Working Document No. 47

CURRENT TOPICS IN BREEDING
OF COMMON BEAN

Proceedings of the
International Bean Breeding Workshop

7-12 November, 1988

Centro Internacional de Agricultura Tropical
(CIAT)
Cali, Colombia

Editor: S. Beebe

Correct citation:

Beebe, S. (ed.). 1989. Current topics in breeding of common bean. Working Document No. 47. 438 pp. Bean Program, CIAT; Cali, Colombia.

TABLE OF CONTENTS

Papers presented:

Page

INTRODUCTION

Many of the production problems which limit yields of common bean (Phaseolus vulgaris L.) in tropical Latin America and Africa lend themselves to a genetic solution. The CIAT Bean Team has long considered that genetic solutions are the most economical and frequently the most readily adopted, particularly by small farmers, and therefore, has dedicated a major part of its effort to the breeding of new varieties.

On various occasions CIAT has invited bean breeders from national programs to participate in workshops to review progress of research and to refine objectives and priorities. However, the audience which CIAT serves - the national program researchers - has changed greatly since CIAT's initiation. Most breeders now have earned higher degrees in plant breeding, either at Ms. or Ph. D. levels. Furthermore, as simpler, first-order problems, such as BCMV, have been solved, attention is being directed to more complex problems, such as yield potential. These factors, among others, led us to seek to present to national program scientists - and to our colleagues here in CIAT - topics which are not only useful and practical, but also intellectually stimulating and challenging. Four general areas were chosen: genetic resources; earliness; breeding for quantitative traits; and the future of bean production. Furthermore, in addition to speakers from national programs and CIAT, we endeavored to bring to CIAT scientists from the United States and Europe who could be of interest to the audience. A poster session was included for the first time to give expression to topics not dealt with in the plenary sessions.

We were all very pleased with the results, and we hope that indeed this workshop will stimulate not only our intellectual curiosity but also more effective research and practical results.

ACKNOWLEDGMENTS

We wish to thank María Eugenia Cobo for her invaluable assistance in the organization of this workshop; Patricia Zamorano de Montoya for her efforts in typing and organizing the manuscript; Drs. Judy Kipe-Noot, Julia Kornegay, Jonathan Lynch, Douglas Pachico, Marcial Pastor and Jeff White for their help in revising the manuscripts in English.

35660

IMPLICATIONS FOR BEAN BREEDERS OF STUDIES ON THE ORIGINS OF COMMON BEANS, *Phaseolus vulgaris* L.

D. G. Debouck and J. Tohme*

Summary

A revision is made of three lines of evidence (botanical, archaeological and biochemical results) for a multiple and independent domestication of wild populations of common bean in the Americas. These domestication events took place at least 10.000 years ago from different wild bean populations. In addition to a founder effect, a lower number of populations could have been domesticated in Mesoamerica versus the southern Andes. Some limitations related to the formation of gene pools and the uniformity of the selective pressures are discussed. Practical consequences for bean breeding related to the genetic incompatibility and a possible case of co-evolution are presented.

Part 1. Origins of Common Bean

1. Evidence for multiple origins and independent domestications

1.1 Botanical evidence. We will define as wild beans those which are morpho- and ecologically wild, that is, with all the attributes of a wild legume such as very active seed dispersal mechanisms and growing freely in climax vegetations.

---

* Germplasm Specialist and Bean Breeder, respectively, CIAT, A.A. 6713, Cali, Colombia.

Wild beans were discovered relatively recently in the Americas, and to date only from that continent (see figure 1). They have been reported from:

Mexico : Miranda, 1967; Gentry, 1969; Nabhan, 1985.
Guatemala : McBryde, 1945; Debouck, 1986a.
Honduras : Burkart and Brücher, 1953.
Costa Rica: Debouck et al., 1988.
Colombia : Gepts and Bliss, 1986.
Venezuela : Berglund-Brücher, 1967.
Peru : Berglund-Brücher and Brücher, 1976; Debouck, 1986b, 1987; Debouck and Tohme, 1988.
Bolivia : Berglund-Brücher, 1967; Debouck, 1988a.
Argentina : Burkart, 1941; Burkart and Brücher, 1953.

The fact that they were found in Costa Rica and Colombia allows one infer a nearly continuous distribution (generally above 1000 masl) from Chihuahua in Mexico (Nabhan, 1985) to San Luis in Argentina (Burkart and Brücher, 1953). This represents a nearly continuous distribution in the American tropics and subtropics covering a distance of over 7000 km.

It is possible that some of presumed wild materials could be feral instead of wild, but the argument by Gentry (1969) that the South American wild beans *aborigineus* are just "escapes from early cultivates", has been refuted by Berglund-Brücher and Brücher (1976) on the basis of phytogeographic evidence. Other wild bean populations have been found since then in climax vegetations in Peru (Debouck, 1986b, 1987; Debouck and Tohme, 1988) and Bolivia (Berglund-Brücher, 1967; Debouck, 1988a). Biochemical evidence is revised below.

If we assume that this distribution did not change over the past millennia, it appears that wild *P. vulgaris* is a rather common wild plant growing at mid-elevations (1000-3000 masl), in non extreme climates

($12-24^{\circ}C$; 400-2000 mm rainfall/year with a marked dry season starting at pod setting). It was probably not so difficult for the first American plant gatherers to find wild bean precisely in the zones where they liked to live thousands of years ago.

This nearly continuous distribution of the wild bean does not imply morphological uniformity: it is clear (Burkart and Brücher, 1953; Gentry, 1969) that the two extremes of the range are morphologically distinct, that is the wild beans from Mexico are not equivalent to those from Argentina. Some of these differences are summarized in Table 1. With the addition of wild beans from Costa Rica, Colombia, Peru and Bolivia, the differences are less clear-cut. Larger seed size and annualism have been set forth for considering the Argentinian forms as feral (Gentry, 1969), although some of them were found in rain forest habitats (Burkart and Brücher, 1953; Debouck, 1985). It is perhaps too early to conclude about a single place of origin for wild P. vulgaris on the basis of such arguments, since some true wild Phaseolus species such as P. chiapasanus Piper or P. maculatus Scheele also have large seeds (100 seed weight: 16 and 26 g respectively) and were not domesticated. P. microcarpus Mart., an annual vine from the tropical deciduous forests of Mexico, was not domesticated either.

As it appears in Table 1, several characters display a continuum along the range of distribution. Up to northern Peru (Cajamarca), seeds tend to be small and rounded, while they are larger and parallel-epipedic in the aborigineus sensu stricto type from southern Bolivia to Argentina. For materials from the southern Andes, one can wonder whether it is an adaptation to forest habitats under cloudy climates where larger storage reserves are needed to germinate. Lignified hypocotyl is generally observed on old plants which can survive the first seed set in some materials from Mexico to Colombia. It is linked to the capacity for buds to regrow on the lower stem, a trait also observed in some escapes (DGD and JSMM # 2077 from Queretaro). Bracteole size is somewhat variable within a single population; a clear-cut difference is, however, displayed by the _aborigineus_ form present from southern Bolivia to Argentina. Curiously, the extremes of the range are earlier to flower than the wild forms of Costa Rica and Colombia, the _aborigineus_ being the earliest.

Evidence fot the large range of distribution in the Americas and the morphological differences between the wild forms have been strengthened by recent explorations. These facts have lead several authors (Evans, 1976; Heiser, 1979; Vanderborght, 1986) to hypothesize two centers of bean domestication: Mesoamerica and the Southern Andes. Of particular interest is the fact that some morphological traits separating the wild forms, such as seed size, were also found of some significance to separate groups of cultivated landraces (Evans, 1976; Vanderborght, 1986). In other words, beans, both wild and cultivated from a same origin, share to some extent some similar characteristics. We will return to this later.

To summarize:

- The wild form of common bean has a large distribution in the Americas from Chihuahua to San Luis.

- Throughout its distribution, there are morphological changes which partly reflect its adaptation to different environments (e.g. sunny thickets in Jalisco versus rain forests in Tucuman).

- Part of these morphological traits are shared between the wild beans and their cultivated counterparts domesticated within the same area.

We will now revise some archaeological records indicating ancient and probably independent domestications in the Americas.

1.2 _Archaeological evidences_. Since we will in most cases deal with ancient plant remains, all our observations will be linked to their conservation conditions. One will then not be surprised to find most evidences in dry areas and not in wet tropical America. In this regard, as it appears from the data shown in Figure 2, records from Central America and Colombia are particularly lacking. This bias could be partly corrected in putting more emphasis on pollen records and phytoliths (Pearsall, 1982; Bozarth, 1986), but this approach has just started. On the other hand, one should not forget that archaeological evidence is a non definitive argument, pending the discovery of a novel ancient site. Other problems in interpretation are related to studies of stratigraphy (Engel, 1963) and to the dominant use of ^{14}C dating method with few countermeasures (Lynch et al., 1985).

Bearing this in mind and the fact that the data are still fragmentary, the data of Figure 2 and the related papers (Kaplan, 1956; Kaplan and McNeish, 1960; Brooks et al., 1962; Kaplan, 1965; Kaplan, 1967; Kaplan et al., 1973; Tarrago, 1980; Kaplan, 1981; Ottonello and Lorandi, 1987; Pearsall, in press) indicate that:

- The oldest records are from Huachichocana, on the west side of the Quebrada de Humahuaca, Jujuy, Argentina, then followed by Guitarrero Caves, Ancash, Peru, and then by Tehuacan, Puebla, Mexico.

- The range of very old sites is large (7000 km between Tehuacan and Huachichocana). The most ancient beans are preceramic and found in a context of very incipient agriculture (plant gathering!). As evidenced by Kaplan and Kaplan (1988), the American plant trilogy (maize, beans, squashes) does not exist when the beans are domesticated.

- Taking into account the present distribution of the wild forms, and assuming that the latter did not change over the last millennia, the old archaeological sites fall very close (100 km or less) to their range.

- The archaeological beans appear to be fully domesticated, that is, their seeds do not show any transition from the wild. They also appear to be fully modern. For example, seed sizes and color patterns are comparable to 1900 types still present for some in the same area. There is thus a noticeable stability in these landraces, and an outstanding continuity by the farmers in growing them. Further evidence about continuity is shown by the different dates at the same place (e.g., Huachichocana reported by Tarrago, 1980; Ocampo reported by Kaplan and McNeish, 1960).

The above mentioned elements are in favor of an independent domestication of wild beans in the mountainous regions of Mesoamerica and South America where they were growing. However, with the beginning of ceramics, beans became a major food plant, and long before Columbus, seed trade and crop diffusion took place. In ancient Peru, by at least 4000 B.P., the beans moved from the highlands to the coast (Pickersgill and Heiser, 1978; Pearsall, 1978; Pearsall, in press). In ancient Mesoamerica, the beans moved from northwestern Mexico into the southwestern USA (by 2000 B.P.: Kaplan, 1956; Kaplan and Kaplan, 1988) and probably from there to the eastern USA (by 1000 B.P.: Ford, 1985). How far they changed during these precolumbian seed movements will be discussed later.

1.3 Biochemical evidences. There is no evidence that about 10.000 years ago early agriculturists and/or animals took an active part in the dispersal of wild beans. Rather, the beans were probably self-dispersed. In preceramic contexts (aprox. 8000 years B.P.), in both Ocampo and Guila Naquitz (Kaplan and McNeish, 1960; Kaplan, 1985, respectively), plant gatherers collected wild beans, but these were of hypogeal germination, perhaps wild P. coccineus and P. oaxacanus respectively. Also because wild bean seeds contain antinutritional factors such as phytohaemagglutinins (Jaffe and Brücher, 1968), one can assume that the present distribution of wild P. vulgaris is broadly similar to that of that period.

If one could find a biochemical marker with the following properties, present in both the wild populations and their cultivated counterparts, it would be of great help in clarifying the domestication process:

- Geographic polymorphism: several forms of the marker should exist throughout the range of distribution of the putative ancestor(s).
- High heritability and complexity of each of the variants of the marker, so that there is little probability that the same variant will be produced several times during the history of the crop.
- Environmental stability: the expression of the variants is not influenced by the growing conditions.
- Stability facing the domestication process: the marker is not influenced by the domestication process, the selection pressures being on other characters.

Gepts (1984, 1988) demonstrated that phaseolin, the major seed storage protein, is a useful marker for evolutionary studies in P. vulgaris. As germplasm has been made available by explorations in Latin America, landraces and wild populations have been examined for their phaseolin characteristics (Gepts et al., 1986; Gepts & Bliss, 1986; Debouck et al., 1988; Koenig et al., in press; Tohme & Debouck, in press). The results are shown in Table 2 and Figure 3. Although the range of wild P. vulgaris is not fully covered yet, one can see that:

1) There are more phaseolin types in the wild materials than in the cultivated ones. As discussed below, this shows that only a portion of the genetic diversity existing in the wild forms was domesticated. On the other hand, in the case the actual wild beans will just be feral or weedy types, they would not express such a larger diversity in phaseolin types.

2) There is a good correspondence between the native landraces of a particular country and the wild beans present there. This was expected given the relative stability of landraces as shown by the archaeological records (see above) and the molecular complexity of phaseolin causing its uniqueness (Gepts, 1988). Furthermore the presence of "odd" types in a particular country can be explained by varietal introduction (e.g. the "cacahuate" types in Mexico with 'T' phaseolin, or the "panamitos" in coastal Peru with 'S' phaseolin). There is also evidence of early seed movements, probably precolumbian, with the extension of the 'B' phaseolin cultivars into Central America.

3) More variability exists in the southern Andes as compared to the northern Andes and Mexico both in wild populations and in cultivated materials. Assuming common bean originated in Mexico (as its has been claimed by Gentry, 1969; Heiser, 1979), it would be difficult to explain such a diversity (this statement is valid for the last 10.000 years). One should take into account, however, the polymorphism of the 'M' phaseolin in wild types of Mesoamerica, so far absent in any cultivated type.

Another piece of evidence about a separate domestication in Mesoamerica vs the southern Andes is given by isozyme analysis (Schinkel et al., 1988), since they are coded by genes (probably unlinked) independent of phaseolin. Analyses performed on Latin America landraces reveal contrasting isozyme profiles for the two regions. Similar results were obtained for a collection of Malawian germplasm (Sprecher, 1988a) once the accessions were traced back to their center of origin in the Americas using phaseolin types. Two dominant alternate isozymes patterns were reported for 6 enzymes where polymorphisms were observed. The dominant Andean pattern was present at a frequency of 76%, while the Mesoamerican one was of 15%. The remaining 9% were distributed between the Andean gene pool (8%) and the Mesoamerican one (1%), with variants of the respective dominant patterns (Sprecher, 1988b). These frequencies for Malawi germplasm would lead one to think that, at least for the Andean gene pool, it would be possible to recognize subunits, a conclusion also reached by Schinkel et al. (1988) working on American cultivars. For a better definition of races, it would be very useful to screen additional primitive American varieties as well as populations of wild beans. The fact that more polymorphism has been found in snap beans (Weeden, 1984) also suggests a need to include more loci when evaluating wild populations.

The presence of more phaseolin types in wild populations vs cultivated landraces raises questions about the domestication process, given the characteristics of phaseolin as a marker. Let us now discuss some of them.

2. The founder effect of domestication

We will adopt the concept developed by Ladizinsky (1985) and thus define the founder effect as the reduction in genetic variability when individuals giving rise to a new population only carry part of the original genetic variability.

The founder effect in bean domestication could be considered under the following aspects:

1 The number of individuals taken from the wild populations and included in the domestication process was small.

2) Gene flow between the domesticated stocks and their wild counterparts was limited.

2.1 The limited initial gene stock. Evidence that parts of the geographic range were touched is found in the phaseolin patterns of the cultivated types vs the wild ones (Table 2). In Mesoamerica, the phaseolin type found so far in the cultivated materials is 'S', while the polymorphic and common 'M' type has not been found in any cultivated genotype examined to date. One could think that the phaseolin 'M' would be linked to a negative character rejected during the domestication process; it has been transferred in experimental breeding lines without expressing any negative character regarding to yield, etc. (F. Bliss, pers. comm.). In the southern Andes, the types 'I' and 'J' have not been found in cultivated materials so far, while the 'T', 'C', 'H' are present in both wild and cultivated genotypes. The fact that the 'A' type (found only in Ayacucho so far) is present in a landrace and not in a wild population is, to us, more illustrative of the incomplete survey for both cultivated and wild materials from the southern Andes than anything else. In examing Figure 1, it is obvious that the range of the wild populations is not fully covered yet, and that perhaps only 10% of all the American landraces have been processed.

As seen in Table 2 and Figure 3, the situation in Mesoamerica could be different from the situation in the southern Andes, i.e. a very few wild populations could have been domesticated in Mexico while several wild populations over a broader range of distribution could have been domesticated in a zone from mid-Peru to northwestern Argentina. As indicated by Gepts (1984, 1988), the truly wild types in Mexico showing no sign of introgression from cultivated forms are concentrated in western Mexico which could then be a place of bean domestication. One should, however, keep in mind that when those studies were made little was known about wild beans in the region from Chiapas to Nicaragua, where they are known to be present and still to be collected. The possibility of finding more places of bean domestication in Middle America thus remains open. To identify a single site of domestication in the southern Andes is, for the time being, more difficult and perhaps irrelevant. After considering the latitudinal extension of the wild beans in South America, Brücher (1968) and Harlan (1971) doubted that there was a specific center of origin for the common bean, but were thinking about a multiple domestication there. More detailed informations could be obtained looking at the mitochondrial DNA but this approach is just beginning to be developed.

Another piece of evidence that part of the wild populations and perhaps just a few plants were included into the domestication process is shown by work on bruchid resistance. Thousands of cultivated genotypes have been screened for resistance to that pest, but not a single one has shown resistance (Schoonhoven and Cardona, 1982). However, a reduced number of wild populations of P. vulgaris from Mexico have shown resistance (Schoonhoven et al., 1983). It was demonstrated that the resistance, an antibiosis reaction, was linked to the presence of the protein arcelin (Osborn et al., 1986, 1988). Some polymorphism exists in arcelin (Osborn et al., 1986), those types with the highest levels of resistance being concentrated in Guerrero and Michoacan, Mexico where, as claimed by Gepts (1984, 1988), domestication did not take place. The reason why no source of bruchid resistance was found in cultivated bean may simply be because the trait of interest, the right arcelin type, was not present in the domesticated population(s).

Although evidence is fragmentary, it thus seems that a few populations along their long range in the Americas were in fact domesticated. Although evidence is even more scarce, it also seems reasonable to conclude that just a few plants within those populations actually participated in the domestication process. Wild beans are still harvested as emergency food in some parts of the Andes (Argentina: Brücher, 1954; Peru: Debouck and Tohme, 1988). Any particular variant (e.g. colored seed, non dehiscent pod) might have been noticed and selected by early agriculturists. Since many traits of high anthropic value are highly heritable (see Table 3), progress in selecting for those traits would have been rapid.

As pointed out by Ladizinzky (1985), there was no need to continue to grow wild types once a more suitable genotype had been obtained (although we will comment on that later on). As is still done today in traditional agriculture in Peru, farmers frequently exchange seeds on an individual basis. When they see an interesting plant they do not have, they pick up a few seeds (in some cases just one), walk back to their huts, and plant them next season to see how they grow.

This form of selection could explain the diffusion of the 'S' types throughout Mesoamerica starting from a few plants once domesticated in western Mexico. This is also illustrated in Colombia: although the early Colombian Indians began with selecting bean populations with 'B' phaseolin (Gepts and Bliss, 1986), they were eager to import 'S' types in northern Colombia and 'T' types in southern Colombia.

Another evidence of this form of selection is suggested by the work on bruchid resistance. A possible explanation of the absence of resistance in any cultivated genoytpe would be that the right populations were not touched by domesticating farmers. One should also remember that right arcelins occur in low frequencies in the original wild bean populations (around 20%: Osborn et al., 1986). Given this, the few plants with interesting seed, pod, or plant characteristics would not include most probably the arcelin conferring resistance to bruchids.

A remaining question is to consider whether there was (or is) any genetic flow from wild populations and/or early cultivars in recently domesticated stocks.

2.2 The gene flow between bean genotypes. The problem of a possible genetic flow to increase diversity in cultivated P. vulgaris, and so to limit the founder effect, can be considered in two aspects: first, the gene exchange during domestication between sympatric wild forms and primitive cultivars, and second the crossing between cultivated genotypes outside the range of the wild forms. But we should first examine whether the gene flow is physically possible based on the rate of natural outcrossing in P. vulgaris.

Cross-pollination apparently exists in the wild forms. For Mexican materials, Wall and Wall (1975) and Vanderborght (1982) reported high levels of outcrossing (3 to 50%), although Brücher (1988) spoke about "an outspoken cleistogamy" for the P. aborigineus forms. Conflicting figures are also reported for cultivated P. vulgaris genotypes (see Table 4). Although these results need further confirmation particularly with respect location effects, ecological conditions, and to pollinating agents (carpenter and bumble bees seem quite active in this regard: Delgado et al., 1988 and personal observations), it appears that cleistogamy is perhaps not as constant as it was thought before and that high rates of cross-pollination (> 10%) could be found in both wild and cultivated common bean.

Crossing between wild forms and primitive cultivars can perhaps be inferred from what can be seen now where both are still growing together. Among Phaseolus species, wild P. vulgaris behaves as a weed in some places, entering human made or disturbed habitats (in Mexico: Delgado et al., 1988; in Peru: Debouck, 1987; Debouck and Tohme, 1988; in Bolivia, Berglund-Brücher and Brücher, 1976). There is thus a possibility to find both the wild forms and some traditional cultivars growing together. This situation has been studied recently in Cuzco, Peru (Debouck and Tohme, 1988; Debouck et al., in press). There, the farmers eat the wild and the weedy types and keep the large grain type "Amarillo Gigante" to be sold on Sunday market. Indeed, beside the wild and the truly cultivated types, a dozen of weedy or intermediate types were also found in the same field and sometimes eaten on the farm. That situation and the comments made by the farmers led these authors (Debouck et al., in press) to hypothesize a "weed-crop complex" after Harlan (1965) and Harlan and de Wet (1965), where the weedy types result from crosses between the wild and the cultivated forms. Similar situation and subsequent use by man have been observed in other crops including, potato (Schmiediche et al., 1980), maize (Wilkes, 1977) and chili peppers (Pickersgill, 1981). There are thus strong indications that the wild types have enriched the primitive landraces, and apparently this is still occurring in 1988 in parts of the range! As shown in Table 3, most of the "wild" characters are dominant in the progenies of natural hybrids involving cultivated and wild forms. As pointed out by Ladizinsky (1985), this could lead to the formation of more weedy races on the one hand and to the rejection of unwanted types by traditional farmers on the other. In the case of beans, one wonders, however, how strong is that rejection, since many traditional landraces of Peru and Bolivia still exhibit a strong pod dehiscence (see also Brücher, 1988). On the other hand, in one place in Cuzco, Peru, Debouck and Tohme (1988) observed that farmers consumed weedy types on the farm.

As a concluding remark, one will note that crossing between wild and cultivated forms is taking place within a restricted geographical area resulting perhaps in a closer morphological likeness between the landraces and their wild ancestors (see also Vanderborght, 1986). This could contribute to the formation of gene pools too, as we will discuss it below.

Crossing between landraces in or outside the range of wild ancestors could be another way to reduce the founder effect. It can also be studied in secondary centers. In traditional landraces of Malawi, natural outcrossing occurs at a low frequency (around 1%, Martin and Adams, 1987), but this is high enough to produce recombinants that can be selected by farmers. How far does outcrossing allow the creation of new variability? The work by Sprecher (1988b) on the same Malawi collection indicates that new genetic variability appears but principally within gene pools and very little between gene pools (partly due to male sterility and other genetic disturbances). It would then be interesting to quantify the intercrossing between gene pools where they were in contact for longer periods (e.g. in Colombia or in northern Peru) to see whether those genetic barriers are also present.

3. Travels of Phaseolus beans and their subsequent genetic consequences.

We will consider successively the travels of the beans within the Americas before and after Columbus, then the travels to Europe, Africa and Asia after Columbus. We will also discuss about some genetic changes which have made possible to grow beans there successfully.

3.1 Travels within the Americas before Columbus. Evidence that beans were exchanged in precolumbian times is obtained from archaeological and biochemical studies, and studies on cultural contacts. This survey cannot be exhaustive, will only present a few general movements.

Related to Mesoamerica:

1) There are some indications (Soustelle, 1979) that the Olmecs had commercial contacts with Oaxaca and Guerrero, and from their homeland in Veracruz up to southwestern Costa Rica (1500-2000 years BP). This could explain the diffusion of some tropical black beans, frequent around the Gulf of Mexico and neighbouring regions.
2) Cultural contacts have also been argued around 1500 years BP (Snarskis, 1985) between Colombia and Panama and Costa Rica. This could explain the diffusion of some 'B' phaseolin cultivars, originally from Boyaca, Colombia to Costa Rica and even Guatemala (Gepts and Bliss, 1986; Koenig et al., in press). On the reverse, the same contacts could explain the presence of 'Sb' cultivars in Southeastern Brazil.

3) Tributes payed to the Aztecs would have presented another opportunity for exchanges of large amounts of seeds in prehispanic Mesoamerica (Torres, 1985). The dominant rule of this group would have

contributed on a large scale to the diffusion of 'S' phaseolin cultivars in Mesoamerica (see Gepts et al., 1986).

Related to South America:

1) The presence of a sieva type of lima bean in the uppers levels at Huaca Prieta (northern coast of Peru) (Towle, 1961) indicates cultural contacts at about 2500 years BP between that part of Peru and Colombia or perhaps Mesoamerica where those beans originated (Pickersgill and Heiser, 1978).
2) The presence of large seeded lima beans in Norcinti, Bolivia (Debouck, 1988a) outside the range of distribution of their wild relatives (Debouck et al., 1987) would indicate an introduction there and thus cultural contacts between southern Bolivia and western Peru.
3) The presence of 'T' phaseolin cultivars in southern Colombia (Nariño; where wild beans are not known) would indicate introduction from the southern Andes where these types of phaseolin are common both in the wild forms and landraces (Gepts et al., 1986; Tohme and Debouck, in press).

Little information is available about the genetic changes occurred in the materials during these millenia. As judged on seed characters, many grain colors were already selected including yellow (Kaplan, 1980). By 800 years B.P., at Ocampo, Tamaulipas, bush types as well as a somewhat snap bean are already present (Kaplan and Mc Neish, 1960).

3.2 Travels within the Americas after Columbus related to Mesoamerica.

1) A movement already perceptible during the last precolumbian period will continue in the Greater Southwest with more beans entering that part of the USA (Carter, 1945; Kaplan, 1956).

2) Soon after the Spanish Conquest, there was an active exchange of germplasm between Mexico and Peru (E. Hernandez X., pers. comm.). This could explain the presence of 'T' phaseolin cultivars in Mexico such as certain "Cacahuates" or "Japones". In the opposite direction there is the small seeded white variety in Peru called "Panamito" with 'S' phaseolin (Gepts, 1984).

3) Haiti, part of Hispaniola, serving as a stop for the spanish galleons on their way to Europe, became soon a secondary center of diversity, with a special emphasis on earliness (C. Messiaen, pers. comm.), resulting in the "Pompadour" group with 'T' phaseolin (Gepts et al., 1988).

Again little information is available. One can hypothesize that as the beans were moved towards higher latitudes especially in the northern hemisphere, some selection was made for day neutral cultivars, i.e. able to bloom under longer days. Also perhaps for bush types, as the growing season becomes shorter at higher latitudes.

3.3. Travels from and outside the Americas after Columbus. Columbus discovered central America in 1492. Less than 60 years later common bean was grown extensively in western Europe (León, 1987; Brücher, 1988). From there, it was distributed much further: southeastern Europe and the Middle East, Iran and India, other places in Asia, Africa and back to the Americas. Let us illustrate a few cases.

1) Most of the varieties in Europe come from the southern Andes displaying 'T' and 'C' phasolins (Gepts and Bliss, 1988). This raises the following questions:
   - Were they better adaptated to longer photoperiods and/or cooler temperatures?
   - Did early travelers prefer them for their larger grain size?
   - Was there a higher mutation rate for snap bean characteristics in

these gene pools"

2) Several European varieties were brought back to the Americas, particularly the USA and Argentina. Several specific cases are well documented (Gepts et al., 1988).

3) Beans were also introduced successfully in Africa, both directly from Brazil (Evans, 1976) and indirectly from the southern Andes through Europe since the Andean types of phaseolin are dominant in Africa (Gepts and Bliss, 1988).

Because of the extension of the geographic range, day neutral cultivars were developed. Also to mention is the appearance of several recessive characters (waxy pods, yellow pods,very long pods) according to specific selection pressures in the secondary center.

Part 2. Implications for Breeders

In the first part, we have presented three groups of facts about the origin of the common bean, *P. vulgaris*, which are:

- Origins of the common bean are multiple and the different domestications about 10.000 years ago were then independent.
- Domestication was not neutral towards genetic diversity included into the domesticated stocks: a founder effect took place with regional differences, also with differences in intensity.
- Genetic changes at a few loci resulting in new characters of high anthropic significance (related to seed, pod, growh habit) appeared early in bean crop history.

Let us now discuss some of their consequences.

1. Gene pools formation and incompatibility problems

Independent domestications using morphologically different wild populations led to formation of morphologically distinct groups of cultivated genotypes. As we have seen above and as has been observed in other crops (Harlan and de Wet, 1965; Johns and Keen, 1986; Wilkes, 1977), there is a strong possibility that crosses between wild and/or weedy populations and early cultivars contributed to the likeness between these two. Multilocal domestications had other consequences: physical isolation of groups of early cultivars from each other for thousands of years (2000-4000 years as can be deduced from the above mentioned figures) led to their genetic isolation and the formation of gene pools. If so, one should experience problems of genetic incompatibility when crossing between gene pools and first of all between regions of origin. In Table 5, some of these crosses are reported.

Although this survey is far from being complete, it appears that crossing between small seeded Mesoamerican cultivars and large seeded southern Andean cultivars is likely to fail with little or no true recombination. As we have seen above and in Sprecher (1988b), in Africa, while crosses occur, genetic barriers prevent the formation of recombinants between the gene pools brought there and planted together.

In crosses investigated so far, F_1 hybrid weakness is apparently controlled by 2 complementary genes: DL1 (for dosage dependent lethal, Shii et al., 1980) attributed to Mesoamerica and DL2 to the southern Andes. The F_1 hybrids DL1 dl1 DL2 dl2 give crippled plants at high temperatures, less abnormal plants at lower temperatures. The fact that some crosses between 'S' and 'T' phaseolins in both cultivated and wild parents can give a normal offspring would discard a direct linkage between the genes coding for phaseolin and the expression of F1 weakness. But, on the reverse, DL1 and DL2 are respectively unseparable from certain phaseolin types. This was indirectly evidenced by Sprecher (1988a) on a small sample including the standard lines for phaseolin types and 27 lines producing F1 hybrid weakness. These materials displayed alternate isozyme profiles between the Mesoamerican (wiht 'S' and 'B' phaseolins) and the Andean gene pools (with 'T', 'C', 'A' and 'H' phaseolins). Now the fact that crippled plants can also be observed in crosses with 'S' and 'B' phaseolin types would indicate that there would be more genes responsible for F1 weakness. Although obviously more data are needed, it would be indicative of an incipient separation of the Colombian materials with 'B' from the Mesoamerican stocks, despite their similarity in isozyme profiles (Schinkel et al., 1988).

Once more, we need more data about crossability problems in beans, also because of its practical consequences. But there is increasing evidence that the extremes of the range when cultivated are not always easy to cross. It would be of interest to test the following hypothesis:

- Are there cases of incompatibility in 'T' phaseolin types?
- Are there other cases of incompatibility between genuine Mesoamerican and Colombian cultivars?
- Is the incompatibility a result of domestication?

Although the type of phaseolin can be very useful in predicting successful crosses, it does not constitute a definitive insurance. It would be therefore useful to develop other (molecular?) markers. On the other hand, as these hypotheses are progressively examined, it will be possible to increase the variability by crossing between gene pools. Although difficult (see above), it could be rewarding on the long run, as indicated by the larger number of loci where polymorphism is expressed in snap beans (Weeden, 1984; Sprecher, 1988a).

2. Are we facing a case of co-evolution between the crop and its biotic and abiotic environment?

If as we hypothesize above early landraces were domesticated in isolate plots and were separated from each other for thousands of years, then there would be strong cases of co-evolution between these landraces and the agents either biotic or abiotic present in their environment. In other words, one should find strong correlations between some particular landraces and some strains of diseases, some climatic stresses, etc. This approach in beans, suggested by Gepts and Bliss (1985), has just started and evidences are accumulating. We will consider two cases: diseases and *Rhizobium*.

Stavely (1984 and 1988) reported about the variability of rust in the US, showing the differential susceptibility of bean cultivars to rust races: some snap bean cultivars highly susceptible to US races reacted in the same way, suggesting a kind of specific host-pathogen reaction. Compuesto Negro Chimaltenango, originally a mixture of black beans from Guatemala, showed the highest level of resistance to a large series of races (Stavely, 1986), perhaps because of its larger genetical basis. Later on, other lines were tested (Stavely, 1988) and PI 181996 and 189013 both from Guatemala were also highly resistant to US races. Another interesting cultivar Ecuador 299 has a 'S' phaseolin, as does Compuesto Negro Chimaltenango (P. Gepts, pers. comm.).

After a electrophoretical study on 55 isolates of angular leaf spot, Correa (1987) found that the resulting two patterns of four enzymes could be associated with the kind of beans they infect, one pattern being found on large seeded types and the other being found on small seeded types. A confirmation is needed to be sure that one pattern is found only on large seeded materials in a specific geographic zone and vice versa. But these two examples indicate that pathogen variability is not distributed at random. In this case, many agronomical practices and screening methods should be revised.

Rennie and Kemp (1983a, b) showed that when testing several bean cultivars for their efficiency in nitrogen fixation using a single strain of Rhizobium, the effect of cultivars was significant, as was the interaction strain-cultivars. If these results prove true on more materials (wild beans for instance), nitrogen fixation could be improved by choosing the right counterparts.

3. Practical consequences for breeding and germplasm management

The above mentioned results, although fragmentary in some cases, clearly indicate that bean breeding from now onwards will be more concerned about the origin of the materials used as potential genitors. Three kinds of needs can be formulated:

1) Need for information about the materials: a free access to the full passport data about any accession appears as a requisite in any breeding work. Without all geographic information and coordinates, germplasm accessions lose much of their value. Around 60% of the cultivated materials of P. vulgaris held in germplasm banks would lack their full passport data, thus limiting their future use. Hopefully, thanks to biochemical markers (isozymes, nuclear and mitochondrial DNA) and well documented collections of wild P. vulgaris, it will be possible to improve this situation.

2) Need for information about genetic relationships: future bean breeding will take more into account to which gene pool belongs a potential genitor, in order to avoid compatibility problems or to assure better complementarity between parents. Biochemical markers which can indicate these compatibilities at nuclear and/or cytoplasmic levels will be used intensively. Here also, the wild beans can play a key role in showing a broad sample of variability.

3) Need for a synthetic approach to the bean biodiversity: it becomes more evident that much genetic diversity was lost both during the domestication process, and through the operations of germplasm collection and handling. Examples of interesting traits being present at low frequencies in original populations are increasing: bruchids (Osborn et al., 1986), I gene in wild bean accessions (J. Tohme, pers. comm.). Guidelines have been published elsewhere (Debouck, 1988b) on how to pick up these rare variants at the collection site. Losses of genetic variability inside germplasm collections (Roos and Centner, 1984; Klein et al., 1988) should be avoided by improved procedures. It must be kept in mind that breeders currently do not and will not have access to the original variability, i. e. in its original context. It is thus of paramount importance to sample the original populations trying to preserve as much of the real genetic diversity as possible throughout the whole process of germplasm conservation. In the future, it would be also highly useful to know more about the variability of diseases, pests and Rhizobium in the original sites, and to correlate this information with the diversity in bean germplasm. In the case co-evolution and local concentration of interesting traits can be further evidenced, then breeders and germplasm specialists should focus more on very primitive landraces and wild beans, since the distribution of the later could reflect more the regional distribution of the biotic and abiotic constraints.

References

Berglund-Brucher, O. 1967. Wildbohnen-Funde in Sudamerika. Naturwiss. 54(17):466-468.

Berglund-Brucher, O. and H. Brucher. 1976. The south american wild bean (Phaseolus aborigineus Burk.) as ancestor of the common bean. Econ. Bot. 30: 257-272.

Bliss, F.A. 1971. Inheritance of growth habit and time of flowering in beans, Phaseolus vulgaris. J. Amer. Soc. Hort. Sci. 96(6): 715-17.

Bozarth, S. 1986. Morphologically distinctive Phaseolus, Cucurbita, and Helianthus annuus phytoliths. p. 56-66. In I. Rovner (ed.). Plant opal phytolith analysis in archaeology and palaeoecology. Proc. 1984 Phytolith Research Workshop, North Carolina State University, Raleigh, NC, U.S.A,

Brooks, R.H., L. Kaplan, H.S. Cutler and T.W. Whitaker. 1962. Plant material from a cave on the Rio Zape, Durango, Mexico. Amer. Antiquity 27(3):356-369.

Brucher, H. 1954. Argentinien, urheimat unserer bohnen. Umschau in Wiss. u Technik 54(1):14-15.

Brucher, H. 1968. Die evolution der gartenbohne Phaseolus vulgaris L. aus der sudamerikanischen wild bohne P. aborigineus Burk. Angew. Botanik. 42(3-4):119-128.

Brucher, H. 1988. The wild ancestor of Phaseolus vulgaris in South America. p. 185-214. In P. Gepts (ed.). Genetic resources of Phaseolus beans. Kluwer Academic Publishers, Dordrecht, Holland.

Brunner, B.R. and J.S. Beaver. 1988. Estimation of outcrossing of dry beans in Puerto Rico Ann. Rept. Bean Improvement Coop. 31:42-42.

Burkart, A. 1941. Sobre la existencia de razas silvestres de "Phaseolus vulgaris y "Phaseolus lunatus" en el Norte Argentino. Resoluc. y Resumenes Botánica, Primera Reunión Argentina de Agronomía, Buenos Aires: 52.

Burkart, A. and H. Brucher. 1953. Phaseolus aborigineus Burkart, die mutmabliche andine stammform der Kultur Bohne. Der Zuchter 23(3):65-72.

Carter, G.F. 1945. Plant geography and culture history in the American Southwest. Viking Fund Publications in Anthropology 5:1-140.

Correa, V.F.J. 1987. Pathogenic variation, production of toxic metabolites, and isoenzyme analysis in Phaeoisariopsis griseola (Sacc.) Ferr. Ph.D thesis, Michigan State University, East Lansing Michigan, USA, 154 pp.

Coyne, D.P. 1965. A genetic study of "crippled" morphology resembling virus symptoms in Phaseolus vulgaris L. J. Hered. 56 (4):162.

Crispin, M. 1960. Cruzamiento natural en el fríjol. Agricultura Técnica México 11:38-39.

Debouck, D.G. 1985. Trip report to Peru and Argentina. Intern. Board for Plant Genetic Resources, Rome, Italy AGPG/IBPGR, 85/123:31p.

Debouck, D.G. 1986a. *Phaseolus* germplasm collection in western Guatemala, C.A. International Board for Plant Genetic Resources, Rome, AGPG/IBPGR, 86/40:30p.

Debouck, D.G. 1986b. *Phaseolus* germplasm collection in Cajamarca and Amazonas, Peru. International Board for Plant Genetic Resources, Rome, Italy, AGPG/IBPGR, 86/161:38p.

Debouck, D.G. 1987. Recolección de germoplasma de *Phaseolus* en el Centro y Centro-Sur del Perú. International Board for Plant Genetic Resources, Rome, Italy, AGPG/IBPGR, 87/112: 36p.

Debouck, D.G. 1988a. Recolección de Germoplasma de *Phaseolus* en Bolivia. Centro Internacional de Agricultura Tropical, Cali, Colombia, mimeographed, 24 pp.

Debouck, D.G. 1988b. *Phaseolus* germplasm exploration. p. 3-29. In P. Gepts (ed.). Genetic resources of *Phaseolus* beans. Kluwer Academic Publishers, Dordrecht, Holland, p.3-29.

Debouck, D.G., R. Araya, W.G. Gonzalez and J. Tohme. 1988. Presencia de formas silvestres de *Phaseolus vulgaris* L. en Costa Rica. Actas XXXIV Reunión Anual Programa Centroamericano para el Mejoramiento de Cultivos Alimenticios, PCCMCA, San José, Costa Rica, 21-25 marzo 1988, p. 75.

Debouck, D.G., F.M. Gamarra, A.V. Ortiz and J. Tohme. Presence of a wild-weed-crop complex in *Phaseolus vulgaris* L. in Peru?. Ann. Rept. Bean Improvement Coop., submitted.

Debouck, D.G., J.H. Liñan Jara, S.A. Campana and J.H. De La Cruz Rojas. 1987. Observations on the domestication of *Phaseolus lunatus* L. Plant Genetic Resources Newsl. 70: 26-32.

Debouck, D.G. and J. Tohme. 1988. Recolección de Germoplasma de *Phaseolus* en el Centro-Sur del Perú. Centro Internacional de Agricultura Tropical, Cali, Colombia, Mimeografo, 23 pp.

Delgado, S.A., A. Bonet and P. Gepts. 1988. The wild relative of Phaseolus vulgaris in Middle America. p. 163-184. In P. Gepts (ed.). Genetic resources of Phaseolus beans. Kluwer Academic Publishers, Dordrecht, Holland.

Engel, F.A. 1963. Datations a l'aide du radio-carbone 14, et problemes de la préhistoire du Pérou. J. Soc. Américanistes 52:101-132.

Evans, A.M. 1976. Beans Phaseolus spp. (Leguminosae- Papilionatae). p. 168-172. In N.W. Simmonds (ed.). Evolution of crop plants. Longman, London, New York.

Ford, R. 1985. Patterns of prehistoric food production in north America. p. 341-364. In R.I. Ford (ed.). Prehistoric food production in north America. Univ. Michigan, Mus. Anthropol. Papers, No. 75.

Gentry, H.S. 1969. Origin of the common bean, Phaseolus vulgaris. Econ. Bot. 23(1):55-69.

Gepts, P.L. 1984. Nutritional and evolutionary implications of phaseolin seed protein variability in common bean (Phaseolus vulgaris L.) Ph.D. thesis, Univ. Wisconsin, Madison, USA, 209 pp.

Gepts P. 1988. Phaseolin as an evolutionary marker. p. 215-241. In P. Gepts. (ed.). Genetic resources of Phaseolus beans. Kluwer Academic Publishers, Dordrecht, Holland.

Gepts, P. and F.A. Bliss. 1985. F1 hybrid weakness in the common bean: differential geographic origin suggest two gene pools in cultivated bean germplasm. J. Hered. 76:447-450.

Gepts, P.L. and F.A. Bliss. 1986. Phaseolin variability among wild and cultivated common beans (Phaseolus vulgaris) from Colombia. Econ. Bot. 40(4):469-478.

Gepts, P. and F.A. Bliss. 1988. Dissemination pathways of common bean (Phaseolus vulgaris, Fabaceae) deduced from phaseolin electrophoretic variability. 2. Europe and Africa. Econ. Bot. 42(1):86-104.

Gepts, P., K. Kmiecik, P. Pereira and F.A. Bliss. 1988. Dissemination pathways of common bean (Phaseolus vulgaris, Fabaceae) deduced from phaseolin electrophoretic variability. 1. The Americas. Econ. Bot. 42(1):73-85.

Gepts, P.L., T.C. Osborn, K. Rashka and F.A. Bliss. 1986. Phaseolin protein variability in wild forms and landraces of the common bean (Phaseolus vulgaris evidence for multiple centers of domestication. Econ. Bot. 40(4):451-468.

Harlan, J.R. 1965. The possible role of weed races in the evolution of cultivated plants. Euphytica 14:173-176.

Harlan, J.R. 1971. Agricultural origins: centers and non-centers. Science 174:468-474.

Harlan, J.R. and J.M.J. de Wet. 1965. Some thoughts about weeds. Econ. Bot. 18:16-24.

Heiser, C.B. 1979. Origins of some cultivated new world plants. Ann. Rev. Ecol. Syst. 10:309-326.

Jaffe, W. and O. Brucher. 1968. La presencia de fitohemagglutinina en Ph. aborigineus y su identidad con la de Ph. vulgaris como argumento quimotaxonómico de la íntima relación entre estas dos especies. Res. Acta. Cient. Venez. 19:20.

Johns, T. and S.L. Keen. 1986. Ongoing evolution of the potato on the altiplano of Western Bolivia. Econ. Bot. 40(4):409-424.

Kaplan, L. 1956. The cultivated beans of the prehistoric Southwest. Ann. Mo. Bot. Gard. 43:189-251.

Kaplan, L. 1965. Archeology and domestication in American Phaseolus (beans). Econ. Bot. 19:358-368.

Kaplan, L. 1967. Archaeological Phaseolus from Tehuacan. p. 201-210. In D.S. Byers (ed.). The prehistory of the Tehuacan Valley. Environment and subsistence. vol. 1, Chapt. 10, Univ. Texas Press, Austin.

Kaplan, L.. 1980. Variation in the cultivated beans. p. 145-148. In T.F. Lynch (ed.). Guitarrero cave: early man in the Andes. Chapt. 7, Academic Press, New York.

Kaplan, L. 1981. What is the origin of the common bean? Econ. Bot. 35(2):240-254.

Kaplan, L. 1985. Preceramic Phaseolus from Guila Naquitz. p. 281-284. In K.F. Flannery (ed.). Guila Naquitz: archaic foraging and early agriculture in Oaxaca, Mexico. Academic Press, New York.

Kaplan, L. and L.N. Kaplan. 1988. Phaseolus in archeology. p. 125-142. In P. Gepts (ed.). Genetic resources of Phaseolus beans. Kluwer Academic Publisher, Dordrecht, Holland.

Kaplan, L., Th.F. Lynch and C.E. Smith, Jr. 1973. Early cultivated beans (Phaseolus vulgaris) from an intermontane Peruvian Valley. Science 179:76-77.

Kaplan, L. and R.S. MacNeish. 1960. Prehistoric bean remains from caves in the Ocampo region of Tamaulipas, Mexico. Bot. Mus. Leafl. Harvard Univ. 19(2):33-56.

Klein, R.E., S.D. Wyatt and W.J. Kaiser. 1988. Bean common mosaic virus and the USDA Phaseolus germplasm collection. Ann. Rept.Bean Improvement Coop. 31:68-69.

Koenig, R.L., S.P. Singh and P. Gepts. Novel phaseolin types in wild and cultivated common bean (Phaseolus vulgaris, Fabaceae). Econ. Bot. in press.

Ladizinsky, G. 1985. Founder effect in Crop-plant evolution. Econ. Bot. 39(2):191-199.

Leakey C. L. A. 1988. Genotypic and phenotypic markers in common bean. p. 245-237. In P. Gepts (ed.). Genetic resources of Phaseolus beans. Kluwer Academic Publishers, Dordrecht, Holland.

León, J. 1987. Botánica de los cultivos tropicales. Editorial Instituto Interamericano de Cooperación para la Agricultura, IICA, San José, Costa Rica, 445 pp.

Lynch, T.F., R. Gillepsie, J.A.J. Gowlett and R.E.M. Hedges. 1985. Chronology of Guitarrero Cave, Peru. Science 229:864-867.

Mackie, W.W. and F.L. Smith. 1935. Evidence of field hybridization in beans. J. Americ. Soc Agron. 27:903-909.

Martin, G.B. and M.W. Adams. 1987. Landraces of Phaseolus vulgaris (Fabaceae) in northern Malawi. 2. Generation and maintenance of variability. Econ. Bot. 41(2):204-215.

McBryde, F W. 1945. Cultural and historical geography of southwest Guatemala. Smithsonian Inst. Washington, Publ. 4:184p.

Miranda Colin, S. 1967. Origen de Phaseolus vulgaris L. (Frijol común). Agrociencia 1 (2):99-109.

Miranda Colin, S. 1971. Cruzamiento natural en frijol. Agricultura Técnica México 3(2):48-52.

Nabhan, G.P. 1985. Native Crop Diversity in Aridoamerica: Conservation of regional gene pools. Econ. Bot. 39(4):387-399.

Norton, J.B. 1915. Inheritance of habit in the common bean. Amer. Nat. 49(585):547-59.

Osborn, T.C., T. Blake, P. Gepts and F.A. Bliss. 1986. Bean arcelin. 2. Genetic variation, inheritance and linkage relationships of a novel seed protein of Phaseolus vulgaris L. Theor. Appl. Genet. 71(6):847-855.

Osborn, T.C., D.C. Alexander, S.S.M. Sun, C. Cardona and F.A.Bliss. 1988. Insecticide activity and lectin homology of arcelin seed protein. Science 240:207-210.

Ottonello, M.M. and A.M. Lorandi. 1987. Introducción a la arqueología y etnología. Diez mil años de historia argentina. Editorial Universitaria de Buenos Aires, EUDEBA, Buenos Aires, Argentina, 210p.

Pearsall, D. M. 1978. Paleothnobotany in western South America: Progress and problems. p. 389-416. In R.I. Ford (ed.). The nature and status of ethnobotany. Anthropological Papers, Museum of Anthropology, Univ. of Michigan, no. 6.

Pearsall, D.M. 1982. Phytolith Analysis: applications of a new paleoethnobotanical technique in archaeology. Amer. Anthropol. 84(4):862-871.

Pearsall, D.M. in press. The origins of plant cultivation in south America. In P.D. Watson and C.W. Cowan (eds.). Origins of agriculture in world perspective. Smithson. Inst., Washington.

Pickersgill, B. 198.. Biosystematics of crop-weed complexes. Kulturplanze 29:377-388.

Pickersgill, B. and C.B. Heiser. 1978. Origins and distribution of plants domesticated in the New World Tropics. p. 133-165. In D.L. Bowman (ed.). Advances in Andean Archaeology. Mouton Publishers, The Hague, Paris.

Prakken, R. 1934. Inheritance of colours and pod characters in *Phaseolus vulgaris* L. Genetica 16:177-294.

Rennie, R.J. and G.A. Kempt. 1983a. N_2-fixation in field beans quantified by ^{15}N isotope dilution. (1) Effect of strains of *Rhizobium phaseoli*. Agron. J. 75:640-644.

Rennie, R.J. and G.A. Kemp. 1983b. N_2-fixation in field beans quantified by ^{15}N isotope dilution. (2) Effect of cultivars of beans. Agron. J. 75:645-649

Roos, E.E. and M.S. Centner. 1984. Characterization and maintenance of genetic variability in germplasm collections. Ann. Rept. Bean Improvement coop. 27:68-70.

Schinkel, C., S.P. Singh and P. Gepts. 1988. Patterns of genetic diversity in *Phaseolus* beans. Ann. Rept. Bean Improvement Coop. 31:40-41.

Schmiediche, P.E., J.G. Hawkes and C.M. Ochoa. 1980. Breeding of the cultivated potato species *Solanum* x *juzepczukii* Buk. and *Solanum* x *curtilobum* Juz. et Buk. 1. A study of the natural variation of *S*. x *juzepczukii*, *S*. x *curtilobum* and their wild progenitor, *S*. *acaule* Bitt. Euphytica 29:685-704.

Schoonhoven, A.v. and C. Cardona. 1982. Low levels of resistance to the mexican bean weevil in dry beans. J. Econ. Entomol. 75:567-569.

Schoonhoven, A.v., C. Cardona and J. Valor. 1983. Resistance to the Bean and the Mexican Bean Weevil (Coleoptera: Bruchidae) in non cultivated common bean accessions. J. Econ. Entomol. 76(6):1255-1259.

Shii, C.T., M.C. Mok, S.R. Temple and D.W.S. Mok. 1980. Expression of developmental abnormalitites in hubrids of *Phaseolus vulgaris* L. J. Hered. 71(4):218-222.

Singh, S.P. and J.A. Gutierrez. 1984. Geographical distribution of the DL_1 and DL_2 genes causing hybrid dwarfism in *Phaseolus vulgaris* L., their association with seed size, and their significance to breeding. Euphytica 33:337-345.

Snarskis, M.J. 1985. The comparative iconography of metal work and other media in precolumbian Costa Rica. p. 121-136. In Precolumbian American Metallurgy, 45th International Congress of Americanists, Banco de la Republica, Bogota.

Soustelle, J. 1979. Les Olmeques. Arthaud, Paris, 221 p.

Sprecher, S.L. 1988a. Isozyme genotype differences between the large seeded and small seeded gene pools in *Phaseolus vulgaris* L. Ann. Rept. Bean Improvement Coop. 31:36-37.

Sprecher, S.L. 1988b. Allozyme differentiation between gene pools in common bean (*Phaseolus vulgaris* L.), with special reference to Malawian germplasm. Ph.D. thesis, Michigan State University, East Lansing Michigan, USA, 207 p.

Stavely, J.R. 1984. Pathogenic specialization in *Uromyces phaseoli* in the United States and rust resistance in beans. Plant disease 68(2):95-99.

Stavely, J.R. 1986. Pathogenic variability, resistance sources, and progress towards developing stable resistance to bean rust. Ann. Rept. Bean Improvement Coop. 29:24-25.

Stavely, J.R. 1988. Rust resistance in beans: the plant introduction collection as a resource and resistance development. Ann. Rept. Bean Improvement Coop. 31:64-65

Stoetzer, H.A.I. 1984. Natural cross-pollination in bean in Ethiopia. Ann. Rept. Bean Improvem. Coop. 27:99-100.

Tarrago, M.N. 1980. El proceso de agriculturización en el noroeste argentino, zona vallíserrana. p. 181-217. In Actas de V Congreso Nacional de Arqueología Argentina, Tomo 1. Universidad Nacional de San Juán, Instituto de Investigaciones Arqueológicas y Museo, San Juan, Argentina.

Tohme, J. and D.G. Debouck. Towards a broader area of domestication of the common bean, Phaseolus vulgaris L., in the Southern Andes? Ann. Rept. Bean Improvement Coop., submitted.

Torres, B.W. 1985. Las plantas útiles en el México antiguo según las fuentes del siglo XVI. p. 53-128. In T. Rojas Rubiela and W.T. Sanders (eds.). Historia de la agricultura, época prehispánica siglo XVI. Vol 1, Instituto Nacional de Antropología e Historia, México, DF, México.

Towle, M.A. 1961. The Ethnobotany of Pre-Columbian Peru. Viking Fund Publ. Anthrop. 30:1-180.

Tucker, C.L. and J. Harding. 1975. Outcrossing in common bean, Phaseolus vulgaris L. J. Am. Soc. Hort. Sci. 100:283-285.

Vanderborght, T. 1982. Seed increase and evaluation of the wild Phaseolus vulgaris germplasm. Centro Internacional de Agricultura Tropical, Cali, Colombia, mimeographed: 69 pp.

Vanderborght, T. 1986. L'étude de la variabilité chez le haricot commun (Phaseolus vulgaris) par l'utilisation de méthodes statistiques multivariées appliquées a une banque de données. These de Doctorat, Faculté des Sciences Agronomiques de l'Etat, Gembloux, Belgique, 229p.

Wall, J.R. and S.W. Wall. 1975. Isozyme polymorphisms in the study of evolution in the Phaseolus vulgaris - P. coccineus complex in Mexico. p. 287-305. In C.L. Markert (ed.). Isozymes, Vol. 1, Genetics and Evolution. Academic Press, New York.

Weeden, N.F. 1984. Distinguishing among white seeded bean cultivars by means of allozyme genotypes. Euphytica 33:199-208.

Wells, W.C., W.H. Isom and J.G. Waines. 1988. Outcrossing rates of six common bean lines. Crop Sci. 28:177-178.

Wilkes, H.G. 1977. Hybridization of maize and teosinte in Mexico and Guatemala and the improvement of maize. Econ. Bot. 31:254-293.

Table 1. Some morpho-physiological characters of wild *P. vulgaris* observed in Palmira and Popayan, Colombia.

Origin	100 Seed weight (g)	Hypocotyl texture	Bracteole size/shape	Days to flowering
Mexico	5-8	Lignified	Large, ovate	40-50
Guatemala	6-9	Lignified	Large, orbicular	50-65
Costa Rica	5-6	Herbaceous?	Large, ovate	>100
Colombia	8-12	Lignified	Large, ovate	65-75
Peru				
Northern	15-16	Lignified?	Medium to large, ovate	55-65
Southern	10-16	Herbaceous	Large, lanceolate	45-55
Bolivia	9-12	Herbaceous	Large, lanceolate & small, triangular	40-50
Argentina	12-16	Herbaceous	Small, triangular	35-40

Table 2. Phaseolin types of wild populations and landraces of *P. vulgaris* from different Latin American countries.

Country	Wild Populations	Landraces	Sources
Mexico	M, S	S, Sd, T	1, 4
Guatemala	M, S	S, B	1, 4
Costa Rica	M	S, B	3, 1, 4
Colombia	CH, B	S, T, C, B	2, 4
Peru			
North	I	T, C, H, S	1, 4
Center	T,C	T, C, H, A, S	5, 1
South	T,C,K	T, C, H, S	5, 1
Bolivia	T	T, C, S	5, 1
Argentina (NW)	T, H, C, J	T, H	4, 1

Sources: 1. Gepts et al., 1986
2. Gepts and Bliss, 1986
3. Debouck, et al., 1988
4. Koenig et al., in press
5. Tohme and Debouck, in press

Table 3. Some morphological traits of high anthropic significance and their heritabilty.

Trait	Number of Loci	Inheritance	Reference
Dehiscent/non dehiscent pod	2 or 3	Dominant/recessive	Prakken, 1934; Leakey, 1988
Colored/pure white seed seed	9	Dominant/recessive	Leakey, 1988
Indeterminate/determinate growth habit	1	Dominant/recessive	Norton, 1915; Bliss, 1971
Internode length: long/ short lower internodes	1	Dominant/recessive	Leakey, 1988

Table 4. Estimated outcrossing rates for cultivated *P. vulgaris*

Place	Rate (%)	Reference
Berkeley, California	0.7	Mackie and Smith, 1935
Davis, California	0-0.007	Tucker and Harding, 1975
Irvine, California	9-69	Wells et al., 1988
Lilongwe, Malawi	0.8	Martin and Adams, 1987
Awassa, Ethiopia	3-5	Stoetzer, 1984
Several places, Mexico	1-4	Crispin, 1960
Chapingo, Mexico	1-3	Miranda Colin, 1971
Mayaguez, Puerto Rico	0.04-17.6	Brunner and Beaver, 1988

Table 5. Some crosses of cultivated P. vulgaris from different origins and problems encountered.

Origins	Phaseolin types	Symptoms/ abnormalities	Reference
South Andean/Mesoamerican via Kenya via USA	T x S	Crippled plants	Coyne, 1965
Guatemala/Bolivia and its reciprocal	S x T	Chlorosis and lethality	Shii et al, 1980
South Andean/Mesoamerican via Turkey via Brazil	T x S	Dwarf plants	Singh and Gutiérrez, 1984
South Andean/Mesoamerican via USA via Brazil	T x S	Absence of roots	Gepts and Bliss, 1985 (also for a review)
Guatemala/Chile	S x C	Cripples	Temple, 1977 (unpublished)
Costa Rica/South Andean via Haiti	S x T	Cripples	Temple, 1977 (unpublished)
Mexico/Colombia	S x B	Cripples	Temple, 1977 (unpublished)

Figures

Figure 1. Distribution of seed accessions of wild _Phaseolus vulgaris_ L. as of 1988.

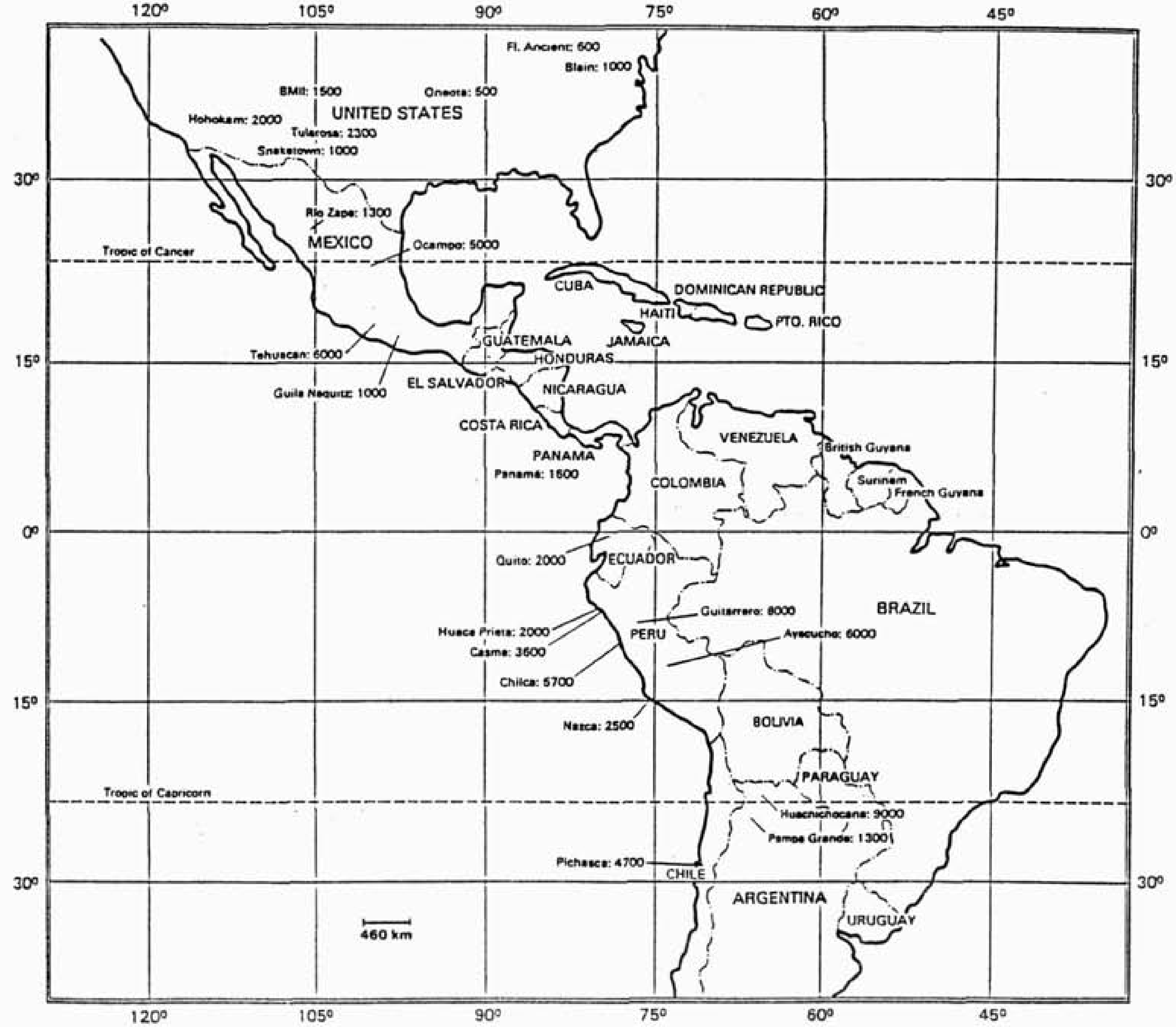


Figure 2. Archaeological findings of Phaseolus vulgaris L.: places and years before present.

Figure 3. Phaseolin types in wild <u>Phaseolus vulgaris</u> L. as of 1988.

35661

THE BEAN GERMPLASM BANK OF MEXICO

Francisco Cárdenas R.*

Introduction

From the time that man appeared on the earth, his sustenance has depended, directly or indirectly, on vegetables, since animals are incapable of synthesizing their own food intake from soil minerals, gases in the atmosphere, and sunlight. As a consequence of natural selection and selection practiced by man from the beginnings of farming, in bean (Phaseolus vulgaris L.), as for all plants, great genetic variability has been created. Certain regions exist in the world where physiographic characteristics favor the development and existence of a large number of ecotypes, and they are known as primary centers of genetic variability. Mesoamerica is considered to be one of the primary centers of genetic variability for bean.

Genetic variability of Phaseolus vulgaris L., as in other vegetable species, is being reduced as a result of the following: change in soil use; development of improved varieties from parental-crossed pure lines; planting in large areas of the same crop or closely [illegible]lated cultivars; the generalized use of cultural practices that minimi[illegible]mental effect on the plants, such as in the case of the use o[illegible] insecticides, fungicides, growth regulators, etc.; and i[illegible] materials, overgrazing.

---

* Director, CENID-Recursos Genéticos, Instituto Nacional de Investigaciones Forestales y Agropecuarias, Apartado Postal 10, Chapingo, Méx., México.

Upon analyzing the items mentioned in the previous paragraph, we observe that the causes of genetic erosion have been and will be a consequence of the evolution of farming. Undoubtedly, this pressure will continue to be greater in coming years, especially in developing countries.

In order to reduce as much as possible loss of genetic variability, it has been necessary to collect and conserve the largest possible number of bean samples from materials planted by farmers in Mexico. The same is also true for materials that have evolved without man's intervention.

Make-up of the Germplasm Bank

Since 1942, work on bean prospecting and collecting in Mexico has been carried out. In the last few years, together with CIAT, wild materials principally of the Phaseolus genera have been collected.

The Germplasm Bank is made up of 10,651 accessions, 90.7% of which are cultivated species, vulgaris, coccineus, lunatus, and acutifolium; and 9.3% represent 24 wild species. In both cases, vulgaris represents 83.5% (Table 1).

88.4% of the vulgaris accessions were collected in America, with 9.2% coming from Europe, 1.7% from Asia, and 0.7% from Africa (Table 2). On the other hand, 66.1% have been collected in Mexico and 12.0% in Central America; thus, more than 78% of the bank is made up of materials coming from Mesoamerica. And, as was indicated before, the bank is located in a primary center of bean genetic diversity.

Of material not originating in Mexico, approximately 80% has been obtained from CIAT.

In Mexico, an annual average of two million hectares of beans are grown and it can be affirmed that they are planted in practically all of the federated entities, with an average yield of around 650 kg/ha. These low yields are explained if one takes into account that in more or less 60% of the cultivated area, rainfall is very low, planting is done on relatively small surface areas, and it is done by farmers who practice traditional farming. Average per capita consumption is approximately 18 kg per year.

Because of all this, the collection of materials has been and is being carried out in all the national territory, taking into consideration ecological and ethnic variability of the country's diverse regions. Table 3 presents the number of accessions existing in the germplasm bank collected in each of the federated entities in the country.

Characterization and Preliminary Evaluation

During the last seven years at the Campo Experimental del Valle de México (CEVAMEX), in Chapingo, 6,284 accessions of *Phaseolus vulgaris* have been characterized and evaluated preliminarily. The following descriptors are evaluated:

1. Color of hypocotyl
2. Length of hypocotyl
3. Length of the fifth odd foliolate
4. Width of the fifth odd foliolate
5. Number of internodes at the beginning of flowering
6. Number of internodes at the end of flowering
7. Growth habit
8. Angle of the secondary branches
9. Number of days from planting to beginning of flowering
10. Number of days from planting to end of flowering
11. Plant height
12. Number of days from planting to maturity
13. Stem diameter
14. Number of pods per plant

15. Number of seeds per pod
16. Total plant weight at maturity
17. Grain yield per plant
18. Harvest index
19. Weight of 100 seeds
20. Volume of 100 seeds
21. Seed density
22. Seed form
23. Seed color
24. Brightness of cover
25. Reaction to diseases
26. Reaction to insects

In all the descriptors cited, there exists a great variation in each one of them, as does a broad combination among them. Within some characteristics that are important in improvement programs, the following variations have been observed in plantings at CEVAMEX:

Days from planting to first flower: 40 to 120
Days from planting to last flower: 20 to 65
Days from planting to maturity: 95 to 180
Total plant weight: 31 to 535 grams
Yield per plant: 6 to 180 grams
Harvest index: 0.03 to 2.3
Number of pods per plant: 11 to 270
Weight of 100 seeds: 15 to 55 grams
Volume of 100 seeds: 15 to 50 cc
Density: 0.85 to 1.5 g/cc
Growth habit: I to V

The five types of growth habit are defined as follows:

I. Determinate, bush, pods well-distributed on the plant, pods almost touch the ground. Type: Canario 101.

II. Indeterminate, bush, with small guides which almost entwine, well-distributed pods, pods rarely touch the ground. Type: Jamapa.

III. Indeterminate, guides of intermediate size with little tendency to entwine, pods concentrated on the lower part of the plant and which are frequently in contact with the ground. Type: Negro 150.

IV. Indeterminate, large and tangling guides, well-distributed pods; for this type to develop well, it needs to be planted with a support. Type: Accession 2068.

V. The same as the previous one, but with more vigor and a greater number of secondary branches; it is generally later. Type: Accession 3476.

Specific Evaluations

Stability of 17 descriptors in 197 accessions, in 5 environments

One of the objectives of bean improvement is to develop cultivars that will have a broad adaptation radius and at the same time their behavior will be the most stable possible. On the other hand, when *Phaseolus vulgaris* accessions are characterized, it is necessary to use those characters that will be less influenced by environmental changes.

With these ideas in mind, 197 accessions were planted, and they were selected as representative of broad variation which exists in the germplasm bank, in five different environments. In Annexes 1 and 2, information on year of collection, altitude, latitude and longitude of the collection site for the trial materials, as well as their common name, is presented. Regarding the testing sites (Chapingo, Celaya, Cotaxtla, Zacatecas, and Zapopan), climatic parameters; altitude, latitude, and longitude; maximum, minimum, and average temperatures; and average monthly rainfall from May to October are presented.

From each one of the accessions, rows six meters long were planted, separated from each other by 80 cm, with 30 cm between plants. Supports were used on those parcels where necessary. Five plants with uniform competency were labeled and pertinent observations were made on them; the average was used to make different comparisons.

The characteristics of flower color, seed shape and brightness, as well as angle of the primary branches in relation to the main stem are maintained almost constant. Nevertheless, in the case of seed color, in some original accessions of mild climate planted in winter (November and December) in a dry tropic, the color of harvested seeds is less intense.

Results obtained regarding stem diameter can be summarized in the following manner:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range in mm	4-11	4-10	4-10	6-13	4-12

Most stable accessions: 508, 559, 688, 943, 949, 1031, 1215, 2374, 2748.

With greater diameter in Chapingo and Zacatecas: 51, 307, 543, 553, 888, 903, 963, 969, 1546, 1651, 1657.

With greater diameter in Celaya and Zapopan: 1553, 1571, 2475, 3476.

With greater diameter in Cotaxtla: 508, 960, 963, 1049, 1152, 2374.

The most stable materials in all environments have growth habits II and III, some being early and others intermediate, with an average plant yield and with large and small seeds. Accessions of the types Cacahuate and Negro Tropical are being found.

Materials with a greater diameter in Chapingo and Zacatecas have medium- to large-sized seeds; plants with habits III, IV, and V; are generally late; types known as Canelo, Rebocero, and Morado de Agua are found in this group.

Flor de Mayo, Caña bean, and Zenete are types which have a large and stable stem diameter in Celaya and Zapopan, they have intermediate-sized seeds, with habits III, IV, and V, and, in general, they are late and have an intermediate number of pods.

In Cotaxtla, materials with greater diameter are from habit II, with small or large seeds of medium earliness, and with few pods per plant except for accession 508. In addition, their yield per plant is good. The types Cacahuate, Japones, and Huasteco are present in this group.

The following results were found for the characteristic number of internodes:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	8-37	5-47	8-32	6-49	9-35

Most stable materials: 627, 642, 643, 663, 790, 895, 963, 1035, 1460, 1629, 2021, 3287.

Accessions with a greater number of internodes in Chapingo and Zacatecas:

530, 1597, 1638, 1697, 1603, and 3420.

In Celaya and Zapopan, accessions with a greater number of internodes were: 96, 101, 701, 809, 1571, 1596, 1597, 1638, 2650, 2708, and 3476.

Accessions 518, 530, 959, 1049, 1597, 1651, 1818, 3505, and 3613 are those which had a greater number of internodes in Cotaxtla.

The majority of stable materials are of types I, II, and III and are generally early and intermediate plants, with low and intermediate yields with small and large seeds. Types Cuarentano, Negro Tropical, and Almendrillo are found in this group. Materials with a larger number of internodes in all sites are of habits IV and V with small- and intermediate-sized seeds, plants with medium to late earliness and generally low yields. The following types are present: Rosa de Castilla, Mexicano, Acalete, and Moro.

The range of variation in the number of days from planting to initiation of flowering was as follows:

	Chapingo	Cotaxtla	Zacatecas	Jalisco
Range:	44-120	29-48	36-109	34-79

The most stable accessions in the four sites mentioned were the following: 187, 508, 627, 647, 663, 688, 949, 957, 959, 960, 1024, 1035, 1152, 1460, 1629, and 2021. All these materials initiate their flowering between 35 and 45 days after planting, the majority have habits I and II, generally small or large seeds, with a small to intermediate number of pods, and average yield per plant is often low and in some cases intermediate. Common names of some of these accessions are Cuarentano, Ejote, Cacahuate, Japones, Frijola, Huasteco, De Vega, Bonbon, etc.

Stable collections and those with a reduced number of days from planting to the appearance of the first flowers in Chapingo and Zacatecas were 187, 627, 647, 895, 960, 1024, 1035, 1152, 1629, 3288, and 3475, those which have the same characteristics mentioned in the previous paragraph.

In Zapopan, collections with a short period from planting to initiation of flowering were 187, 409, 539, 575, 627, 643, 647, 823, 895, 899, 960, 1011, 1024, 1035, 1152, 1215, 1434, 1466, 1469, 1629, 1638, 2736, 3288, and 3475. Characteristics of these materials are similar to those indicated in the case of stable accessions in all environments. In addition, some early materials are added, with large seed and with an intermediate number of pods per plant. Those are known as Ojo de Cabra, Cuarentano, Canelo, and Pastilla.

Under tropical conditions, such as in Cotaxtla, all the materials initiated their flowering between 35 and 45 days after being planted.

The flowering period, number of days from first to last flowers, had the following ranges of variation:

	Chapingo	Cotaxtla	Zacatecas	Zapopan
Range:	29-60	11-31	10-44	22-54

Materials which showed themselves to be the most stable were 188, 539, 544, 547, 555, 581, 627, 688, 728, 849, 889, 902, 904, 907, 947, 965, 1011, 1460, 1466, 1651, 1818, 2681, and 3362. Of these accessions, 75% have growth habits III and IV and the rest have II and V. Fifty percent have large seeds and in the other 50%, medium-sized seeds predominate; earliness is intermediate to lateness; and yield per plant generally ranges from intermediate to high. Some of the materials are known by the following names: Bonbon, Vaquita, Panza de Venado, Bayo Rata, Grullo, etc.

In Zacatecas and Chapingo, materials which showed stability and a short flowering period were 85, 145, 299, 586, 627, 688, 701, 895, 904, 1033, 1035, 1152, 1215, 1460, 1629, 1798, 1818, 1868, 2310, 2375, 2533, 2748, and 3475. Twenty-five percent have growth habits I and II, 35% have habit III, and the rest have habits IV and V. Intermediate and late early materials, with intermediate and large seeds, and with small, intermediate, and large yields per plant are found. Cuarentano, Cacahuate, Ejote, Español, Garbancillo, etc., are common names by which the previously cited materials are known.

The number of days from planting to maturity showed the following variation:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	107-184	82-130	72-86	82-161	72-133

The most stable accessions in the five environments were 187, 895, 949, 1011, 1024, 1035, 1152, 1469, 1629, 1798, and 3888; 75% of which have growth habit I and the rest have growth habits II and III. All have large seeds, with a low number of pods per plant, and their yields are generally low. Some common names for these materials are Cuarentano, Canario, Cacahuate, Ejote, Ojo de Cabra, Peruano, Palacio, etc.

In Chapingo and Zacatecas, stable materials with a short period from planting to maturity were 187, 895, 1011, 1024, 1035, 1469, 1629, 3288, 3402, and 3475. These accessions have already been mentioned in the group of those with good stability in all environments.

Stable accessions with a short period from planting to maturity in Celaya and Zapopan were 187, 575, 643, 647, 807, 895, 960, 1011, 1024, 1035, 1215, 1409, 1469, 1629, 1638, 1798, 1845, 2533, 3288, and 3475. Half of these materials were already mentioned in the case of broad stability and the other half have the same characteristics of growth habit, seed size, number of pods per plant, and yield.

In Cotaxtla, differences in earliness were very small; 95% of the material planted matured between 74 and 80 days.

Yield per plant, expressed in grams, had the following variations:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	6-180	11-149	9-92	19-388	11-224

In the five test environments, materials which showed stability were 72, 145, 187, 508, 627, 728, 889, 957, 963, 1023, 1035, 1152, 1818, 2374, and 3397. Within this material, representatives are found for the five growth habits, seed size varies from small to large, the same as earliness and yield per plant. It is common within these materials to find the names of Cuarentano, Cacahuate, Huasteco, Bonbon, Moro, Almendrillo, and Apetito.

Collections with greatest yield and stability in Chapingo and Zacatecas were 200, 307, 575, 969, 1596, 1651, 2021, 2068, 2300, 2316, 2337, 2681, 3338, and 3362. Growth habit of these materials can be IV or V, with intermediate or large seeds, number of pods per plant is high, and, in general, plants are late, with more than 135 days from planting to maturity. They are commonly known as Morado de Agua, Grullo, Higuerilla, Zarco, Moro, etc.

In Zapopan and Celaya, the following accessions stood out for their stability and yield: 96, 121, 145, 307, 727, 889, 957, 963, 969, 1019, 1075, 1657, 1868, 2068, and 3362. These accessions, the great majority of which have large seeds and growth habits IV and V, are intermediate or late. They are known by the following common names: De Enredo, Moro, Almendrillo, Blanco Grande, Arroz, etc.

Stable materials with good yield per plant in Cotaxtla are 72, 83, 96, 489, 508, 518, 688, 807, 903, 957, 1409, 2748, 3476, and 3613. Ten of these accessions have growth habit IV, three have habit V, and one has habit I. Seed size for half is small and for the other half it is large. They have a medium number of pods per plant and the largest majority are of intermediate earliness. They are commonly known by the names Huasteco, Grullo, Rebocero, Flor de Mayo, Negro Opaco, Isiche, etc.

Total plant weight at maturity, expressed in grams, showed the following ranges of variation:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	31-535	31-283	17-156	36-752	42-604

Accessions that showed themselves to be stable with a high total plant weight were 121, 307, 555, 1546, 1596, 1651, 2021, 2316, 2681, 2337, and 3420. Plants from these materials are of growth habits IV and V, are late, have a high number of pods and a large yield per plant. They are commonly known as Borrego, Parreleña, Obalado, Pecoso, etc.

In the five environments, materials mentioned as follows were stable in Chapingo and Zacatecas: 299, 508, 627, 642, 643, 963, 994, 1023, 1035, 1152, and 3748. These materials have growth habits I, II, and III, and, in general, their seeds are intermediate-sized. In addition, their yield per plant is intermediate, and they can be early or intermediate and have a low or medium number of pods per plant. Common names with which they are frequently designated are Cuarentano, Cacahuate, Huasteco, Bonbon, Zamorano, Flor de Mayo, Rosita, etc.

In Celaya and Zapopan, materials which had a high total plant weight and which showed stability are 96, 121, 969, 1019, 1075, 1571, 1634, 1676, 1868, 1908, 2650, and 3362. They are commonly known as De Enredo, De Caña, Isiche, Morado de Agua, Ejotero, etc.

Accessions which had a high total plant weight in Cotaxtla were 508, 518, 555, 688, 1045, 1049, 1075, 1129, 1221, 2748, 3476, and 3613. The great majority have growth habits IV or V, with low-yielding small seeds and medium earliness. Common names of these materials are Negro Opaco, Manzano, De Enredo, De Pascua, Ancho, Zinguiño, etc.

Harvest index was defined as the relation between yield per plant divided by total dry plant weight, from which yield per plant was subtracted. Variation observed in this character was the following:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	0.30-2.25	0.28-3.11	0.10-3.75	0.10-3.30	0.15-2.47

In test environments, the most stable materials were 51, 188, 544, 575, 586, 637, 647, 663, 688, 849, 994, 1651, 1845, 1868, and 3288. They mainly have growth habits I, II, and III, and occasionally habit IV. Seed size varies from small to large, the same as number of pods per plant and yield per plant. These collections are known as Colima, Flor de Mayo, De Vega, Huasteco, Arroz, Borrego, etc.

Stable materials in Chapingo and Zacatecas that at the same time have a high harvest index were 508, 575, 637, 663, 688, 790, 969, 1460, 1676, 1868, 2558, and 2748. These collections, except for two, have growth habit IV, intermediate and large seeds, and an intermediate to long period from planting to maturity. The number of pods per plant and yield are high. Huasteco, De Mata, Pastilla, Morado de Agua, Arroz, Tigre, etc., are common names of these materials.

In Celaya and Zapopan, accessions 602, 637, 762, 907, 963, 993, 1001, 1031, 1460, 1676, and 2374 are stable and have a good harvest index.

Eighty percent of them have growth habit III, and growth habits II and IV are found in equal proportion. Nine of the eleven materials have large seed, and the rest have small. The number of pods per plant is low, yield per plant varies from low to intermediate, and the number of pods per plant varies in the same manner. These materials are commonly known as Almendrillo, Azufrado, Perla, Cacahuate, Bayo Rata, etc.

Materials which were outstanding for their high harvest index in Cotaxtla were 145, 508, 823, 903, 957, 963, 1215, 1409, 1547, 1603, 1629, 1909, 3362, 3475, and 3613. Seventy percent of these have growth habit IV and the rest have growth habits I and II. Around 50% have large seeds and the rest have small to intermediate ones. Yield per plant and number of pods per plant are high. Burro, Rebocero, Bola, Huasteco, Almendrillo, etc., are common names by which these accessions are known.

Variation observed in the number of pods per plant was the following:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	11-279	11-111	7-61	16-278	24-198

The following accessions stood out at the five sites for their stability: 84, 508, 627, 675, 701, 728, 888, 949, 1023, 1033, 1035, 1152, 1469, and 1629. The five growth habits are found in these accessions, seed size ranges from small to large, yield per plant runs from low to intermediate, and the number of days from planting to maturity fluctuates from earliness to lateness. Names by which these materials are known are Cacahuate, Cuarentano, Huasteco, Bonbon, Canelo, Patachete, etc.

Materials which had a high number of pods per plant and at the same time were stable in Zacatecas and Chapingo were 51, 121, 188, 286, 307, 555, 575, 809, 965, 1603, 1868, 2021, 2068, 2337, 2375, 3007, and 3368. Predominant growth habits for these accessions are IV and V, seed size goes from small to large, plants are late, they have a high number of pods per plant, and they have a good yield. They are commonly known as Vaquita, Franelo, Arroz, Garbanza, Pastilla, Pecoso, etc.

In Zapopan and Celaya, the following accessions were stable and had a high number of pods per plant: 70, 96, 121, 188, 307, 581, 701, 728, 1571, 1634, 1676, 1868, 1908, 1919, and 2068. They have growth habits IV and V, intermediate to late earliness, intermediate to high average yield per plant, and medium to large seed size. They are commonly known as Vaquita, Moro, Ejotero, Arroz, Guadalupano, etc.

Accessions which stood out in Cotaxtla for number of pods per plant were 167, 286, 299, 489, 508, 518, 1225, 1547, 1603, 2558, 2748, 3288, 3613, and 4016. Growth habit IV predominates, yield per plant is average to good, earliness is medium, and seeds are medium-sized. These materials are known by the names Negro Opaco, Aceitunado, Zamorano, Amapolo, Zacapeño, Colima, etc.

The range of variation observed in the number of grains per pod in the five test environments were:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	3-6	2-8	2-8	4-7	3-7

At the five sites, materials which showed stability for this characteristic were 489, 508, 543, 663, 688, 919, 957, 969, 1023, 1152, 1215, 1551, 1597, 1909, 2139, 2374, 2744, 3287, 3402, 3475, and 3505. Growth habits for these accessions vary from I to V, and seed size, number of pods per plant, and yield per plant are equal, ranging from small to large. Cacahuate, Huasteco, Cuarenteño, Grullo, Tzama, Lenteja, etc., are common names by which these beans are known.

In Chapingo and Zacatecas, materials which had a high number of grains per pod and showed stability were 489, 508, 530, 555, 663, 804, 895, 1033, 1651, 1657, 1697, 1868, 1909, 2316, 3476, and 3613. These materials have plants with growth habits II to V, with those having small seeds predominating. They have medium to late earliness, and yield per plant and number of pods per plant vary from average to high. These types of bean are known as Huasteco, Español, Borrego, Bonbon, Arbolito, Jarocho, Acalete, etc.

Accessions with a high number of grains per pod and that were stable in Zapopan and Celaya are 508, 555, 642, 653, 663, 688, 701, 943, 1019, 1034, 1215, 1551, 1908, 1909, 2708, 3287, and 3505. Growth habits for these materials varied from II to V, the great majority have small seeds, the number of pods per plant varies from low to intermediate, the same as yield per plant. Blanco Chico, Berrendo, Barreton, Peruano, Mantequilla, and Huasteco are names by which these beans are known.

In Cotaxtla, accessions which had a high number of grains per pod were 187, 508, 530, 663, 688, 1215, 1225, 1409, 1551, and 2744. Growth habit IV predominates, seed size is small, yield is from low to intermediate, and the number of pods per plant is intermediate, the same as earliness.

Weight of 100 seeds varied in the following manner:

	Chapingo	Celaya	Cotaxtla	Zacatecas	Zapopan
Range:	12-51	12-59	17-61	12-56	16-50

Stable accessions in the five environments were 40, 89, 187, 347, 489, 508, 530, 539, 559, 581, 602, 637, 663, 688, 728, 809, 904, 947, 957, 993, 1019, 1031, 1547, 1868, 1909, 2068, 2316, 2508, 2533, and 3505. Growth habits I, II, and III predominate for these materials, with less frequency for habits IV and V. Yield per plant ranges from low to high, the same for number of days from planting to maturity. Low and intermediate numbers of seeds per pod predominate. These accessions are commonly known as Frijola, Huasteco, Manquilla, Grullo, Arroz, Moro, Palacio, Bayo Rata, etc.

Stable materials with heavier seeds in Chapingo and Zacatecas were 145, 200, 544, 547, 559, 711, 804, 892, 899, 903, 923, 957, 960, 969, 997, 1950, 2558, 3288, 3633, and 3888. Plants from these accessions generally have growth habits IV or V, they are late, they have a medium to large number of pods and yield per plant. Farmers call them Japones, Burro, Grullo, Morado de Agua, Panza de Venado, Canelo, Rebocero, etc.

In Zapopan and Celaya, collections that showed stability in 100-seed weight were 347, 539, 544, 559, 575, 899, 902, 903, 907, 919, 957, 969, 1152, 1434, 1651, 3007, 3288, 3362, 3633, 3885, and 3888. Growth habit III is the most common for these plant accessions. They are early to intermediate, they have a low number of seeds per pod, and yields are low and intermediate. They are commonly known as Cacahuate, Borrego, Rebosillo, Grullo, Canelo, Pastilla, Franelo, Ojo de Liebre, etc.

Under tropical conditions in Cotaxtla, materials which had the greatest 100-seed weight were 347, 539, 544, 575, 804, 899, 901, 902, 957, 969, 1152, 1434, 1629, 1950, 3362, 3475, and 3633. Their plants have growth habits I, III, and IV. They possess a low number of seeds per pod, their yields can be low and average, the number of pods per plant is low, and they have an intermediate earliness.

Accessions which showed less variation in the greatest number of descriptors in the five environments can be considered stable in general. Collections which showed stability in three or more characters are shown in Table 4. In this table, one can observe that materials have growth habits I, II, and III, they are early, and seeds can be large or small.

Search for sources of drought tolerance

From just over six years ago, the Bean Department began systematic work in order to identify materials which showed the greatest tolerance possible to stress produced by the lack of water in the most critical season for grain production. For that, under controlled humidity conditions, research was begun to initially test the 197 accessions to which we have previously referred. From this initial work, it was concluded that collections with growth habits I, II, IV, and V, under the ecological conditions of Francisco I. Madero, Durango, had few probabilities for success. Therefore, from that time on, more than 7200 materials of growth habit III have been tested. Some of the materials collected in Mexico that have shown the greatest tolerance to drought are presented in Table 5.

Sources of resistance to eleven physiological races or pathotypes of Colletotrichum lindemuthianum

Of the 197 accessions that are shown in Annex 1, 179 were inoculated with eight physiological races or pathotypes of C. lindemuthianum under greenhouse conditions with the goal of discovering the reaction of the materials to each one of the races and to detect the most resistant ones. The pathotypes were originated from isolations made from pods and/or infested seeds, which were collected in Chapingo, Mexico; Victoria and Madero, Durango; and Tepame, Jalisco. They were designated as MA-11, MA-16, MA-23, MA-24, MA-25, MA-26, and MA-30.

The 14 collections that are presented in Table 6 were resistant to the 8 pathotypes; 22 were susceptible to all of them and the rest showed great variability in susceptibility and resistance.

Upon examining Table 6, we become aware that there were no materials from habit II that were resistant to all the pathotypes, there being great variation in relation to days from planting to maturity, in 100-seed weight, and in other descriptors.

Tolerance to high temperatures

In order to search for materials that would produce acceptably when bean plants (in the period from flowering to maturity) find themselves developing at high temperatures and at relative humidities that vary from 45% to 70%, they were planted at Cd. Obregón. They are the materials that are mentioned in Annex 1.

Planting was carried out on March 12, so that plants (during the period from beginning of flowering to maturity) were submitted to maximum temperatures of 33 to 36 °C during the month of May and of 34 to 38 °C in June. Only 73 accessions produced seed and of the remaining 124, 23 did not produce flowers and 101 flowered but did not produce pods.

In Table 7, some accessions whose yield and number of pods per plant were superior are presented. Upon analyzing the information, one sees that the material collected in the state of Chiapas and especially that which originated in Acala is the most tolerant.

Perspectives for using the Bank

In a short- and medium-term future, the use of the materials deposited in the bank will depend on the information with which one can count on now. And on that which will be collected, it can be transmitted appropriately to breeders so that they will be convinced of the importance of its incorporation into improvement programs. It is necessary for people who work in bean breeding genetic resources to receive from breeders needs for specific materials for their programs. Those programs should focus their work in that direction.

Because of human resources and economic limitations in Mexico and perhaps in all national agricultural research centers in Latin America, it is necessary to look for working agreements within the institution itself, or with national and international entities, which will allow a maximizing of resources to be able to adequately satisfy demands for information and materials.

On the other hand, and because of limitations mentioned, it is necessary to prioritize bank activities, working on problems that should be attacked. It is almost impossible, with the current state of the bank's knowledge, to be able to comply satisfactorily with specific requests for certain materials.

Taking into consideration the number of accessions of some large banks, it would be convenient, as in the case of work which has been described previously, to look for some manner of having, with an appropriate but reduced number of materials, a broad representation of the stored materials. This allows detection, in a given case, of what type or type of materials the characters sought are found in. Afterward, more intense research with a greater number of materials can be directed specifically toward this type of accessions.

Table 1. Composition of the *Phaseolus* germplasm bank of the INIFAP, Mexico, 1988.

Cultivated forms		9.662
P. vulgaris	8.395	
P. coccineus	904	
P. acutifolius	218	
P. lunatus	145	
Wild forms		989
P. vulgaris	499	
P. coccineus	210	
P. acutifolius	60	
P. lunatus	40	
P. maculatus	29	
P. pedicellatus	25	
P. leptostachus	23	
P. macrocarpus	22	
Other 16 species	81	
Total		10.651

Table 2. Geographic origin of the *P. vulgaris* accessions in the germplasm bank of the INIFAP, Mexico, 1988.

América	
North America	183
Mexico	5.545
Central America	1.009
The Caribbean	40
South America	642
Total	7.419
Europe	
Central	120
Western	387
Eastern	58
Mediterranean	198
Northern	10
Total	773
Africa	58
Asia	143
Oceanía	4
Total	8.395

Table 3. Collections of cultivated *P. vulgaris* made in each federated entity of Mexico, 1988.

Entity	Number	Entity	Number
Aguascalientes	276	Nayarit	52
Baja California N.	3	Nuevo León	24
Baja California S.	8	Oaxaca	215
Campeche	27	Puebla	901
Coahuila	41	Querétaro	59
Colima	15	Quintana Roo	9
Chiapas	745	San Luis Potosí	163
Chihuahua	112	Sinaloa	27
Durango	181	Sonora	48
Distrito Federal	1	Tabasco	1
Guanajuato	232	Tamaulipas	15
Guerrero	86	Tlaxcala	139
Hidalgo	104	Veracruz	208
Jalisco	289	Yucatán	2
México	286	Zacatecas	178
Michoacán	239	Unknown	279
Morelos	81	To be documented	507
Total		5.046	

Table 4. Accessions with three or more stable characters, Mexico, 1988.

Accesion number	No. of characters	Common name	Growth Habit	Days to maturity	100-seed* weight* (g)
508	7	Huasteco	II	98	19
627	6	Bonbon	II	97	23
688	6	De Mata	II	98	25
1035	6	Cuarentano	I	85	39
1152	6	Cacahuate	II	93	50
663	5	De Vega	II	100	20
949	4	Cacahuate	II	85	38
957	4	Grullo	III	113	51
1023	4	Amarillo	III	97	28
1629	4	Ejote	I	85	39
187	4	Frijola	I	85	37
728	4	Moro	III	115	25
963	3	Almendrilla	III	111	30
1460	3	Bayo Rosa	III	99	43
2374	3	Cacahuate	II	98	43

* Mean of the five environments.

Table 5. Materials tolerant to drought in Francisco I. Madero, Durango, Mexico, 1988.

Accesion number	Collection site Alt. (m)	 Lat.	 Long.	Days to maturity	100-seed weight (g)	Grain color
282	1.941	19:43	101:11	88	28	Purple with cream
339	1.611	19:26	102:05	124	25	Bay
342	1.456	19:36	102:29	157	27	Bay with pink
637	1.800	16:50	92:25	110	30	Red
867	1.600	20:23	100:00	115	17	Bay
975	1.979	21:53	102:18	109	27	Black
1419	---	28:12	105:34	101	29	Bay with purple
1514	1.981	21:27	100:53	103	32	Bay
1673	---	18:56	99:47	103	21	Bay
1678	---	---	---	110	21	Black
1710	---	---	---	114	45	Bay
1698	35	16:30	100:53	81	10**	Gray with black

* Information provided by Dr. Jorge Acosta.

** Wild material.

Table 6. Accessions resistant to eight pathotypes of *C. lindemuthianum*, Mexico, 1988.*

Accesion number	Collection site	Growth Habit	Days to marurity	200-seed weight
187	El Mirador, Gto.	I	85	38
518	Jalacingo, Ver.	V	130	18
530	Atzalán, Ver.	V	128	17
701	Teapizca, Chis.	V	142	28
902	Pabellón, Ags.	V	140	50
1049	San Cristóbal de las Casas, Chis.	V	135	38
1549	Taxco, Gro.	IV	121	21
1603	El Grullo, Jal.	V	140	18
1629	Tequila, Jal.	I	85	40
1798	Zitacuaro, Mich.	I	89	37
2175	Puebla, Pue.	IV	115	20
2604	Cd. Victoria, Tamps.	III	101	22
2708	Estanzuilla, Ver.	IV	108	21
3505	San Cristóbal de las Casas, Chis.	V	145	27

* Information generated in thesis work done by Eduardo R. Garrido R.

Table 7. Accessions that were most tolerant to high temperatures in the period from flowering to maturity, Mexico, 1988.

Accesion number	Collection site	Days to flower	Days to maturity	Yield/ plant (g)	Pods per plant	Growth Habit
76	Yahualica, Jal.	53	100	17.0	35	IV
77	Teocaltiche, Jal.	57	104	16.9	15	V
637	Oxchic, Chis.	47	104	19.8	26	IV
650	Acala, Chis.	65	100	15.7	24	I
659	Acala, Chis.	57	100	18.4	24	III
674	Acala, Chis.	59	100	17.7	25	II
685	Bejucal, Chis.	65	100	24.8	29	III

Annex 1. Idenfication data of 197 *P. vulgaris*. accesions. Mexico, 1988.

Accession number	Year of collect.	Altitude (m)	North Latitude	West Longitude	Common name
40	—	1.700	18:51	98:25	Manguito
51	1945	1.700	21:10	102:28	Tempranillo
70	1948	2.240	21:27	102:35	Burro Bola
72	1950	—	19:38	103:36	Apetito
83	1948	1.880	21:08	102:52	Chicharo
84	1948	—	21:36	102:24	Tepetate
85	—	2.240	21:27	102:35	Tepetate
89	1948	—	20:08	103:11	Pildora
96	1950	1.960	20:49	102:46	Moro
101	1947	—	19:32	103:24	Mexicano
121	1949	1.589	20:41	103:20	—
145	1952	1.932	22:23	103:11	Burro
167	1948	1.736	20:13	101:08	Amapola
187	—	1.777	20:56	101:35	Frijola
188	1945	1.895	21:09	100:56	Vaquita
200	1946	1.852	20:57	100:45	Alubia
286	1948	1.575	20:03	102:44	Zacapeño
299	1950	1.575	20:03	102:44	Zamorano
303	1950	1.575	20:03	102:44	Canutillo
307	1948	1.540	20:16	102:20	Pecoso
347	1948	2.675	—	—	Rebocillo
489	1955	30	19:04	96:09	De arbolito
508	1955	—	—	—	Huasteco
518	1955	1.944	19:49	97:18	Negro Opaco
530	1966	1.600	19:48	97:13	Acalete
539	1948	1.850	22:34	102:13	Aceitito
543	1948	1.850	22:34	102:13	Lenteja
544	1948	1.850	22:34	102:13	Panza de Venado
547	1948	1.850	22:34	102:13	Morado
553	1948	1.800	21:22	100:52	Lagunero
555	1948	1.800	21:22	100:52	Manzanero
559	—	1.800	22:47	102:36	Manteca
575	1948	—	—	—	Pastilla
581	1948	—	22:28	103:09	Origuelo
586	—	1.300	22:34	102:13	Cuarenteño
592	1954	1.300	22:34	102:13	Pardo Barqueño
602	—	2.612	22:38	103:40	Jacalito
627	—	200	16:06	93:45	Bonbon
637	1946	1.800	16:50	92:25	Tigre

Annex 1. Cont.

Accession number	Year of collect.	Altitude (m)	North Latitude	West Longitude	Common name
642	1946	1.200	16:20	92:34	Shanquil
643	1946	1.530	16:15	92:08	Barreton
647	1946	600	16:18	92:25	Huet
651	1946	550	16:31	92:44	Tsajal-Chelnek
663	1947	1.635	16:15	92:08	De Vega
675	---	600	16:45	93:09	Patachete
688	1950	1.500	15:25	92:07	De Mata
691	1950	1.500	15:25	92:07	De Vara
701	1950	1.500	16:33	92:28	---
711	1948	2.435	20:09	98:43	Alimonado
725	1943	1.102	20:22	99:39	Higuerilla
728	1948	1.102	20:22	99:39	Moro
747	1948	2.435	20:09	98:43	Garambullo
752	---	2.435	20:29	99:13	Franciscano
762	---	2.050	20:14	99:13	---
785	1952	1.734	23:50	104:14	---
790	1952	1.898	24:03	104:40	Champurrado
804	---	1.668	24:47	104:27	Jarocho
807	1976	---	23:43	103:49	Ojo de Cabra
809	1976	---	23:57	104:03	Negro Brillante
820	1976	---	24:31	104:21	Amarillo Brillante
823	1955	3	23:12	106:25	Bañarta
849	---	200	21:15	98:47	Huatusco
888	1952	1.609	25:32	103:28	Canelo
889	1945	1.950	22:14	102:19	Bayo
892	1945	1.979	21:53	102:18	Manchado
895	1945	1.979	21:53	102:18	Español
899	1945	1.950	22:14	102:19	Canelo
901	1945	2.217	22:11	102:21	Panza de Puerco
902	1945	2.217	22:11	102:21	Grullo
903	1945	2.217	22:11	102:21	Rebocero
904	1945	2.217	22:11	102:21	Guero
907	1945	2.217	22:11	102:21	Bayo Rata
919	---	1.950	22:14	102:19	Ojo de Liebre
923	---	1.979	21:53	102:18	Garrapata
943	1952	1.979	21:53	102:18	Mezquitillo
947	1954	1.979	21:53	102:18	Bayo Palacio
949	---	1.979	21:53	102:18	Cacahuate
955	---	1.979	21:53	102:18	Garbancillo
957	---	1.979	21:53	102:18	Grullo

Annex 1. Cont.

Accession number	Year of collect.	Altitude (m)	North Latitude	West Longitude	Common name
959	—	1.979	21:53	102:18	Alubia Mediana
960	—	1.979	21:53	102:18	Japones
963	—	1.979	21:53	102:18	Almendrilla
965	—	1.979	21:53	102:18	Garbanza
969	—	1.979	21:53	102:18	Morado de Agua
972	—	1.979	21:53	102:18	Chivitas
993	—	1.979	21:53	102:18	Flor de Mayo
994	—	1.979	21:53	102:18	Flor de Mayo
997	—	1.979	21:53	102:18	Bayo Rosado
1001	—	—	23:20	109:45	Azufrado
1011	1948	1.610	15:26	100:52	Peruano
1019	1952	1.840	28:41	100:33	Blanco Grande
1023	1952	1.140	25:32	103:28	Amarillo
1024	1965	1.589	25:25	101:00	Canario
1031	1954	494	19:15	103:44	Perla
1033	1954	494	19:15	103:44	Rosita
1034	1954	494	19:15	103:44	Berrendo
1035	1946	2.755	16:46	92:38	Cuarentano
1045	1954	2.755	16:46	92:38	Trapichito
1049	1954	2.755	16:46	92:38	Frijol Ancho
1975	1954	1.530	16:15	92:08	De Enredo
1129	1954	1.500	16:46	93:23	Zinacatan
1152	—	137	14:55	92:16	Cacahuate
1215	1972	564	16:39	93:48	Cuarenteño
1221	—	—	—	—	De Pascua
1225	—	—	—	—	Concecionero
1351	1976	500	16:34	92:48	Nandalume
1392	1976	1.770	16:34	92:28	Gato
1409	—	—	28:32	107:30	Ojo de Cabra
1434	1966	2.440	—	—	Chicharo
1439	—	900	28:10	108:30	De Verano
1445	—	900	28:10	108:30	Granizo
1460	1977	1.600	27:57	106:07	Bayo Rosa
1466	1977	1.500	31:38	106:20	Amarillo Flojo
1469	1978	1.490	31:38	106:20	Ojo de Cabra
1490	1952	1.734	23:50	104:14	—
1492	—	—	23:57	104:03	Pinto
1546	1946	—	—	—	Parraleño
1547	—	1.735	18:33	99:36	Bola
1549	—	1.735	18:33	99:36	Acerado

Annex 1. Cont.

Accession number	Year of collect.	Altitude (m)	North Latitude	West Longitude	Common name
1551	1952	290	18:19	101:45	Pan Caliente
1553	1952	38	17:58	101:48	Plomo
1571	1966	—	—	—	De Caña
1592	1955	2.181	20:05	98:22	Serrano
1596	1945	—	20:08	103:03	Rosa de Castilla
1597	1945	1.500	19:32	103:45	Rayado
1603	—	952	18:48	104:13	Café Claro
1623	—	1.280	20:50	104:43	Garbancillo Grande
1629	1965	1.215	20:52	104:51	Ejote
1634	1965	—	20:20	102:46	Guadalupano
1638	1965	1.215	20:52	103:51	Fríjol del Diezmo
1651	1965	1.550	20:33	101:31	Borrego
1657	1965	1.550	20:33	102:31	Zarco
1659	—	—	—	—	—
1675	1957	1.847	19:12	100:08	Criollo
1676	—	—	18:56	99:47	Ejotero
1667	—	—	—	—	Chamacuro
1768	—	2.600	19:28	98:21	—
1769	1965	1.751	19:48	102:42	Rebozo
1798	1965	1.993	19:26	100:23	Palacio
1818	1972	—	—	—	—
1845	—	1.291	18:48	98:57	—
1868	—	915	21:31	104:53	Arroz
1884	1965	1.020	21:05	104:20	Capulina
1980	1948	2.150	16:42	94:48	Cuarenteño
1909	1948	—	—	—	Chatito
1979	—	1.526	16:47	96:40	Coral
1922	—	1.526	16:47	96:40	Cocona
1950	1965	1.572	17:48	97:47	—
1954	1965	1.563	17:04	96:43	Mixteco
1963	—	—	—	—	Colorado
2021	1943	1.676	18:25	97:26	—
2061	1943	2.458	18:52	97:22	Vaquita
2068	1943	2.458	18:52	97:22	Vaquita
2123	1943	1.285	19:22	98:33	Ojo de Venado
2124	1943	2.278	19:17	98:27	De Temporal
2132	1946	1.213	18:12	98:13	Tabaquillo
2139	1952	—	18:51	98:25	—
2151	1952	—	19:53	98:37	Tlapeño
2161	1948	2.676	18:59	98:27	Mantequilla

Annex 1. Cont.

Accession number	Year of collect.	Altitude (m)	North Latitude	West Longitude	Common name
2175	1952	2.209	19:02	98:11	Frijol de Milpa
2300	1966	—	20:08	97:15	Bayo Arriñonado
2310	1966	350	18:40	97:40	Frijol Shinaliea
2316	1966	2.315	19:02	98:02	Parrañelo
2337	1966	—	19:06	97:33	Pinto
2374	—	1.790	19:49	97:48	Cacahuate
2375	—	—	—	—	Garbancillo
2400	1965	1.676	18:25	97:26	Garabato
2475	1972	350	18:40	97:40	Zenete
2508	—	—	—	—	Bayo Rata
2533	—	—	—	—	Lagunero Mantequilla
2558	1973	—	20:49	100:00	Aceitunado
2559	1973	—	20:49	100:02	Pardo
2604	1954	321	23:44	99:08	Bayo Chiquito
2650	1966	2.100	19:19	98:19	Enredador
2681	1963	2.340	19:18	96:46	Charreado
2708	1966	—	—	—	Ochenteño
2724	1965	—	18:48	97:11	Charro
2736	—	1.258	18:51	97:06	Abalado
2744	1968	—	—	—	Tzoma
2748	1954	—	22:34	102:13	Zinguiño
3007	1946	1.951	24:28	104:22	Franelo
3287	—	—	—	—	Blanco Chico
3288	—	—	—	—	Colima
3362	1973	—	17:08	97:44	—
3338	1973	—	—	—	Amarillo de Mata
3397	1976	—	—	—	De Carrizo
3402	1976	—	16:43	93:01	Patashite
3420	1977	—	18:54	97:44	Blanco Abolado
3475	1977	—	—	—	—
3476	1978	—	—	—	Flor de Mayo
3505	1977	—	—	—	—
3613	1978	—	15:34	92:19	Isiche
3633	1978	—	—	—	Cara de Cabra
3885	—	—	—	—	—
3888	—	—	—	—	—
4016	1979	—	23:36	100:42	Huevo de Viejito

Annex 2. Meteorological parameters of five sites, Mexico, 1988.

	May	June	July	August	September	October	November
Chapingo Altitude: 2.250 msnm - Latitude: N-19:29 - Longitude: W-98:54							
Average mean temperature	26.9	25.7	24.3	24.3	23.5	23.5	23.4
Averge mean temperature	17.3	17.3	16.2	16.0	15.8	14.6	12.8
Average minimum temperature	8.0	9.9	9.2	9.0	9.0	6.4	3.5
Total rainfall mm	66.4	109.7	123.8	115.3	104.5	46.9	15.5
No. of days with frost	0.86	0.15	0.00	0.09	0.36	2.40	7.52
Zacatecas Altitude: 2.446 msnm - Latitude: N-22:47 - Longitude: W-102:35							
Average mean temperature	26.8	25.9	24.4	24.5	23.8	22.7	19.8
Averge mean temperature	19.0	19.0	17.8	17.9	17.2	16.2	14.5
Average minimum temperature	5.6	7.0	7.5	5.8	4.1	1.0	-3.5
Total rainfall mm	14.7	69.1	75.1	102.1	78.4	38.1	10.2
No. of days with frost	0.00	0.00	0.00	0.00	0.00	0.34	3.23
Celaya Altitude: 1.752 msnm - Latitude: N-20:31 - Longitude: W-100:49							
Average mean temperature	32.2	30.6	28.5	28.6	27.4	26.6	25.4
Averge mean temperature	23.3	22.8	21.4	21.4	20.6	19.0	15.2
Average minimum temperature	14.4	15.1	14.3	14.3	13.8	11.4	8.7
Total rainfall mm	26.5	106.0	115.6	114.7	93.4	44.1	12.4
No. of days with frost	0.00	0.00	0.00	0.00	0.00	0.44	2.43
Zapopán Altitude: 1.589 msnm - Latitude: N-20:40 - Longitude: W-103:23							
Average mean temperature	31.2	28.7	26.0	26.0	25.6	25.5	25.2
Averge mean temperature	23.2	22.3	20.5	20.5	20.1	19.0	17.2
Average minimum temperature	14.0	15.9	15.3	15.1	15.1	12.4	9.1
Total rainfall mm	24.6	164.6	250.3	195.6	148.8	59.7	11.3
No. of days with frost	0.00	0.00	0.00	0.00	0.00	0.06	1.50
Cotaxtla Altitude: 30 msnm - Latitude: N-19:32 - Longitude: W-96:06							
Average mean temperature	32.8	32.6	31.7	32.3	31.9	30.8	27.3
Averge mean temperature	27.7	27.9	26.9	27.2	27.0	25.7	23.6
Average minimum temperature	22.7	23.3	22.1	22.2	22.1	20.7	18.6
Total rainfall mm	50.4	253.2	313.5	247.9	245.5	83.6	39.0
No. of days with frost	0.00	0.00	0.00	0.00	0.00	0.00	0.00

35662

RACES OF COMMON BEAN, Phaseolus vulgaris L.

Shree P. Singh, Daniel G. Debouck, and Paul Gepts*

Summary

A large genetic variation in common bean (Phaseolus vulgaris L.) is found, but this is probably not distributed at random. Based on the ancestral and adaptive characteristics and the ecological habitat, six races have been tentatively identified in cultivated common bean germplasm. Three of these each were of Middle-American (races D, J, and M) and Andean-American (races C, N, and P) origin. Distinguishing characteristics of each of these races are described.

Criteria Used for Race Identification

Leaf, stem, inflorescence, flower, pod, and seed characteristics and the extent of crossability, chromosome pairing, and gene exchange have been utilized for species characterization and establishment of the primary, secondary and tertiary gene pools within the genus Phaseolus (Smartt, 1980, 1985). It is believed that present day cultivated common bean (Phaseolus vulgaris L.) evolved from its immediate relative, the wild common bean. The wild common bean crosses easily with cultivated forms and produces normal, fertile progenies (Weiseth, 1954; Harmsen et al., 1987), and hence falls within its primary gene pool (Smartt, 1984). The geographical distribution of the wild common bean extends from northern Mexico to the southern tip of the Andes in Argentina (Debouck and Tohme, this volume).

---

* Bean Breeder, and Germplasm sepecialist, respectively, CIAT, A.A. 6713, Cali, Colombia. Asstt. Professor, Dept. of Agronomy and Range Science, U.C. Davis, CA 95616, USA.

There are striking differences in leaf, inflorescence, flower, and seed characteristics and habitats of wild bean from the two extreme northern and southern regions of Latin America (Burkart and Brücher, 1953; Vanderborght, 1987) although some accessions, from Venezuela to Peru, exhibit intermediate traits (Debouck and Tohme, this volume). Present day cultivars of common bean differ strikingly from their wild ancestors; nevertheless, some of the traits from the wild bean are still conserved in the cultivated types. These will be refered to as ancestral traits and will be described later.

Variability in morpho-agronomic and molecular traits in cultivated common bean follows similar patterns as those of wild bean of different regions. Harlan (1971, 1975) considered common bean as a noncentric crop - without a specific and localized center of origin, but with wide geographical distribution of its wild relatives and multiple centers of domestication. Using phaseolin seed protein patterns, Gepts and Bliss (1985) and Gepts et al. (1986) separated both the wild and cultivated common bean of Meso-America from those of Andean South America, and suggested two major domestication centers.

Variability for growth habit, seed, pod, maturity, and adaptation characteristics is much greater in cultivated forms than in wild common bean. Did this variability evolve after initial domestications? If so, this might reflect preferences and needs of the precolombian civilizations within their original environments. Nonetheless, we have at our disposal two groups of traits, namely the ancestral and adaptive, to study the patterns of variation in cultivated germplasm. The term race is used here to define groups of germplasm accessions that share in common some ancestral and adaptive traits, occupy similar ecological niches, and differ from other such groups in these attributes. A brief description of traits used for race identification are below.

Ancestral traits

As noted earlier these are traits from wild bean that are still preserved in cultivated landraces and hence help identify the domestication centers: Middle America (MA) vs. Andean America (AA). These include:

Leaf shape. The shape of the terminal leaflet of the trifoliate leaf can be ovate (MA) or rhombohedric (AA). These differences have been pointed out by Brücher (1988) in the wild bean throughout their range.

Bracteoles. Bracteoles of MA are large ovate exceeding the calyx and those of AA are small lanceolate or slender, not exeeding calyx length (Gentry, 1969). Small bracteoles are typically found in the aborigineus form, distributed in southern Bolivia and Argentina (Debouck and Tohme, this volume).

Standards. Striped and colored outer base of standard (MA) vs. smooth and greenish (AA).

Inflorescence. Multi-insertions (2-5) (MA) vs. few (1-2) insertions (AA). Their striking character, measured by the number of primary bracts, was first observed by Vanderborght (1983)

Phaseolin seed protein. The cultivated as well as wild bean from MA carry phaseolin patterns of S, Sb, and Sd types and those from AA possess T, C, H, A, I, and J types (Gepts et al., 1986; Koenig et al, 1989). The B phaseolin patterns have been found in small-seeded accessions of cultivated and wild beans from Colombia. Some cultigens from Brazil and Central America also possess B phaseolin patterns. In general, there is much larger variability in phaseolin protein patterns in wild populations, a smaller proportion of which are found in cultigens (Gepts et al., 1986; Koenig et al., in press).

Isozyme patterns. A survey of nine polymorphic isozyme loci has confirmed the existence of the Mesoamerican and Andean races. At several isozyme loci, Mesoamerican and Andean genotypes display contrasting alleles. For example, Mesoamerican genotypes, in general, display the F (fast) allele of the enzymes ribulose biphosphate carboxylase/oxygenase and shikimate dehydrogenase, and the S (slow) alleles of the enzymes diaphorase-1 and leucine aminopeptidase3; Andean genotypes, on the other hand, display the S and F alleles, respectively.

One or more of these ancestral traits helps to divide cultivated germplasm in two groups, one each belonging to MA and AA domestication centers. It should, however, be noted that intermediate forms for most of these traits do occur and some accessions may carry one or more traits of MA and other traits typical of AA populations.

Adaptive traits

Leaf hairiness. Small and reduced hairs or trichomes (MA) vs. large and dense hairs (AA). This distinction does not refer to the hooked hairs which are always present in any Phaseolus sensu stricto species (Marechal et al., 1978). Since the wild beans of both MA and AA possess hairy leaves, its reduction in cultivated MA germplasm could be the consequence of domestication.

Pod tip. Extending straight from the dorsal suture (MA) vs an intermediate position between ventral and dorsal (AA).

Climatic adaptation. Common bean is originally a short-day species favoring mild temperatures. In the zone between the tropics of America, however, common bean grows from about sea level (mean growing temperature of 25 C) to 3000 m altitude (mean growing temperature of 12 to 15 C). Consequently marked differences in photo-thermal responses are found among common bean accessions from contrasting environments (Gniffke, 1986) within the centers of domestication such that when germplasm from the highlands are grown in lowlands it may not come to flower and vice versa. Common bean germplasm from each of the domestication center can grossly be divided into those from highlands (1800 to 3000 m), lowlands (0 to 500 m), and intermediate altitudes.

Seed size. Variation in seed size of cultivated common bean is very large(from < 15 g to 90g/100 seeds) . These are arbitrarily grouped into small (< 25 g), medium (25 to 40 g), and large (> 40 g/100 seeds) (Voysest, 1983). Wild bean from South America has relatively larger seed than their MA counterparts; however, both are small-seeded (>5 to < 25 g/100 seeds) (Debouck and Tohme, this volume), and it is believed that evolution has been from small to large-seeded forms. The cultivated common bean seeds of MA are on the average smaller than those from AA (Evans,1976; Voysest, 1983).

Seed shape. Seed shape depends upon the length, height and width of fully developed dry seed. Taken all together in descriptive terms these can be round, oval, elliptical, rhomboid, kidney, and cylindrical shapes. Seed shape of MA forms are often eliptical and rhomboid while cylindrical, kidney, and round types predominate in AA germplasm.

Growth Habit. The type of growth of the terminal bud (vegetative or indeterminate vs. reproductive or determinate), stem stiffness (strong vs. weak), twining ability (absent, weak, or strong), and distribution of pod load or fruiting patterns (basal, along the entire length, or largely in the upper portion of the plant) can be utilized to characterize and classify common bean germplasm in four principal growth habits (Singh, 1982). Determinate upright (I), indeterminate upright (II), and indeterminate prostrate non-climbing and semi-climbing (III) growth habits are commonly referred to as bush type. These require no support for normal growth and development, and are grown extensively in sole crop as well as in various intercropping systems. On the other hand, weak-stemmed, tall, indeterminate or determinate (IV) plants with long guides or leaders (i.e., elongated terminal internodes, which are weak and possess ability to intertwine) are known as climbing or pole bean. These always require support, and therefore are either intercropped with maize and other crops or are grown on stakes or trellises.

Principal ancestral and adaptive morpho-agronomic and molecular traits distinguishing Meso-American and Andean-American common bean are summarized in Table 1.

Characterization of Races

Evans (1973, 1976) grouped genetic diversity in cultivated *Phaseolus vulgaris* from its primary centers of domestication in Middle (small-seeded) and South America (large-seeded) into five races based on growth habit, number of nodes on the main stem, climbing ability, and seed size. She put small- and large-seeded climbing types from Middle and South America in Race 1 and differentiated them by adding subscripts A and B, respectively. Some important groups of germplasm of medium- and large-seeded cultivars from the highlands of Meso-America and South America were not covered by her classification. Vanderborght (1987) found four stable natural groups characterized by their different growth habits in landraces of common cultivated bean from each of Meso-America and Andean mountains.

Among germplasm from each domestication region, Singh (1988, 1989) found marked differences in leaf, growth habit, inflorescence, flower, pod, and seed characteristics, and adaptation specificity. Based on these characteristics he classified dry common bean into 12 gene pools. The green or snap bean was grouped in two additional gene pools.

Based on germplasm evaluations carried out thus far it was possible to identify and separate common cultivated dry bean germplasm from each of Middle America and Andean South America into the following races.

Middle American

Race M (for Meso-America). This includes small-seeded (< 25 g/100 seed) common bean of all seed colors (often solid) and growth habits. Leaf size and internode length are small, intermediate or large. The group is characterized by an ovate terminal leaflet and short, thick ovate bracteoles. The standards of flowers possess marked stripes at the outer base. Multi-poded inflorescence are found in some accessions. Pods are 8-15 cm long, slender, fibrous, and easy to thresh; they possess six to eight seeds. Phaseolin seed protein patterns are predominantly 'S', but can also be 'Sb' and 'B'. The race is distributed throughout the tropical lowlands and intermediate altitudes of Meso-America, Colombia, Venezuela, and Brazil.

Race D (for Durango). Cultivars and landraces are predominantly of indeterminate prostrate growth habit III (and IV), which is characterized by relatively small to medium leaves, thin stems and branches, short internodes, and by fruiting commencing from and concentrated in the basal nodes. Germplasm in this group possesses medium-sized (5 to 8 cm) flattened pods with four to five flattened rhomboid or elliptical seeds of medium size (25 to 40 g/100 seeds). Seed colors are often bayo-like or with a cream gray or pink background. Phaseolin types are predominantly 'S', but some accessions can carry the 'Sd'type. The race is distributed in semi-arid central and northern highlands of Mexico and the south western USA.

Race J (for Jalisco). This race is characterized by indeterminate, climbing growth habit IV. Plant height can be over 3 m. The terminal leaflet of trifoliate leaves are ovate and relatively large. Stem and branches are weak and have long internodes. Fruiting is either along the entire length or mostly in the upper part of the plant. Pods are 8-15 cm long and have five to eight medium-sized seeds, often of round, oval or slightly elongated shape. These carry 'S' phaseolin patterns. Their natural habitat is the humid highlands of Central Mexico and Guatemala where maximum diversity is found.

Andean South American

Race N (for Nueva Granada). Germplasm is mostly of growth habits I, II, and III with medium and large seeds (> 40 g/100 seeds) of kidney and cylindrical shapes which vary greatly in color. Leaves are often very large and pubescent, with rhomboid terminal trifoliate leaflets. Stem internodes are intermediate to long. Bracteoles are thin, elongated or lanceolate. Dry pods are fibrous, hard, medium to long (10 to 20 cm), leathery, and possess four to six seeds. The origin of pod tips is between ventral and dorsal sutures. Predominant phaseolin protein patterns are of the 'T' type. The race is distributed in intermediate altitudes(< 2000 m elevation) of the northern Andes in Colombia, Ecuador, and Peru, but it is also found in Brazil and some Caribbean countries including the Dominican Republic, Haiti, and Cuba.

Race C (for Chile). Landraces and cultivars are predominantly of indeterminate growth habit III. These are characterized by relatively small elongated (rhomboid) leaves, short internodes, medium-sized (5-8 cm) pods often with reduced fibre, and round to oval seeds (three to five per pod). Morphologically, these largely resemble germplasm from race D of Middle America, except that seeds of race C are round or oval, and fruiting is more sparse and along the length of stem and branches. In some of the landraces, striped pod color becomes attractive, and in many countries these are harvested for physiologically mature green seeds (green shelled or 'granados') before drying begins. The most common phaseolin patterns are 'C' and 'H' types.

This race is distributed in relatively drier regions at lower altitudes in the southern Andes (Bolivia, Chile, and Argentina).

Race P (for Peru). Key morphological characteristics of germplasm belonging to this race are large rhomboid leaves, long and weak internodes with either determinate or indeterminate type IV climbing growth habit. Pods are often long (10 to 20 cm) and leathery. Fruiting is either along the entire stem length or in only the upper part of the plants. Seeds are large, often round or oval. Predominant phaseolin protein patterns are C, H, and T types.

This group is highly photoperiod-sensitive and is adapted to moderately wet and cool temperatures. The race is distributed from northern Colombian highlands (> 1500 m altitude) to Argentina.

Discussion

By far the largest differences are found between common bean germplasm from Middle America and Andean South America. These observations are in general agreement with those of Evans (1973, 1976), Gepts and Bliss (1985), Gepts et al. (1986), and Vanderborght (1987). In both regions, however, there seems to be a parallel between climate and growth habit. In both centers of domestication, for example upright bush types are more common in relatively warmer lower altitudes, prostrate non-climbing beans are more common in cool semi-arid regions, and aggressive climbers predominate in cool and wet highlands. Furthermore, in both Middle and South America, relatively smaller-seeded forms predominate in warmer climates and seed size increases with altitude.

The race D · of Meso-America morphologically resembles, to some extent, race C from South America. But the two groups, however, possess different phaseolin-proteins, are geographically separated, and there are differences in allelic frequencies and in genetic associations of traits which predominate in one group but are rare in the other.

Frequency of alleles for elongated, cylindrical, and kidney shaped seed was high among germplasm from race N of South America. On the contrary, the accessions of race D of Middle America had predominance of somewhat flattened and rhomboid seed shapes. Similarly, the allelic frequency of genes determining various types of marbling, spotting, mottling, striping, speckling and other marks on seed coats was extremely low in the Middle American race M, but it was very high in races D and J of Middle America and all three races of South America. Green-brown spotting, a characteristic of pinto bean, brown striping found in 'Ojo de Cabra', and speckling or circular mottling of pink and other colors found in 'Flor de Mayo' and 'Flor de Abril' of Middle America were rare in South American races. Similarly, red mottling of 'Calima', 'Cargamanto', and 'Cranberry' genotypes and the ring or eye around the hilum and large blotches found on 'Vaquita' were virtually nonexistent in the races of Middle American domestication center.

Whether or not each of theses races is a consequence of different domestication events each tracing back to a different population of wild bean is still unknown, but the genetic distances both between and within Meso-American and Andean-American races seem to be considerable. As a consequence, although hybridization among these races is easily effected, various degrees and kinds of hybrid problems (Coyne, 1965, 1969; Evans, 1970; Gepts and Bliss, 1985; Gutiérrez and Singh, 1982; Provvidenti and Schroeder, 1969; Rabakoarihanta and Baggett 1983; Singh and Gutiérrez, 1984) is observed beginning in the F_1 and subsequent generations, thus, interfering with effective introgression of genes among races. Of course, these phenomena are more pronounced in crosses between parents belonging to MA and AA races. This all suggests that an incipient speciation had begun in cultivated common bean.

Future Outlook

Morphological characteristics and molecular markers available at present may not suffice to adequately classify the range of variation found in common bean germplasm. It may be desirable to combine information on these traits with other information on genetic and breeding behavior and adaptive characteristics, for further refinements of the races described here.

A minimum number of accessions representing each race and the entire range of variability should be established to facilitate further experimentation and utilization of common bean germplasm.

References

Brücher, H. 1988. The wild ancestor of Phaseolus vulgaris in South America. In Genetic resources of Phaseolus beans, P. Gepts (ed.), Kluwer Academic Publishers, Dordrecht, Holland, p. 185-214.

Burkart, A. and Brücher H. 1953. Phaseolus aborigineus Burkart, die mutmabliche andine stammform der kultur bohne. Der Zuchter 23(3):65-72.

Coyne, D. P. 1965. A genetic study of "crippled" morphology resembling virus symptoms in Phaseolus vulgaris L. J. Hered. 56:162.

Coyne, D. P. 1969. Breeding behavior and effect of temperature on expression of a variegated rogue in green beans J. Am. Soc. Hortic. Sci. 94:488-491.

Evans, A. 1970. Heterosis for yield in Phaseolus vulgaris crosses. Annu. Rep. Bean Impr. Coop. 13:52-54.

Evans, A. 1973. Exploitation of the variability in plant architecture in Phaseolus vulgaris. Pages 279-286. In Potentials of field beans and other food legumes in Latin America. CIAT, Cali, Colombia. Series, Seminar 2E.

Evans, A. 1976. Beans. Pages 168-172. In N. W.Simmonds, ed., Evolution of crop plants. Longman, London.

Gentry, H. S. 1969. Origin of the common bean, Phaseolus vulgaris. Econ. Bot. 23(1):55-69.

Gepts, P., and F. A. Bliss. 1985. F_1 hybrid weakness in the common bean: Differential geographic origin suggests two gene pools in cultivated bean germplasm. J. Hered. 76:447-450.

Gepts, P., T. C. Osborn, K. Rashka, and F. A. Bliss. 1986. Phaseolin protein variability in wild forms and landraces of the common bean (Phaseolus vulgaris): Evidence for multiple centers of domestication. Econ. Bot. 40:451-468.

Gniffke, P. A. 1986. Studies of phenological variation in the common bean (Phaseolus vulgaris L.) as modulated by mean temperature and photoperiod. Diss. Abst. 46:2895B.

Gutiérrez, J. A., and S. P. Singh. 1982. Hybrid dwarfism in Phaseolus vulgaris L. and its implications in genetic improvement. Ann. Rep. Bean Improvement Coop. 25:96-97.

Harlan, J. R. 1971. Agricultural origins: Centers and noncenters. Science 174:468-474.

Harlan, J.R. 1975. Geographic patterns of variation in some cultivated plants. J. Hered. 66:184-191.

Harmsen, R., F. A. Bliss, and T. C. Osborn. 1987. Breeding beans resistant to bruchids. Ann. Rept. Bean Improvement Coop. 30:44-45.

Koenig, R. L., S. P. Singh, and P. Gepts. 1989. Novel phaseolin types in wild and cultivated common bean (Phaseolus vulgaris, Fabacea). Econ. Bot. (in press).

Marechal, R., J. M. Mascherpa, and F. Stainier. 1978. Etude taxonomique d'un group complexe d'especies des genres Phaseolus et Vigna (Papilionaceae) sur la base de donnees morphologiques et polliniques, traitees per l'analyse infmatique. Boissiera 28:273.

Provvidenti, R., and W. T. Schroeder. 1969. Three heritable abnormalities of Phaseolus vulgaris: seedling wilt, leaf rolling, and apical chlorosis. Phytopathology 59:1550-1551.

Rabakoarihanta, A., and J. R. Baggett. 1983. Inheritance of a leaf distortion tendency in bush lines of beans, *Phaseolus vulgaris* L., a Blue Lake background. J. Am. Soc. Hortic. Sci. 108:351-354.

Singh, S. P. 1982. A key for identification of different growth habits of *Phaseolus vulgaris* L. Ann. Rep. Bean Improvement Coop. 25:92-95.

Singh, S.P. 1988. Gene pools in cultivated dry bean. Ann. Rep. Bean Improvement Coop. 31:180-182.

Singh, S.P. 1989. Patterns of variation in cultivated common bean (*Phaseolus vulgaris*, Fabaceae). Econ. Bot. (in press).

Singh, S.P., and J. A. Gutiérrez. 1984. Geographical distribution of the DL_1 and DL_2 genes causing hybrid dwarfism in *Phaseolus vulgaris* L., their association with seed size, and their significance to breeding. Euphytica 33:337-345.

Smartt, J. 1980. Evolution and evolutionary problems in food enzymes. Econ. Bot. 34:219-235.

Smartt, J. 1984. Gene pools in grain legumes. Econ. Bot. 38:24-35.

Smartt, J. 1985. Evolution of grain legumes 4. Pulses in the genus *Phaseolus*. Experim. Agric. 21:193-207.

Vanderborght, T. 1983. Evaluation of *P. vulgaris* wild types and weedy forms. Plant Gent. Resources Newsl. 54:18-25.

Vanderborght, T. 1987. The study of common bean (*Phaseolus vulgaris* L.) variability by the use of multivariate statistical methods applied to a data base. Diss. Abstr. 47:3190B-3191B.

Voysest, O. 1983. Variedades de fríjol en América Latina y su orígen. Centro Internacional de Agricultura Tropical, Cali, Colombia, 87 p.

Weiseth G. 1954. Una variedad silvestre del poroto común (*Phaseolus vulgaris*), autóctona del Noroeste Argentino y su relación genética con variedades cultivadas. Rev. Agron. Noroeste Argentino 1(2):71-81.

Table 1. Principal characteristics of common beans from Meso-American and Andean American domestication centers.

	Meso American	Andean American
Ancestral		
Terminal trifoliate leaflet	Ovate	Rhomboedric, elongated
Bracteole	Broad ovate	Thin, elongated or lanceolate
Base of standard	Striped (often)	Smooth
Inflorescence	Multinoded	Fewer nodes
Phaseolin seed protein patterns	S, Sb, Sd, B	T,C, H, A, I, J
Isozyme	Rbcs^{F}, Skdh^{F}, Me^{F} or Me^{M} Diap-1^{S}, Lap-3^{S}	Rbcs^{S}, Skdh^{S}, Me^{S}, Diap-1^{F}, Lap-3^{F}
Adaptive		
Leaf hairs	Sparse & small	Dense & large
Pod tip position	Dorsal suture	Between dorsal & ventral sutures
Seed size	Small & medium	Medium & large
Seed shape	Elliptical, rhomboid, & round	Cylindrical, kidney, oval, & round

Table 2. Some characteristics of the races of common bean and their habitats in primary centers of domestication in America.

Race	Seed size[a]	Seed color	Landraces	Growth habit	Phaseolin protein type Isozyme	Mean growing temperature °C	Habitats
Middle American							
D	Medium	All Colors	Pinto, Great Northern, Red Mexican, Sutter Pink, Bayo, Ojo de Cabra, Dermason.	Indeterminate weak-stemmed, non-climber or semi-climbing III.	S, Sd	20	Semi-arid highlands of Mexico and south western USA.
J	Medium	Beige Pink Yellow	Garbancillo Zarco, Frijola, Flor de Mayo, Rosa de Castilla, Conejo, Apetito, Cacahuate Criollo.	Indeterminate: weak-stemmed, climbing IV.	S	18	Humid highlands of Mexico and Guatemala.
M	Small	All Colors	Brazil 2, Oaxa 892, Kupal, Jamapa, Porrillo, Rojo de Seda, Zamorano, Mulatinho, Carioca, Rosinha.	Determinate I, Indeterminates II, III, and IV.	S, Sb, B	22	Lowlands and intermediate altitudes of Meso-America, Colombia, Venezuela, Brazil.
Andean South American							
C	Medium oval, round	Cream Pink Beige Gray White	Cranberry, Tortolas, Coscorron, Borlotos, Suaves, Bolita Cristal	Indeterminate weak-stemmed, non-climber or semi-climbing III.	C,H	22	Southern Andes and Chile.
P	Medium & large oval round	Red Pink Beige Cream White	Overitos, Caballeros, Nuñas, Bolon Bayo, Bola Canario, Bola Roja, Cargamanto, Mortiño.	Determinate and indeterminate climber IV.	T,C H,A	16	Highlands of Colombia, Ecuador, Peru, Bolivia and Argentina.
N	Medium and large elongated	Red Pink Cream Beige Yellow	Cargabello, Uribe, Calima, Canario, Pompadour, Chabelo, Antioquia 8, San Martin 8, Chaucha Colorada, Cavalho Amarelo, Jalo, Cacahuate Largo.	Determinate I, Indeterminate II and III.	T	20	Intermediate altitudes of Andean Colombia, Ecuador, and Peru; Bolivia, Brazil Haiti, Dominican Republic.

[a] Weight of 100 seeds of small is < 25 g, medium varies between 25 to 40 g, and large is >40 g.

35663

USE OF WILD *Phaseolus vulgaris* TO IMPROVE BEANS FOR RESISTANCE TO BRUCHIDS

Cesar Cardona and Julia Kornegay*

Introduction

The Mexican bean weevil, *Zabrotes subfasciatus* (Boheman) and the bean weevil, *Acanthoscelides obtectus* (Say) are the two most important storage pests of beans in the world. Losses in storage have been estimated at 13%. Among the different methods of bruchid control, CIAT has emphasized the search and development of bean materials with resistance to their attack. In this paper, we attempt to summarize present knowledge on the utilization of resistant wild bean accessions to improve cultivated varieties for resistance to bruchids.

Sources of Resistance

The search for sources of resistance to bruchids was initiated in 1978. More than 8,000 cultivars were screened, but no adequate levels of resistance were found (Schoonhoven and Cardona 1982). In 1981 and 1982 a small collection of wild accessions collected in Mexico, were submitted to routine screening. A handful of these materials showed very high levels of resistance to both bruchid species (Schoonhoven et al 1983). Out of 380 accessions evaluated, 12 have been rated as highly resistant to *Z. subfasciatus* and 14 have been reconfirmed as highly resistant to *A. obtectus*.

---

* Bean Entomologist and Bean plant breeder, respectively, CIAT, A.A. 6713, Cali, Colombia.

So far, no sources of resistance have been detected among wild accessions originating elsewhere in Latin America. All bruchid resistant materials are climbers, usually with a viney growth habit. They tend to be dehiscent and small seeded (6-7 g per 100 seeds). Hard seed coat is a common characteristic. These materials can easily be crossed with cultivated varieties.

Mechanisms of Resistance

It has been shown that antibiosis is the mechanism responsible for resistance to both bruchid species (Schoonhoven et al 1983; Cardona et al 1988). The data in Table 1 show that there is a significant, deleterious effect on the biology of the insects and their survival: adult emergence in resistant accessions is drastically reduced, the life cycle of surviving insects is prolonged and progeny weight is reduced. More recent studies revealed that the antibiosis results in negative population growth rates; prolonged, staggered life cycles; high mortality of late first instars and early second instars; reduced female fecundity; and male-biased sex ratios.

Even though the testa may occasionally act as a physical barrier, it was demonstrated by Cardona et al (1989) that factors responsible for resistance are chemical in nature and are present in the seed cotyledons. When the testa are removed and insects are reared on "artificial" seeds, resistant and susceptible responses can easily be distinguished (Table 2).

Resistance Factors

1. *Zabrotes subfasciatus*

Research on the factors responsible for resistance was initiated in 1983. A new protein, present only in wild accessions resistant to *Z. subfasciatus*, was identified at the University of Wisconsin (Osborn et al 1986). This protein was called arcelin (after Arcelia, the town in Mexico where most of the resistant accessions had been collected) and was postulated as the factor responsible for bruchid resistance. There are four variants of arcelin which can easily be detected by SDS-Page electrophoresis (Figure 1). The protein can also be detected serologically.

Although the presence of arcelin was correlated with resistance to Z. subfasciatus, it was necessary to test whether resistance was associated with transfer of the arcelin gene. Romero Andreas at al., (1986), using an inbred backcross breeding strategy, demonstrated that arcelin is inherited as a single dominant gene. They introduced the arcelin-1 allele from G 12882 into the bean cultivar Sanilac. Seeds of backcross lines were tested for resistance to Z. subfasciatus (Table 3). All arcelin-1 homozygous lines showed high levels of resistance (prolonged life cycle, reduced emergence). Lines lacking arcelin-1 were fully susceptible compared to Calima and heterozygous lines showed intermediate levels of resistance (Osborn et al 1988). Analogous sets of backcross lines from different cultivated bean types further demonstrated that resistance is associated with transfer of the arcelin gene.

To further prove that arcelin was the factor conferring resistance to Z. subfasciatus, "artificial" seeds containing different levels of purified arcelin-1 were prepared and tested (Osborn et al 1988). As shown in Table 4, there was a dosage response to the increasing levels of arcelin-1 in articial seeds. The LD50 in that, and subsequent tests, has been ca. 6.5%. The insecticidal activities of arc-2 and arc-4 have been demonstrated in more recent, as yet unpublished tests.

These findings have greatly facilitated breeding for resistance to Z. subfasciatus. All segregating populations are tested on a routine basis for the presence or absence of arcelin by means of a simple, reliable serological technique, the Ouchterlony plate. Seeds devoid of arcelin are discarded, those containing the protein are selected and handled as described below.

2. Acanthoscelides obtectus

It is known from multiple tests that the presence of arcelin does not necessarily confer resistance to this species. It has been postulated by researchers at the University of Durham (Gatehouse et al 1987) that resistance to A. obtectus is due, at least in part, to the presence of a heteropolysaccharide which has an unusually high arabinose and fucose content. This hypothesis has not been reconfirmed at CIAT or elsewhere nor has a simple method been developed for detecting the presence of the carbohydrate. The lack of a quick, reliable, screening technique for resistance to A. obtectus has been a major drawback in the development of materials resistant to this species.

Breeding for Resistance

1. Zabrotes subfasciatus

A backcross breeding scheme is being utilized to improve beans for resistance to this species.

As shown in Table 5 the scheme is largely based on selection for the presence of arcelin in F1 and F2 generations. This facilitates selection in a large number of segregating populations and has the additional advantage that the desirable commercial characteristics of the recurrent parent are quickly recovered. At present, homozygous F5 lines with high levels of resistance and acceptable seed characteristics have been developed (Table 6).

2. Acanthoscelides obtectus

Following an inheritance study which suggested that resistance to A. obtectus may be controlled by one or two recessive genes, a backcross breeding scheme was also adopted to improve beans for resistance to this species. As shown in Table 7, the disadvantange is the lack of a quick screening technique to select for resistance in early segregating populations. This has forced us to perform large numbers of individual seed feeding tests with the insect, a lengthy process. Thus, breeding for resistance to A. obtectus has progressed more slowly. At present, the first BC_2F_2 resistant materials are being planted to be selected and then tested in replicated trials for resistance to the bruchid.

References

Cardona, C., C.E. Posso, J. Kornegay, J. Valor & M. Serrano. 1989. Antibiosis effects of wild dry bean accessions on the Mexican bean weevil and the bean weevil (Coleoptera: Bruchidae). J. Econ. Entomol. 82, (in press; accepted for publication September 3, 1988).

Gatehouse, A.M.R., P. Dobie, R.J. Hodges, J. Meik, A. Pusztai & D. Boulter. 1987. Role of carbohydrates in insect resistance in Phaseolus vulgaris. J. Insect Physiol. 33:843-850.

Osborn, T.C., T. Blake, P. Gepts & F.A. Bliss. 1986. Bean arcelin. 2. Genetic variation, inheritance and linkage relationships of a novel seed protein of Phaseolus vulgaris L. Theor. Appl. Genet. 71:847-855.

Osborn, T.C., D.C. Alexander, S.S. Sun, C. Cardona & F. A. Bliss. 1988. Insecticidal activity and lectin homology of arcelin seed protein. Science 240:207-210.

Romero Andreas, J., B.S. Yandell & F.A. Bliss. 1986. Bean arcelin. 1. Inheritance of a novel seed protein of Phaseolus vulgaris L. and its effect on seed composition. Theor. Appl. Genet. 72:123-128.

Schoonhoven, A.van & C. Cardona. 1982. Low levels of resistance to the Mexican bean weevil in dry beans. J. Econ. Entomol. 75:567-569.

Schoonhoven, A.van, C. Cardona & J. Valor. 1983. Resistance to the bean weevil and the Mexican bean weevil (Coleoptera: Bruchidae) in noncultivated common bean accessions. J. Econ. Entomol. 76:1255-1259.

Table 1. Levels of resistance to bruchids in selected wild beans compared to cultivated susceptible variety.

Accession	Seed size (g/100 seeds)	Percent emergence	Days to adult emergence	Adult weight (g x 10^{-3})
Zabrotes subfasciatus				
G 12949	7	16.2	63.0	0.7
G 12952	6	17.4	65.2	0.7
G 12953	6	14.8	67.4	0.6
Calima (susceptible)	50	96.1	33.7	1.6
Acanthoscelides obtectus				
G 12891	8	31.6	52.1	1.8
G 12949	7	4.0	62.5	2.0
G 12954	6	7.2	55.1	1.0
Calima (susceptible)	50	58.4	36.6	2.6

Table 2. Biology of *Zabrotes subfasciatus* on "artificial" and intact seeds of four varieties.

Technique	Variety	Rating	Percent emergence	Days to adult emergence
"Artificial" seed	Calima	Susceptible	87.7	37.9
	L 12-56	Susceptible	74.7	38.4
	Sanilac	Susceptible	86.1	37.8
	SARC 1	Resistant	18.4	53.7
Intact seed	Calima	Susceptible	93.0	31.5
	L 12-56	Susceptible	100.0	32.1
	Sanilac	Susceptible	95.9	31.3
	SARC 1	Resistant	7.3	50.7

Table 3. Levels of resistance to Z. subfasciantus in Sanilac backcross-derived lines with arcelin-1 (Arc1/Arc1), without arcelin-1 (arc/arc), and segregating for arcelin-1 (Arc1/arc).

Line No.	Arcelin genotype	Days to adult emergence	Percent emergence
3	Arc1/Arc1	53.0	2.5
5	Arc1/Arc1	47.8	2.1
4	Arc1/arc	33.2	20.9
7	Arc1/arc	37.2	38.7
8	Arc1/arc	38.1	34.6
9	Arc1/arc	35.4	30.2
1	arc/arc	34.2	89.5
2	arc/arc	34.7	76.3
6	arc/arc	34.4	93.8
Calima (susceptible)	arc/arc	34.0	92.9

Table 4. Levels of resistance to Z. subfasciatus in intact and artificial seeds with and without the addition of purified arcelin-1.

Treatment	Days to adult emergence	Percentage emergence
Intact seed		
Sanilac	31.3	95.9
"Artificial" seed		
Sanilac	37.8	86.1
Sanilac + 2.5% arcelin-1	38.9	76.1
Sanilac + 5.0% arcelin-1	44.7	76.1
Sanilac + 10.0% arcelin-1	53.4	18.4

Table 5. Breeding scheme to improve beans for resistance to *Zabrotes subfasciatus*.

Resistant x Susceptible

F_1 : backcrossed to susceptible parent.

BC_1F_1 : serological tests of 10-20 seeds per cross. Arc$^+$ are backcrossed to susceptible parent.

BC_2F_1 : serological tests of 10-20 seeds per cross. Arc$^+$ are planted and individual plants are selected in the field.

BC_2F_2 : serological tests of 10-20 seeds per plant selected in BC_2F_1. Homozygous Arc$^+$ are planted in progeny rows in the field and selected for agronomic characteristics.

BC_2F_3 : seeds are submitted to replicated feeding tests with the insect. Resistant progenies are planted in the field and selected for agronomic characteristics.

BC_2F_4 : best lines are coded BRU.

Table 6. Levels of resistance to *Zabrotes subfasciatus* in some of the F_5 lines selected in 1988.

Line	Percent emergence	Days to adult emergence	Adult weight (g x 10^{-3})
GG 97-1-2-CM	20.2	40.8	1.1
GG 98-10-2-CM	10.8	45.4	1.0
GG 98-22-2-CM	19.8	41.5	1.1
GG 98-28-2-CM	10.3	46.0	1.0
GG 98-28-2-CM	5.3	44.2	1.0
GG 98-33-1-CM	4.3	48.3	0.9
G 12952 (wild, resistant)	9.7	61.3	0.6
Calima (cultivated, susceptible)	97.4	30.5	1.4

Table 7. Breeding scheme to improve beans for resistance to *Acanthoscelides obtectus*.

Resistant x Susceptible

F_1 : seed increase.

F_2 : individual seed (200 seeds per cross) feeding tests with the insect. Resistant seeds are planted and backcrossed to susceptible parent.

BC_1F_1 : seed increase.

BC_1F_2 : individual seed (200 seeds per cross) feeding tests with the insect. Resistant seeds are planted and backcrossed to susceptible parent.

BC_2F_1 : seed increase.

BC_2F_2 : individual seed (200 seeds per cross) feeding tests with the insect. Resistant seeds are planted and selected for agronomic characteristics.

BC_2F_3 : replicated feeding tests with the insect for each of individual plants selected in BC_2F_2. Resistant lines are planted and selected for agronomic characteristics.

BC_2F_4 : replicated feeding tests with the insect for each of individual plants selected in BC_2F_3. Resistant plants are planted and selected for agronomic characteristics.

BC_2F_5 : best lines are coded BRU.

35664

POTENTIAL OF BIOTECHNOLOGY IN GERMPLASM EVALUATION AND THE GENETIC IMPROVEMENT OF Phaseolus BEANS

W.M. Roca, H. Ramirez, P. Chavarriaga, L.C. Muñoz*

Introduction

Plant breeding - the intentional production of genetically different plants and the evaluation of this variability - without doubt has contributed to the production of higher yielding varieties of major important crops. Among the pulse crops, the Phaseolus beans are the most important considering worldwide production and consumption. The common bean (Phaseolus vulgaris) is an important source of dietary proteins and calories in Latin America and Africa (Laing et al., 1984). Farmers' yields in Latin America and Africa are low, averaging 500-600 Kg/ha, eventhough potential yields of 2000 - 3000 Kg/ha have been demonstrated. A great portion of this differential can be attributed to numerous biotic and edapho-climatic factors that limit bean production in developing countries. Common bean breeding at CIAT has been developed to a high standard and progress has been made in developing disease and pest resistant varieties with increased tolerance to drought, to acid soils, improved ability for symbiotic nitrogen fixation and improved architectural characteristics (CIAT, 1987). There are however limitations in the speed and precision with which many useful traits can be identified, selected and utilized in the breeding process. On the other hand, genetic variability for some important traits is not present or occurs at very low frequency in the world germplasm collections of P. vulgaris (Cardona and Posso, 1987). There are also varying degrees of incompatibility between P. vulgaris gene pools as well as between P. vulgaris and other cultivated Phaseolus spp, i.e. P.

---

* Biotechnology Research Unit, CIAT, A.A. 6713, Cali, Colombia.

acutifolius (tepary bean), P. coccineus (runner bean) and P. lunatus (lima bean) (Gepts, 1984; Singh and Gutierrez, 1984). Furthermore, the genetic improvement of common beans would greatly benefit from the availability of information regarding the inheritance of important characters, their precise location on chromosomes and their distribution among genetic stocks.

Rapid advances in recent years from the biological sciences are providing new tools for the study of plants and their genetic improvement. Some of these techniques already offer short cuts in the production of genetically fixed lines as well as aiding in the identification and physical location of important traits on the chromosomes. Future developments promise to allow the selective inhibition or activation of genes and the introduction and expression of DNA sequences in selected genetic backgrounds. These new approaches have widely been termed "biotechnology".

In a more restricted sense, biotechnology can be defined as the application of non-traditional approaches, based on knowledge at the cellular, biochemical and gene level, to constraints that can not be easily resolved through traditional methodologies.

In this paper we cover, in broad outline, the current status and perspectives of biotechnology development in Phaseolus beans, with emphasis on applications to germplasm evaluation and genetic improvement.

Approach to Biotechnology Research in Phaseolus Beans

Constraints to productivity in Phaseolus beans should be reviewed periodically and possible techniques for researching and overcoming the constraints reevaluated. Biotechnology research should focus on areas where a) traditional methodologies have shown limited promise and b) there is reason to believe that emerging cellular and molecular research approaches and tools can aid in solving the problem.

In spite of the importance of common beans in the tropical and sub-tropical areas of the developing world, there has been relatively little basic research conducted on this crop. On the contrary, basic research on common bean problems was, until recently, essentially neglected at both the national and international levels. It has been seen as too costly and as requiring too long a time frame for payoff; thus basic research has been given orphan status in spite of the exciting possibilities that exist.

The identification of constraints to research on important bean production problems, followed by an evaluation of specific research strategies which could conceivably be implemented to resolve those constraints, would facilitate the establishment of a multi-institutional advanced research network for Phaseolus bean biotechnology. A network approach would allow more rational use of resources, prevent wasteful duplication of efforts and facilitate faster advances in research.

The characterization of each constraint should include: a) a clear statement of research objectives; b) biological and economic justification for working on the constraint; c) proposed research strategies to approach the problem; d) main areas of impact; e) estimated time frame for achieving results and impact; f) linkages between the advanced research and the applied research conducted at institutions like CIAT and in developing countries. Current research projects in Phaseolus biotechnology would become part of the larger network.

The approach to advanced research would include both, constraints which can be immediately tackled using biotechnology tools and other constraints which may require basic biochemical and/or genetic information before possibilities of new technologies can be assessed.

While the constraint identification process is being completed, we have been addressing the development of selected techniques which are necessary conditions for many of the biotechnology applications to Phaseolus beans. These techniques can be grouped into two major areas: a) in vitro techniques and b) techniques for genome analysis. These include research on cellular, biochemical and molecular techniques, the development of which will open the way for undertaking work in other biotechnology areas.

Development of Techniques

In vitro techniques

With the exception of P. vulgaris micropropagation through shoot tip culture (Allavena, 1984; Muñoz et al., 1987) and the recovery of plants of certain interespecific crosses through immature embryo culture, i.e. P. vulgaris x P. acutifolius (Andrade-Aguilar, 1987), the development of cell and tissue culture techniques in the common bean is constrained by the difficulty in achieving complete and consistent regeneration of plants from callus cultures.

Micropropagation. This technique can be useful for: a) rapidly multiplying bean F_1 and M_1 plants which show restricted sexual reproduction; b) recovery of mutants after treatment of early stage multiple shoot cultures with radiation or chemical mutagens; and c) multiplication of valuable germplasm which may be available in minimum quantities. At CIAT, this technique has been successfully used in the case of wild relatives of P.vulgaris. Micropropagation of P.vulgaris varieties at CIAT yielded 5-20 shoots per explant.

Embryo culture. This technique has been used in a few selected cases, especially in crosses involving P. vulgaris and P. acutifolius or P. coccineus. The genotype of the recipient parent is critical for achieving embryo growth. A backcrossing and selection program needs to be implemented following the recovery of fertile plants; in some cases, chromosome doubling techniques need to be implemented before backcrossing. A major drawback in wide crossing has been instability of the introgressing trait in advanced generations.

Plant regeneration from callus cultures. Although there has been successful plant regeneration in other grain legumes, e.g. pigeon pea (Cajanus cajan), moth bean (Vigna aconitifolia), broad bean (Vicia faba), soybean (Glycine sp) and peas, in Phaseolus beans there are only two reports of successful plant regeneration, one with the tepary bean (P. acutifolius) (Kumar et al., 1988) and one with the runner bean (P. coccineus) (Allavena et al. 1987).

In a collaborative project between CIAT and the TCCP, Colorado State University, we have repeated the P. acutifolius regeneration and are adapting the technique for P. vulgaris. Because plant regeneration seems to be genotype dependant, our work at CIAT involves crossing the best responding tepary bean genotype with a range of P. vulgaris genotypes. F_1 embryos will be rescued and cultured to plants, explants for culture will be obtained from F_1 and F_2 plants.

The technique basically consists of the induction of callus on leaf sections obtained from seedlings, production of a fine cell suspension and selection of isodiametric, densely cytoplasmic, cell populations for plating on regeneration medium. The selection of cells, which are morphogenetically capable, is carried out through a series of filtration and sub-culturing steps. Recent work with P. vulgaris has reached the pre-organogenic stage similar to the P. acutifolius cultures.

In parallel research at CIAT, plant regeneration has been obtained from callus induced on embryo axes of five wild relatives of P. vulgaris (unplublished results). Because these genotypes are easily crossed with P. vulgaris, a study has been initiated to ascertain, whether the "regeneration capability" of the wild materials can be transferred to the common bean.

Thus, it may just be a matter of a more concerted effort in this area to achieve plant regeneration in P. vulgaris. Some effort should also be allocated to regeneration from immature pollen.

Once plant regeneration has been achieved and tested for reproducibility, the following potential applications can be envisaged:

a) Exploit the chromosomal instabilities of cell cultures to facilitate the introgression of traits in wide crosses. Using haploid cell cultures would increase chromosomal instability. Changes in chromosome number may also provide a means towards polyploidy or aneuploidy in beans;
b) induction of haploid and doubled haploid plants may prove to be useful for conducting genetic studies, to facilitate selection of traits which are highly influenced by the environment, and for accelerating the production of homozygocity in particular breeding strategies such as varietal improvement for long growth cycle ecosystems, i.e. highland beans.
c) transfer and expression of useful traits by genetic engineering techniques will require the capability of plant regeneration.

Screening at the gametophytec level. Some important traits, e.g. heat and cold tolerance may be expressed at the gametophyte level and be associated with pollen germination, (Mulcahy and Mulcahy, 1987). Challenging F_1 pollen with stresses would allow selection of tolerant or resistant genotypes. Following fertilization with selected pollen the progeny would be screened for the desired trait. The beauty of this approach is that large numbers of different genotypes, which are haploid, can be handled quickly in very little space.

Recent work at CIAT has shown a correlation between plant response and pollen germination regarding heat tolerance; there also seems to be a correlation between pollen size and heat tolerance. Work continues to determine if the trait is expressed in progeny following fertilization with heat tolerant pollen.

Techniques for genome analysis

Genome analysis is the area of biotechnology currently receiving most attention. The analysis of genomes is based on the development of biochemical and molecular markers at three levels: proteins (polypeptide analysis), enzymes (patterns in isozyme activity) and DNA (restriction fragment length polymorphisms= RFLPs). These markers, associated with morphological markers, can be used in *Phaseolus* beans for: a) establishing biosystematic relationships among species and sub-species of the geneus *Phaseolus*; b) assessing genetic variability in the *P. vulgaris* germplasm; c) evolutionary and germplasm dispersal studies; d) characterization of *P. vulgaris* gene pools and ascertaining intra- and inter-specific compatibilities; e) developing genetic linkage maps of *P. vulgaris*, and f) identification (tagging) of genes in order to monitor their flow within a breeding program, such as the introgression of traits from other *Phaseolus* and wild germplasm.

Biochemical and molecular markers, have special features that make them very useful in the genetic improvement of *Phaseolus* beans. They occur naturally, thus there is no need for artificial induction; co-linkage of these markers can be evaluated in the progeny from an heterozygous parent; their expression (isozymes) or presence (RFLPs) is free of environmental and epistatic effects, hence a trait can be identified in a population of plants even if it is not visually expressed (Tanskley and Orton, 1983).

Isozyme analysis allows the analysis of gene products even prior to phenotype expression. It is relatively rapid among the genome analysis techniques. The level of isozyme pattern variability (polymorphism) in P. vulgaris varies with the genotype. In recent work at CIAT on the characterization of P. vulgaris land races from Mexico, Peru and Colombia, of 9 isozyme systems, highest polymorphism was found with diaphorase in meso American germplasm and with esterase in south Andean materials. Diaphorase, peroxidase, esterase and acid phosphatase showed variability between gene pools (Vargas, 1988). In work at the University of Florida (E.Vallejos personal communication) high isozyme polymorphism was found in two common bean lines, one carrying resistance to CBB from P. coccineus and the other a susceptible Colombian variety.

Protein analysis. Variability in the electrophoretic pattern of the bean seed protein, phaseolin, has provided a useful tool to study the domestication and dispersal of common bean germplasm (Gepts and Bliss, 1985). Several electrophoretic phaseolin types have been identified, e.g. S, T, and C; they are highly polymorphic and are specific to the major bean gene pools. Additional phaseolin types are being found in wild populations of P. vulgaris from meso-America and the Andes. This technique has been used at CIAT to track the dispersal of P. vulgaris in Eastern Africa (Triana, 1988) and to characterize new collections of wild P. vulgaris from the southern Andes. There are two posters in this workshop dealing with the utilization of phaseolin types in germplasm domestication and dispersal studies.

Polypeptide analysis. Through two-dimensional gel electrophoresis large numbers of polypeptides can be analysed simultaneously. Expression of some polypeptides is influenced by the environment, therefore this analysis may provide clues in associating specific proteins with certain traits. Development of methods for polypeptide fingerprinting in Phaseolus beans may result in the identification of polypeptide fractions which become amplified under stress conditions, and thus pave the way for isolation and characterization of the responsible nucleotide sequences.

RFLP analysis. RFLP analysis is a direct analysis of the DNA (genes), thus RFLPs are true molecular, genetic markers: They are not subject to environmental influences; they are abundant and many are not expressed in morphological differences at the plant level, they have co-dominant alleles and can often be scored at a seedling or tissue level. Using restriction enzymes, the plant DNA is cut into pieces. Since restriction enzymes cut at specific nucleotide sequences, differences in the DNA between plants result in fragments of different sizes. The fragments are separated by electrophoresis, then probes (cDNA clones or low copy number genomic clones frequently labelled with ^{32}P) are hybridized to the DNA fragments. The different lengths of the DNA fragments to which the probe hybridizes gives a pattern on the gel, an RFLP marker. The RFLP markers can be linked to specific heritable traits and thus used for screening in early generations, accelerating a breeding program. The RFLP differences between lines can be attributed to single base pair changes or to insertion-deletion changes (Helentjaris, T. et al., 1985).

It is necessary to find probes that will give polymorphisms in P. vulgaris in order to develop and apply RFLPs. Both genomic and plastome DNA need to be evaluated. Chloroplast (cpDNA), ribosomal (rDNA) probes as well as random repetitive and single copy sequences from related species, e.g. soybean, mungbean, etc. should be tested for homologies with P. vulgaris.

Recent work on the construction of a saturation linkage map of P. vulgaris using RFLPs has resulted in the isolation of over 25 cDNA clones. Out of these, 11 showed polymorphism between the two genotypes compared (E.Vallejos, personal communication). Important single gene traits can be easily maped using RFLPs, however future work should emphasize quantitative traits which are more relevant to Phaseolus genetic improvement.

Since genome analysis by RFLPs is time consuming and more costly than isozyme or protein analysis, a concerted effort by many scientists will be needed to achieve the goal of mapping important Phaseolus bean traits.

The development of RFLP analysis in P. vulgaris will provide information on the presence of specific genes and their location on the chromosomes. This research is expected to accelerate genetic manipulation through genetic engineering techniques.

Gene transfer and expression

As mentioned above, the identification of priority targets for genetic manipulation through the emerging biotechnologies is a pre-requisite for developing research strategies in Phaseolus beans.

P. vulgaris is susceptible to transformation by Agrobacterium vectors (CIAT, 1986). However, it will be necessary to regenerate plants from transformed tissues in order to study the expression and regulation of foreign genes in whole transgenic plants and their progeny. It will also be necessary to test other means of gene transfer in Phaseolus beans; i.e. the particle gun technique which may avoid problems associated with plant regeneration.

References Cited

Andrade-Aguilar, J.A. 1987. Interspecific hybridization between Phaseolus vulgaris L. (common bean) and Phaseolus acutifolius A.Gray (tepary bean) by means of embryo culture. Thesis, Dept. Plant Biology, Univ. of Birmingham, 37 p.

Allavena, A. 1984. Beans (Phaseolus). In: W.K.Sharp, D.A.Evans, P.V. Annirot, Y. Yamada (eds.) Handbook of Plant Cell Culture, Vol. 2. Crop Species, Macmillan, New York, p.137-168.

Allavena, A., AngeliniRota, R. Rossetti, L. Mazzola, 1987. Morphogenesis from immature cotyledos of *P. coccineus* and *P. vulgaris* cultured *in vitro*. Abstract. Internat. Congress Plant Tissue Culture of Tropical Species (A. Angarita, ed.) Bogota - Colombia, p.15.

Cardona, C., and Posso, C.E. 1987. Resistancia de variedades de frijol a los gorgojos del grano almacenado. Fuentes, mecanismos y factores responsables. Hojas de Frijos ISSN 0120-2480, Vol 9:1-4.

Centro Internacional de Agricultura Tropical. 1986. Biotechnology Research Unit, Ann. Report 1985, Cali-Colombia. 66 p.

Centro Internacional de Agricultura Tropical. 1987. Bean Program *In*: CIAT Report 1987, Cali-Colombia. pp. 39-55.

Gepts, P.L. 1984 Nutritional and evolutionary implications of phaseolin seed protein variability in common bean (*Phaseolus vulgaris* L.) Ph.D. Thesis, Univ. Wisconsin, Madison, USA. p. 228.

Gepts, P., and Bliss, F.A. 1985. Usefulness of phaseolin as an evolutionary marker. Bean Improvement Cooperative Ann. Report 28: 60-61.

Helentjaris, T., King, G., Slocun, M., Siedenstrang, Ch., and Wegman, S. 1985. Restriction fragment polymorphisms as probes for plant diversity and their development as tools for applied breeding. Plant Molecular Biol. 5: 109-118.

Kumar, A.S., Gamborg, O.L., and Nabor, M.W., 1988. Regeneration from long-term cell suspension cultures of tepary bean (*Phaseolus acutifolius*). Plant Cell Reports 7: 322-325.

Laing, D.R., Jones, P.R., Davis, J.H.C. 1984. Common bean. *In*: P.R. Goldsworthy, N.M. Fisher (eds.), The Physiology of Tropical Field Crops. Wiley, New York. pp. 305-351.

Mulcahy D.L., and Mulcahy, G.B. 1987. The effects of pollen competition. American Scientist. Vol. 75: 44-50.

Muñoz, L.C., Laignelet, A., Hoyos R., Roca, W.M. 1987. Differentiation of embryo- like structures from immature sexual embryos and in vitro micropropagation of Phaseolus vulgaris and Phaseolus lunatus. Abstract. Internat. Congress Plant Tissue Culture of Tropical Species (A.Angarita, ed.), Bogota-Colombia p.58-59.

Singh, S.P. and Gutierrez, J.A. 1984. Geographical distribution of the DLI and DL2 genes causing hybrid dwarfism in Phaseolus vulgaris L., their association with seed size, and their significance to breeding. Euphytica, 33: 337-345.

Triana, M. 1988. Estudio electroforetico de germoplasma de frijol (Phaseolus vulgaris L.) en centros secundarios de diversidad genética: el caso de Africa suroriental. Tesis, Univ. Nacional de Colombia, Facultad de Ciencias Agropecuarias, Palmira. 92 p.

Vargas, J. 1988. Caracterización de los acervos genéticos de Phaseolus vulgaris L. por medio de electroforesis de isoenzimas. Tesis, Univ. del Valle, Cali-Colombia. 72 p.

35665

THE POTENTIAL OF HYBRID BEANS

H. Bannerot*

Summary

In order to successfully develop F1 hybrid beans, four conditions are prerequisites :

1. To evaluate the magnitude of heterosis.
   A review of 23 papers shows that yield heterosis above the high parent can vary between 20 and 170% depending on combinations and crop conditions. A recent paper reports yield heterosis above the high parent averaging 30% with the maximum exceeding 100%, which correspond to an actual yield of 5t/ha.

   All of the yield components exhibit heterosis, in particular the pod number/m^2. The best combinations involve parents of different growth habit.

2. To find efficient cytoplasmic male sterilities.
   Until now, five cytoplasms inducing a reasonably good level of male sterility in P. vulgaris have been found : 1 at CIAT, 4 in Versailles. These cytoplasms seem to differ by their mtDNA restriction patterns with the enzyme Sal I, but are functional with the same set of maintainers.

   Most of the P. vulgaris genotypes tested are poor maintainers giving partial male sterility when converted.

---

* Directeur de Recherches, Station de Génetique et d'Amelioration des Plantes, I.N.R.A., Route de Saint-Cyr, 78026 Versailles Cedex, France.

Less than 20 genotypes were found with a good maintaining ability. These belong to the different categories : bush, climber, dry, snap, white or colored seeded beans.

After meiosis, the pollen grains of good male sterile plants remain associated in tetrads and less than 10% of them are stainable.

3. To transport pollen from the male to the female parent.
The cross fertilization of male sterile plants was evaluated in the field as insufficient in 1987, but good in 1988, at the Versailles Station.

A selection program for natural crossing ability was started in 1980 in a population deriving from P. vulgaris x P. coccineus multicrosses. It gave lines with a natural hybridization rate (without male sterility) of 20 to 30% in Versailles compared with a natural rate of 3% in control varieties.

4. To restore pollen production in F1 hybrids.
We found 3 lines of P. vulgaris possessing a dominant restoring ability. Their F1s with good male sterile genotypes were not as fertile as the control. They have 30 to 70% stainable pollen grains which are partially coalescent.

Another source of dominant restoration was derived from P. vulgaris x P. coccineus multicrosses. They seem to give F1s with higher stainability levels and more disperse pollen. In 1988, the level of pod fertility of experimental F1s appears to be sufficient to express the yield potential quite well.

We propose to start a program of recurrent reciprocal selection with two complementary groups. The first group will be the source of female parents. Thus, it will incorporate high maintaining ability (in order to be easily transformed to male sterility by back crosses) and high seed number (i.e. small seed size and intermediate growth habit).

On the contrary, the second group must be selected for high restoring ability, large seed size, and high combining ability with group 1.

Climbing beans probably represent the most appropriate target to start hybrid breeding.

Introduction

One of the most difficult challenges of plant breeding is the successful development of F1 hybrids in self pollinated species.

The F1 hybrid model (cross of two pure lines) was almost simultaneously proposed in the beginning of this century by Shull and East, aiming to improve the yield of maize. It took a very long time (about 40 years) to succeed. Despite a significant progress in yield and uniformity, the severe inbreeding depression of the parental lines increased enormously the cost of commercial seeds and thus delayed the development of hybrid varieties. Thanks to the solution found by Jones (double hybrids), it was at last possible to launch hybrids.

Now this type of variety is universally utilized for many heterogamous species : onion, sugar beet, sunflower, asparagus, carrot, cucurbits, etc..

For autogamous species, the rare cases of F1 hybrids are found in vegetables : tomato, pepper, and eggplant where hybrids progressively replace the old true-bred varieties. Nevertheless, in China, 1 million hectares of rice F1 hybrids are cultivated and in Europe the first wheat hybrids were released four years ago, though in fact without great success.

It is indeed difficult to develop F1 hybrids in autogamous species, since pure lines can themselves be productive, adapted to different types of agriculture, are very easy to reproduce and are thus utilized directly as commercial varieties. This is the case for beans where pure lines are quite satisfactory. But that does not mean there is no heterotic effect.

Four prerequisites must be satisfied before embarking on a program of hybrid creation.

First of all, it is necessary to evaluate the magnitude of heterosis which indicates the probability of finding combinations sufficiently better than control varieties.

Heterosis will be measured as the difference between the hybrid and the best parent which in this case, should not be a severely depressed line, but a productive homozygous line. This is why the value of heterosis in autogamous species averages 20 to 30% above the high parent instead of 200% as in maize.

We shall see that in the case of the common bean, we have the good fortune to have available highly diversified types capable of generating unexpected heterosis effects.

The second prerequisite deals with the process of hybridization itself. In hermaphroditic species, it is impossible to emasculate by hand on a large scale. The best solution is to rely on cytoplasmic male sterility or CMS. CMS is based on the interaction of an inducer cytoplasm (or more precisely an inducer mitochondrion) and a maintainer nucleus in the same genotype.

Third, the pollen of the male parent must be carried profusely to the stigmas of the female parent. In legumes, this transport will be carried out by insect pollinators, bees and bumble bees. In strictly autogamous species, pollen transport could be a problem.

Finally, we have to cancel the sterilizing effect of the mitochondrial genome by action of nuclear genes carried by the male gametophyte. We call this pollen fertility restoration or simply restoration. We need to have restoration of the F1 itself, which means that this nuclear restorer genetic system must be dominant.

1) Magnitude of Heterosis

In 1986, Florence Lestienne reviewed the literature relevant to heterosis in common bean. Twenty three references were analyzed from 1932 (Malinovski) to 1986 (Nienhuis and Singh). Generally, due to the difficulty of obtaining hybrid seed in large quantities, evaluations were performed on single plants or plots at very low densities.

Heterosis expressed as the difference between hybrid and high parent can vary to a large extent : 20 to 170%, depending on the parents and environment.

The most recent paper (Nienhuis and Singh, 1986) is probably among the most interesting. The authors used a large dialled cross 9 x 9, with parents chosen in the three existing growth habits of bush beans and of different seed sizes. F1s and F2s were evaluated in two locations (Palmira and Popayan, Colombia) for yield, yield components and architectural traits.

The main results can be summarized as follow :

- Heterosis above mid parent was observed for all traits measured.
- Significant heterosis x location interactions were found for yield, yield components and three architectural traits.
- Yield heterosis above the high parent was significant in 20 crosses at

Palmira (mean heterosis 36%) and in 4 crosses only at Popayan (mean 23%).

- The best crosses showed heterosis of about 100% which corresponds to a yield near 5 t/ha in Palmira compared with a parental mean yield of 2.7 and best parent yield of 3.4.
- Heterosis values tend to increase in crosses of increasingly divergent growth habit, I x II and I x III are better than I x I or II x II.
- General combining ability is greater than specific combining ability suggesting that additive gene action is most important in the inheritance of yield.

In Versailles, we also found good combining ability between different growth habits. For instance, the F1 S102 (type II) x Red Kloud (type I) showed heterosis above high parent (S102) of 30% in the field and 60% in the greenhouse.

Allow me to quote this commentary of Nienhuis and Singh (1986) "Heterosis for all traits measured and especially heterosis above the high parent for yield may be sufficiently large to stimulate interest in the feasibility of commercial production of hybrid bean seed".

2) Cytoplasmic Male Sterility

2.1 Origin of cytoplasms

The first case of CMS in bean was observed at CIAT (Singh et al., 1980). The cytoplasmic nature of this male sterility was confirmed in the USA (Basset and Shuh, 1982).

This CMS originated in G 8063, a typical P. vulgaris genotype where 13 male sterile plants were observed in 1977. Their F1's with G 3807 were sterile or partially sterile, suggesting that G 3807 is a maintainer, later Sprite and Triumph American snap beans were also found as maintainers and were converted to male sterility in Gainesville. Male sterile plants produced less than 10% of stainable pollen and persistent tetrads of unstained pollen. Unfortunately, this CMS appeared to be unstable, reverting erratically to fertility.

It also presents the paradoxical phenomenon of "permanent restoration" already observed in Vicia faba. The F2 P. vulgaris progeny derived from selfed restored F1 CMS Sprite x R351 segregates as expected 3 mf : 1 ms. But the male sterile plants in the F3 generation are absent. It was recently demonstrated by Sally Mackenzie and Chris Chase that a 6 kb fragment of mtDNA was excised in revertants and in F3 deriving from restored F1. We received this cytoplasm very recently, and it was coded (Ci) because of its CIAT origin.

In 1978, in order to study nucleus-cytoplasm interactions in bean, we started to cross several P. vulgaris genotypes as female by several P. coccineus genotype (VUCO program) and reciprocally (COVU program).

The principle of the method which was used is that the progeny of a cross receives the cytoplasm exclusively from the female parent. For example, consider that the cross Desiree (female) x Maxidor (male) followed by nine back crosses to Maxidor (male) results in the transfer of the Maxidor nucleus into the cytoplasm (D) of Desiree. To describe this situation of isogenic alloplasmy, we use the notation (D) Rg Maxidor.

We will here examine only the results of the COVU program (i.e. the transfer of several P. vulgaris nuclei into 17 P. coccineus and 2 P. polyanthus cytoplasms) the only one having given results useful for application (Table 1).

Crosses using P. vulgaris as female x P. coccineus are very easy to carry out and present no problems. In contrast, the cross of P. coccineus as female x P. vulgaris male is considered to be very difficult, indeed impossible with improved genotypes; this we have confirmed. To overcome this obstacle and to initiate the transfer into P. coccineus cytoplasms, we have employed an auxiliary genotype ZBD 1.3 which served as a bridge. This was an F4 individual derived from the complex cross coded ZBD.

ZBD = (Wulma x Colorado) x (P. formosus) x P. coccineus, which we maintain through cuttings. As a male parent, it crosses as well with P. vulgaris as with P. coccineus. There is also the advantage of the presence of dominant markers of the plantlet (anthocyanin) and of the flower (purple color) which can be used as evidence for successful crosses. After a cross with ZBD (and a second cross, if necessary) the systematic back-crosses with recurrent parents can begin.

The principal phenotypic modifications observed were deleterious and specific to certain cytoplasms : loss of vigor, rapid senescence, variegation of leaves and pods, loss of fertility.

The first clear case of male sterility appeared in 1980 with Morelos cytoplasm (Mo) and Rugally nucleus; it was followed by three others (Hq) (Sp) (Da).

2.2 Results

On Table 1, we have summarized the latest results :

- (Hq), (Mo), (Sp) and (Da) cytoplasms are CMS inducers, the others 15 are not.
- Rugally and E02 are maintainers for these 4 cytoplasms and also for (Ci). Contender and Maxidor are very poor maintainers but are not restorers.
- The maintaining ability of a series of genotypes was evaluated by back-cross with the first cytoplasm obtained (Mo).

Most of them appeared to be poor maintainers as they gave partial male sterility when converted, characterized by erratic production of partially self fertilized pods. Relatively few genotypes possess a good maintaining ability (Table 2). They belong to different types of beans (bush or climber, dry or snap) with a tendancy to be more frequent in snap beans.

When converted to male sterile they bear only parthenocarpic pods without seeds as already observed by Singh et al (1980). The pollen grains of these male sterile plants remain associated after meiosis; 90 to 95% of the tetrads possess four empty grains, the rest of them show occasionally 1, rarely 2, never 3 or 4 stained pollen grains (Fig. 1). Less than 5% of the pollen grains are disperse, even this may be an artefact of the stainig procedure (squash effect).

Stainable dispersed or associated pollen grains represent less than 10% of the total pollen. In comparison, the control (the maintainer itself with its own cytoplasm) possess 95% to 99% dissociated stainable pollen grains.

Thus, we need to understand why the so-called male sterile plants which in fact produce 5 to 10% stained pollen grains are not self fertilized. The reason for this appears to be the following. The anthers of these sterile plants are nearly empty so they cannot burst. The rare functional pollen grains which are released are mixed with debris forming a sticky powder. They have little chance to fertilize.

As far as we could observe the maintaining ability (MA) which is efficient with Mo cytoplasm seems to function to the same extent with the 4 other cytoplasms.

It seems that a continuous range of MA occurs : from very good MA with Gitana or Rugally to very poor MA giving converted plants almost as fertile as controls with S102 (brasilian black seeded genotype), Maxidor

(European wax-Snap bean) or Red Kloud (North American light Red Kidney). When crossed as female to Gitana, this converted version gives male sterile F1s! This indicates that they possess a recessive restoration system.

A study of mitochondrial DNA of the five sources of CMS was performed. The electrophoretic patterns obtained with enzyme Sal I were specific to each cytoplasm; Hq, Mo and Sp differ slightly and resemble non inducer P. coccineus but are very different from P. vulgaris. Da (P. polyanthus cytoplasm) is unique, Ci is very similar to normal P. vulgaris. A fragment of 8.4 Kb, present in non-inducing cytoplasms is lacking in Hq, Mo, Sp and Ci, but present in the Da pattern (Fig. 2).

3. Cross-Fertilization of Male Sterile Plants

Producing hybrid seeds on a female (male sterile plant), implies that the pollen produced by the male parent has to be carried to the stigmas of the female male sterile plant where it will germinate and lead to the formation of cross-fertilized seeds.

This task will be carried out by bees and bumble bees which forage the flowers looking for nectar and sometimes pollen. The bumble bees collecting nectar in Versailles often bore the base of the flower bud one day before anthesis, which is ineffective for pollination. We observed male sterile plants in the proximity of normal plants in the field during the two preceding seasons. The cross fertilization was evaluated as poor in 1987, but good in 1988 though less than the control. We don't understand the reasons for this difference between years.

In 1978, fearing an insufficient cross pollination of male sterile plants, perhaps due to a lack of pollinator visits, we started to select for natural out crossing ability.

This selection was based on the utilization of a marker affecting pigmentation which is probably pleiotropic; it is visible in the seed, in the plantlet and in the flower. The two possible states of this marker are the following : recessive (white seeds, green axis and cotyledons, white flowers); dominant (black seeds, purple axis and cotyledons, purple flowers).

Selection was carried out on the KH population mentioned above. This population quickly showed a tendency for allogamy; after two generations of natural reproduction in the field, the characters purple and yellow pods, white and red seeds were found in the population. These characters were not present in the parents of the original crosses and must, therefore, have been introduced by natural crosses with plants of neighboring plots.

Some of the plants had white flowers and gave white seeds. Several groups of white seed progeny were planted in the fall in the greenhouse in square dishes. 200 seeds can be planted in one 36 x 36 cm dish. Among the groups of progeny, the majority of which had green axis and cotyledons, plants with violet axis and cotyledons appeared with variable frequency : these could only have resulted from natural hybridization with plants possessing the dominant markers. The more frequent the anthocyanic plantlets among the progeny, the more the female parent has a tendency for allogamy. Among those giving such plantlets with high frequency, several hybrid plantlets were recovered, grown in the greenhouse during the winter and self fertilized (Fig. 3).

The markers segregated in the F2 progeny with observed ratios of 3 : 1 or, most frequently, 9 : 7. These progenies were sown the following year and those which had white flowers were harvested. The white seeds were selected and the cycle was started again (Fig. 4). A more costly variation of this method consists of fixing the white seed character by cultivating F2 plants with green axis and white flowers. This procedure requires a second generation in an insect-proof greenhouse.

While the average rate natural hybridization of P. vulgaris varies in Versailles between 2 and 3%, lines giving 20 to 30% of natural hybrids were obtained after a single cycle of selection (Fig. 2). We hope to increase this rate even more.

This tendency for heterogamy should permit better fertilization of the male sterile plants which otherwhise give not enough seeds. The frequency of hybridization mentioned above is probably an underestimate, since the pollinators seem to choose one color of flower and pollinate others accidentally.

Unfortunately, after testing by backcross to Mo cytoplasm, the best lines for heterogamy showed a poor maintaining ability. Only the line A1 24 K is a good maintainer but it gives only 7% natural outcrosses. We must now observe CMS lines with neighboring male fertile plants in different locations during several years in order to check the yield of hybrid seeds.

4. Restoration of Pollen Fertility

It is probably a wise precaution to restore the pollen production in the F1 plants in a self pollinated species since outcrossing would probably be insufficient. Thus, when we found good CMS, we looked immediately for dominant restoring ability (DRA). The test cross for DRA is very simple; the restorer candidates are crossed with one or preferably two different good male sterile genotypes. So we found only 3 P. vulgaris genotypes with sufficient DRA among about fifty candidates tested: Borlotto gigante (Borgi), Bo 025 and Ph 257.

In fact, as already observed by Sally Mackenzie with Ci cytoplasm the restoration is not complete. Only 30 to 70% of the pollen is stainable and grains are still predominantly coalescent.

This year, for the first time, restored F1s between different CMS (five different nuclei in the same (Mo) cytoplasm), and the restorers mentioned above were observed in the greenhouse and the field. In the field, the fertilization rate seems to be better than in the greenhouse, maybe because of insect activity or wind effect.

The results of greenhouse trials are promising; if we express the quality of the restoration by the ratio of the mean number of seeds/pod of the F1s divided by the seed number of a theoretical mid parent: ((maintainer + restorer) x 0.5), we found for this ratio 0.74 for Borgi, 0.84 for Bo 25, 0.86 for PH 257. The ideal control would be the same hybrid, obtained by hand crossing. We also looked for restoration in the species which had given the inducer cytoplasm: P. coccineus itself and VUCO genotypes, specially in the KH populations mentioned before.

This time, we have found several genotypes giving in F1s with good CMS, 80% of stained pollen, mainly disperse.

We are currently transferring these dominant gene (s) by backcrossing the restored F1 to a good male sterile. The obtained progeny of the BC segregate, generally 1 mf : 1 ms (one dominant gene) or 1 mf : 3 ms (two dominant genes).

A very good restoration level seems necessary for green beans, because an incomplete fertilization diminishes the quality of the green pod. For dry beans, we hope for a compensation effect of the insufficient number of seeds in pods by an increase in pod numbers.

Conclusion

The magnitude of heterosis found in common bean is higher than generally observed in self pollinated plants; the quality of CMS is satisfactory with maintainers already classified as good; the cross-pollination has to be more precisely evaluated. The restoration level presently obtained must be also tested in practical conditions. We propose to start right now a program of reciprocal recurrent selection with a special attention to the problem of hybrid seed cost.

The first population, source of the future female parents could be oriented to a type of plant yielding a large number of seeds. This means small seed size and high number of pods (i.e. types II, III or IV). Other necessary characters are maintaining and crossing ability.

The complementary population, source of the future male parents must correct or compensate all the "defects" introduced in the first group : large seed size will correct the small size, dominant restoring ability will override the male sterility and high combining ability will enhance the yield.

References

Adams, M.V. 1967. Basis of yield component compensation in crop plants with special reference for the field beans, Phaseolus vulgaris. Crop Science 7:505-510.

Adams, M.V. and Duarte, R. 1961. The nature of heterosis for a complex trait in a field bean cross. Crop Science 1:380.

Albuquerque, M. and De Vieira, C. 1974. Manifestation of heterosis in Phaseolus vulgaris L. beans. Revista Ceres 21(114):148-166.

Bannerot, H.; Bell, J.M.; Bosc, B.; and Camut, R. 1987. Un gene dominant de stérilité male chez le haricot. Agronomie 7(8):563-566.

Bannerot, H. 1983a. Creation of allogamous vulgaris x coccineus populations in order to breed new types of beans. Eucarpia Meeting on Phaseolus Bean Breeding, Hamburg, 19-21 july.

Bannerot, H. 1983b. Transfer of Phaseolus vulgaris nuclei into Phaseolus coccineus cytoplasms and reciprocally. First results. Eucarpia Meeting on Phaseolus Bean Breeding, Hamburg, 19-21 july.

Bannerot, H. and Charbonnier, L. 1987. Induction de stérilités cytoplasmiques par alloplasmie dans le genre Phaseolus : étude génétique et moléculaire. In: Variabilité génétique cytoplasmique et stérilité male cytoplasmique. Colloque de l'INRA, n 45, Sainte-Sabine (France), 22-23 avril 1987.

Basset, M.J. and Shuh, D.M. 1982. Cytoplasmic male sterility in common bean. J. Amer. Soc. Hortic. Sci., 107(5):791-793.

Bell, J.M. 1986. Etude génétique, cytologique et physiologique de différentes stérilités males géniques et cytoplasmique chez *Phaseolus vulgaris* L. These Univers. Paris 11, n d'ordre 111.177 p.

Chung, J.H. and Goulden, D.S. 1971. Yield components of haricot beans (*Phaseolus vulgaris* L.) grown at different plant densities. New Zealand J. Agric. Res. 14:227-234.

Chung, J.H. and Stevenson, E. 1973. Diallel analysis of the genetic variation in some quantitative traits in dry beans. New Zealand J. Agr. Res. 16(2):223-231.

Coyne, D.P. 1965. Component interaction in relation to heterosis for plant height in *Phaseolus vulgaris* L. variety crosses. Crop Science 5:17-18.

Coyne, D.P. 1968. Correlation, heritability and selection of yield components in field beans (*Phaseolus vulgaris* L.). Proc. Am. Soc. Hortic. Sci. 93:388-396.

Evans, A. 1970. Heterosis for yield in *Phaseolus vulgaris* crosses. Annual report of the Bean Improvement Cooperative 13:52-54.

Foolad, M.R. and Bassiri, A. 1983. Estimates of combining ability, reciprocal effects and heterosis for yield and yield components in a common bean diallel cross. J. Agric. Sci. 100(1):103-108.

Ghaderi, A.; Adams, N.W.; and Nassib, A.M. 1984. Relationship between genetic distance and heterosis for yield and morphological traits in dry edible bean and faba beans (*Phaseolus vulgaris*, Vicia faba). Crop. Science 24(1):37-42.

Gutierrez, J.A. and Singh, S.P. 1985. Heterosis and inbreeding depression in dry bush beans, *Phaseolus vulgaris*. Can. J. Plant Sci. 65(2):p.243.

Haq, M.N.; Lane, G.R.; and Smartt, J. 1980. The cytogenetics of *Phaseous vulgaris* L., *Phaseolus coccineus* L., their interspecific hybrids, derived amphidiploid and backcross progeny in relation to their potential exploitation breeding. Cytologia 45:791-798.

Laing, D.R.; Jones, P.G.; and Davis, J.H.C. 1984. Common beans (*Phaseolus vulgaris* L.). In: Goldaworthy, P.R. and Fisher, N. (Ed.). The Physiology of tropical field crop. John Wiley and Sons, New York, 305-352.

Lefort-Buson, M. 1985. Distance génétique et hétérosis. 1. Mise en évidence d'une relation entre heterosis et divergence génétique. In: Lefort-Buson, M. and De Vienne, D. (Eds). Les distances génétiques, estimations et applications, INRA, 111-118.

Lestienne, F. 1986. Etude de l'hétérosis pour le rendement chez le haricot grain. Mémoire de fin d'etudes, ENSH, Versailles, 46p.

Mackenzie, S.A. and Bassett, M.J. 1987. Genetics of fertility restoration in cytoplasmic male sterile *Phaseolus vulgaris* L. 1. Cytoplasmic alteration by a nuclear restorer gene. Theor. Appl. Genet. 74:642-645.

Mackenzie, S.A.; Pring, D.R.; Bassett, M.J.; and Chase, C.D. 1988. Mitochondrial DNA rearrangement associated with fertility restoration and cytoplasmic reversion to fertility in cytoplasmic male sterile *Phaseolus vulgaris* L. Proc. Natl. Acad. Sci. 85:2714-2717.

Mackenzie, S.A.; Pring, D.R. and Bassett, M.J. Large double-stranded RNA molecules in *Phaseolus vulgaris* L. are not associated with cytoplasmic male sterility. Theor. Appl. Genet. 76:59-63.

Malinowski, E. 1932. Phénomenes de l'accroissement de vigueur chez les hybrides de *Phaseolus vulgaris* L. Compte rendus de la Société de Biologie de Paris. 111:1035-1036.

Nienhuis, J. and Singh, S.P. 1984. Diallel analysis of yield components and architectural traits in dry bush beans *Phaseolus vulgaris*. Hortscience 19(3) sect. 2:p.599 (abstract).

Nienhuis, J. and Singh, S.P. 1985. Effects of location and plant density on yield and architectural traits in dry beans. Crop Sci. 25(4):579-584.

Nienhuis, J. and Singh, S.P. 1986. Combining ability analysis and relationships among yield, yield components and architectural traits in dry beans. Crop Sci. 26:21-27.

Sarrafi, A.; Amirshahi, M.C. and Seadati, K. 1973. Heterosis and heritability for yield components in reciprocal F1 and F2 hybrids of two american and iranian bean varieties Phaseolus vulgaris. Agronomy, abstracts p.13.

Sarrafi, A.; Yazdi-Samadi, B.; and Zali, A.A. 1976. Heterosis and heritability for yield and yield components in F1 and F2 generation of a bean cross. Iranian J. Agric. Res. 4(1):3-6.

Singh, S.P.; White, J.W.; and Gutierrez, J.A. 1980. Male sterility in dry beans. Ann. Rep. Bean Improv. Coop. 23:55-57.

Singh, S.P. 1982. A key for identification of different growth habits of Phaseolus vulgaris L. Ann. Rep. Bean Improv. Coop. 25:92-94.

Singh, S.P. and Saini, S.S. 1983. Heterosis and combining ability studies in french bean. Sabrao J. 15(1):17-22.

Srivastava, H.K, 1980. Heterosis for chiasma frequency and quantitative traits in common beans (Phaseolus vulgaris L.). Theor. Appl. Genet. 56(1/2):25-29.

Tonguthaisri, T. 1977. Genetic analysis of morphological characteristics of yield beans (Phaseolus vulgaris L.) as expressed in a diallel cross. Dissertation Abstracts International B. 37(12):5902B-5903B.

Voysest, O. 1972. The effect of heterosis on yield and its primary components in french bean, Phaseolus vulgaris L. Investigaciones Agropecuarias, 3(1):10-16.

Table 1. Transfer of different *P. vulgaris* nuclei in different *P. coccineus* or *P. polyanthus* cytoplasms.

		Number of back crosses on				
Code	Donor of cytoplasm	Contender	Maxidor	Rugally	EO_2	Observed modifications
D	Désirée	10	9	-	2	Severely depressed, variegation
P	Petaco	11	12	-	2	Variegation
T	Tres cumbres (*P. purpurascens*)	14	11	-	2	Loss of fertility, parchment?
Mo	Morelos 662	15	13	21	28	Male sterility
X	Mexique F	12	10	-	2	Normal?
Q	N1 407 (*P. obvallatus*)	4	-	-	-	Strongly-weakened, almost lethal
C	CL 4x	10	11	-	3	Normal? loss of fertility
H	HB 18	9	7	-	-	Depressed, variegation
L	LTE 8	13	-	-	-	Variegation
58	DGD 58	5	1	-	3	Normal?
67	NC 67 (*P. formosus*)	5	-	-	-	Loss of fertility, parchment? as T
125	DGD 125	9	-	-	-	Normal?
141	DGD 141	12	-	-	-	Normal?
726	N1 726=DGD361	7	-	-	2	Severely depressed, loss of fertility
Sp	N1 756=Patzum	16	8	7	17	Male sterility
886	N1 886	9	-	-	2	Normal?
Hq	N1 889	14	10	9	7	Male sterility
757	N1 757 (*P. polyanthus*)	3	-	-	3	Normal?
Da	N1 758 (*P. polyanthus*)	5	3	3	3	Male sterility

Table 2. Levels of maintaining ability (MA) found in *P. vulgaris* with the different CMS inducing cytoplasma (1)

	CI	Da	Hq	Mo	Sp
Good MA					
Gitana (bush, snap)	5(1)	5	5	5	5
Rugally (bush, snap)	4	4	4	4	4
Prélude (bush, snap)	4	4	4	4	4
Sprite (bush, snap)	-	-	5	5	5
Triumph (bush, snap)	4	-	5	5	5
EO$_2$ (bush, dry)	4	4	4	4	4
PH200 (bush, dry)	-	-	4	4	4
GM10 (pole, snap)	-	-	-	5	-
VX193 (pole, snap)	-	-	-	4	-
Copau (pole, dry)	-	-	-	4	-
Al 24K (pole, dry)	-	-	-	5	-
P. mexicanus and progenies	-	-	-	4	-
Intermediate MA					
Most of the screened genotypes fall here (Carioca, navys, Great Northern)	-	-	-	2-3	-
Poor MA					
Contender	2	2	2	2	3
Maxidor	1	1	1	1	2-3
Red Kloud	2	2	2	2	3
S 102	1	1	1	1	2

(1) Score based on pod fertility
0 = fertility of the control = no sterility
5 = complete sterility of converted version

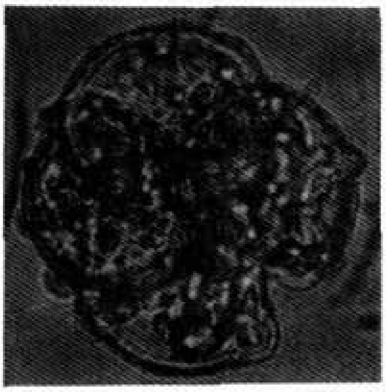
Figures

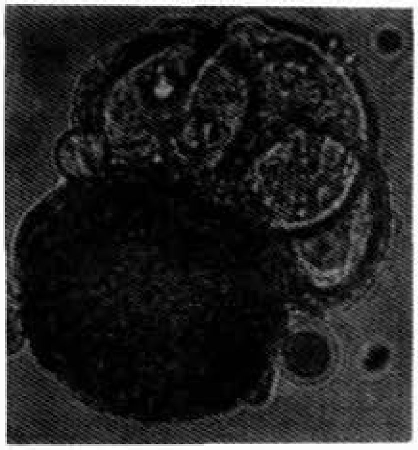
Fig. 1. Tetrads of 1, 2, 3, or 4 strained pollen grains.

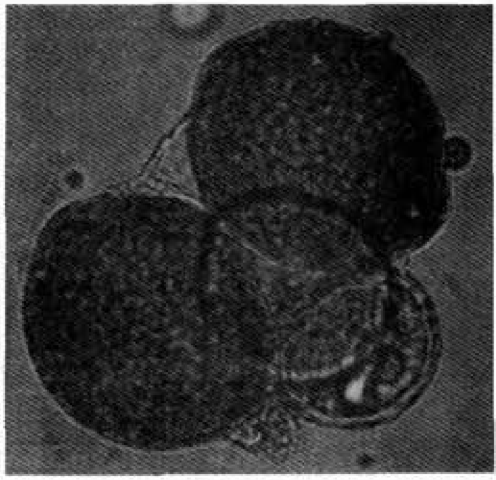
Fig. 2 Comparison of mt DNA patterns (Sal I enzyme).

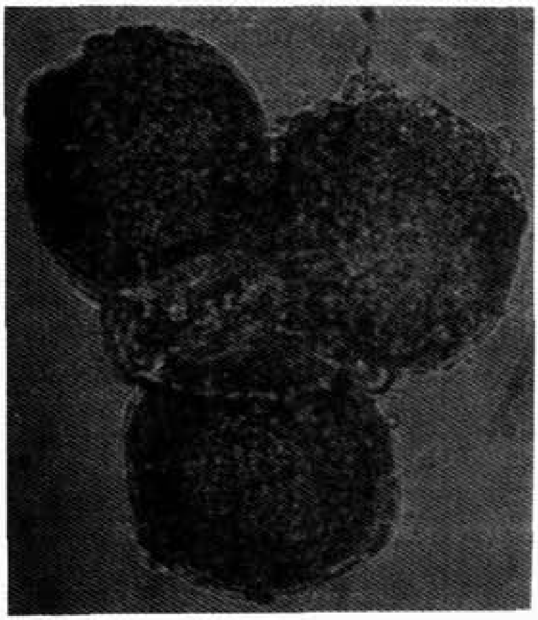
Fig. 3. Percent allogamy in KH in 1983 (200 plants).

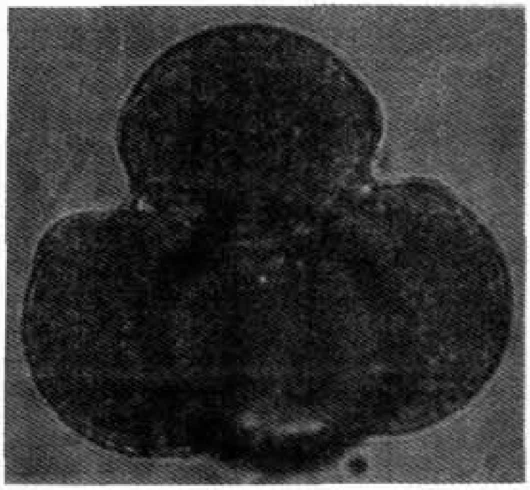
Fig. 4. Selection for increased allogamy.


(0C)


(1C)


(2C)


(3C)


(4C)

Normal control: dispersed stained pollen grains

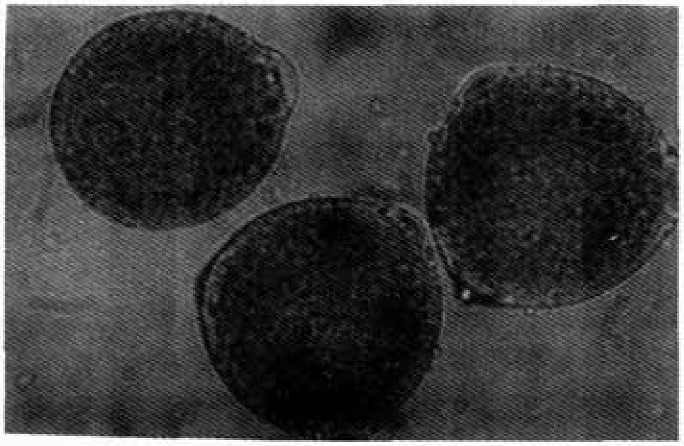

mf plant (anthesis)

Figure 1. Tetrads of 1, 2, 3, or 4 strained pollen grains.

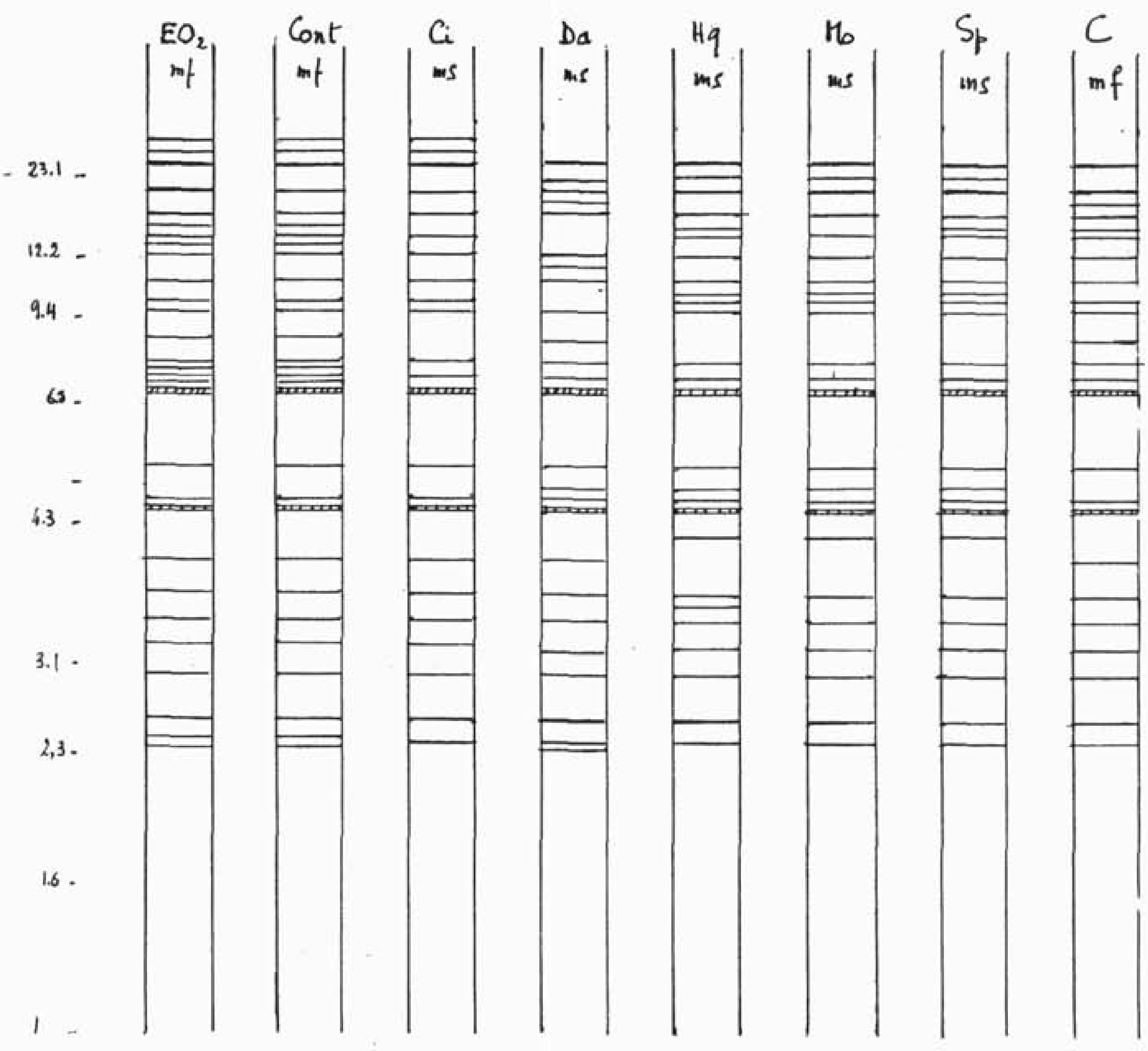
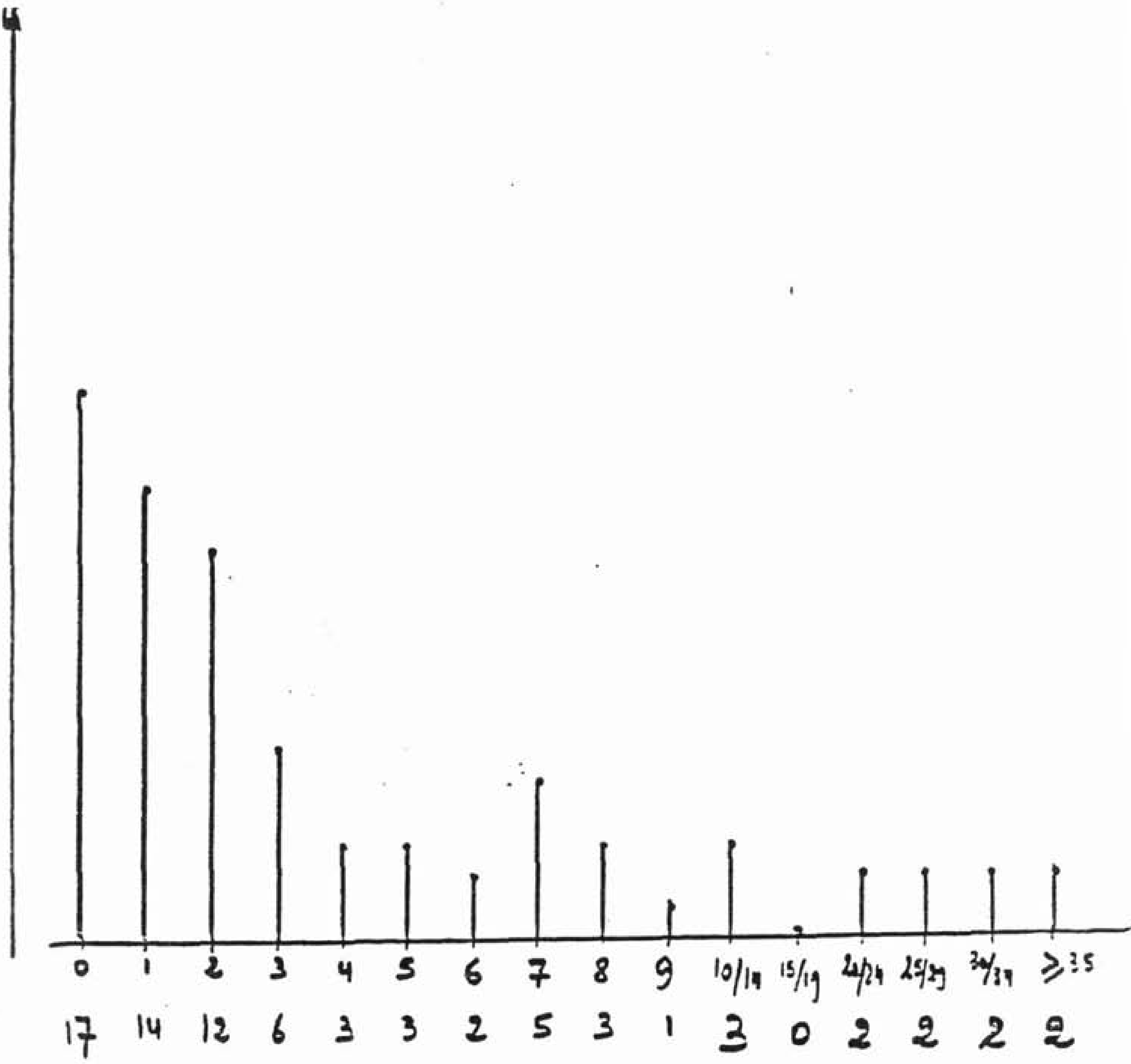


Figure 2. Comparison of mt DNA patterns (Sal I enzyme)

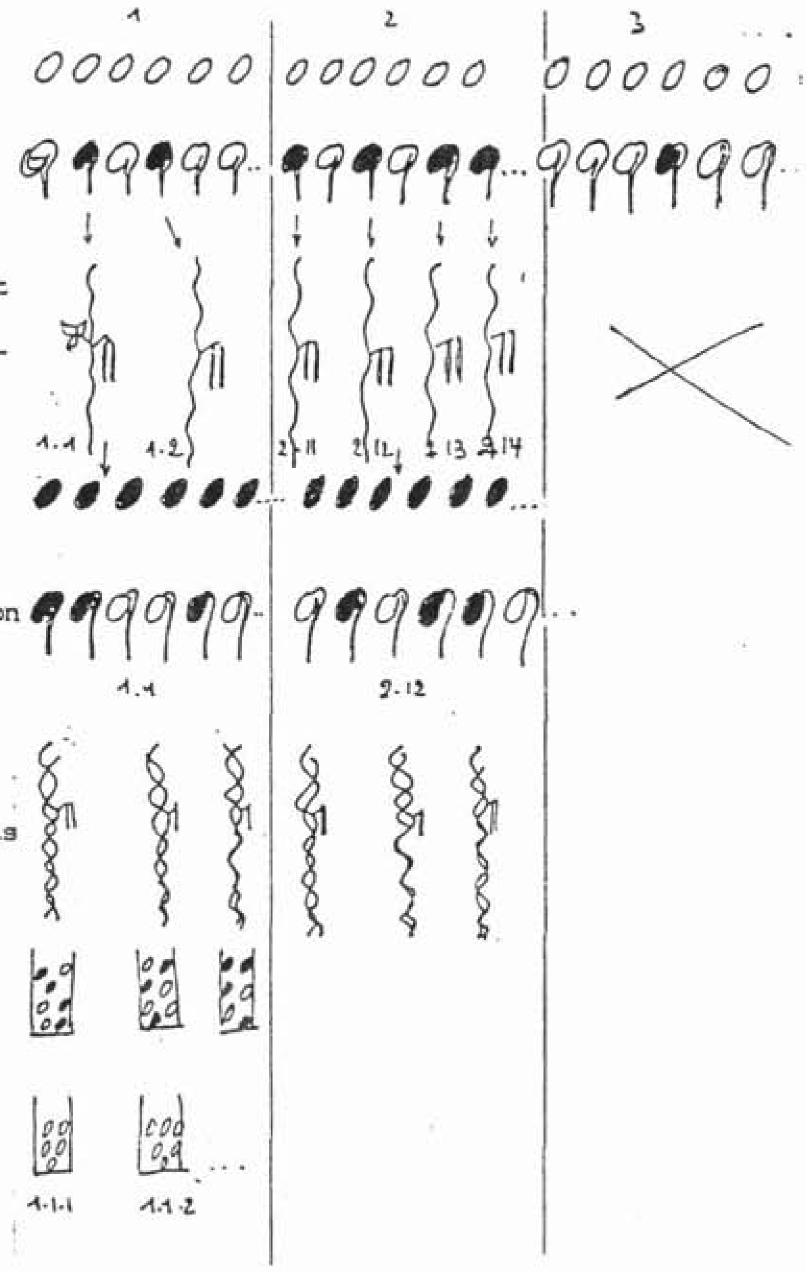
Figure 3. Percent allogamy in KH in 1983 (200 plants)



77 progeny have white grains

Fig.4 Selection for increased allogamy

1. Harvest families with white seeds
2. Test germination
3. Breed several violet plantlets (from high frequency families) in greenhouse
4. Harvest the seeds (black)
5. Check the segregation in F_2 (facultative)
6. Plant in the field the rest of the seeds (hill plot)
7. Harvest hill plots in bulk
8. Separate white seeds
9. Begin again with step 2



35666

A SOCIO-ECONOMIC PERSPECTIVE ON EARLINESS IN BEANS

Willem Janssen*

Summary

Earliness is a breeding and production concept with many different dimensions. It affects risk, crop management, labor, land and capital use, sales possibilities and food availability through the year. The attention to earliness is increasing in part because it has received little attention in the past, which has led to late varieties, with adoption problems.

Because earliness has so many dimensions it can only be understood in a farm systems context. The author believes that the role of earliness as a drought escape mechanism is often overestimated at the cost of its impact on especially labor, land and capital productivity. One of the reasons for the limited attention to the other dimensions of earliness, is that the benefits do not appear within the crop but in the rest of the farm system.

For all dimensions distinguished in earliness, alternatives do exist. The management of a number of alternatives, however, is more complex than the growing of early varieties, which combine a number of advantages in one, easily managed trait. As well, many alternatives have a strong institutional component, which falls outside the reach of the individual farmer. As much as a drought escape mechanism, earliness appears an "institutional deficiency" escape mechannism.

Earliness has a price, in terms of a reduction of yield potential. However very few studies (or none) have been reported that calculate the

---

* Economist, Bean Program, CIAT, A.A. 6713, Cali, Colombia.

value of the trait. This is because the multidimensional character of earliness makes it difficult to measure its value correctly, because it has received little attention in temperate agriculture and because it is not a problem that economists tend to be interested in instinctively.

Some suggestions are made on how its value could be measured. A promising strategy appears to be the generation of methodologies analogous to risk-analysis.

Earliness has to be associated with poor people. Poor people can often not wait until next week in order to receive money or food. To survive, they need it today. Consequently they live with a very short time horizon. Earliness is a trait which helps them in their struggle to survive. Nevertheless, if the small farmers of Latin America and Africa would not need earliness any more, this most probably would imply that their production situation and living conditions would have improved considerably.

Introduction

Earliness as a breeding objective has been a concern in many crops. Its value has been proven in a very convincing way in rice, where the development of early maturing, high yielding varieties allowed the inclusion of a third crop in the annual production cycle (Zandstra et al., 1981). In case of beans, such clear proof on the value of earliness has not been produced. Yet, intuitively the importance of earliness for bean breeding is clear. Many farmers in the developing world praise beans for being a rapid crop. Among the staple foods, it is probably the crop that occupies the field for the shortest time. In fact, a farmer in Costa Rica commented that he liked beans, because "it was all over" in less than three months.

An initial judgement on the value of earliness should be positioned somewhere between two contemporary expressions. The first one is "time is money" and the second one is "haste makes waste". This paper will try to explain in more detail the advantages than the disadvantages of earliness. However, it should be clear that, other things equal, early varieties have less yield potential than late varieties. The benefits of earliness do not come for free.

The expression "time is money" is mostly associated with wealthy businessmen in the United States of America. Not only wealthy businessmen, but also poor people in underdeveloped countries live with this expression in mind. Poor people are almost always short of money and will rather receive a small amount of money today, than a bigger amount next week. They live from day to day, are not able and therefore not accustomed to wait for money or food.

"Haste makes waste" is an expression that represents scientific values. Scientists most often have stable incomes, have spent long years of their life studying, and are trained to produce careful results, rather than to produce rapidly. The challenge of explaining earliness to a scientific public lays in the different value system of farmers and researchers.

What Is Earliness?

Earliness is a relative concept. A variety is early if it completes its crop cycle in less time than the traditional variety. What this means in the number of days is very location specific. In the Southeast of Guatemala early varieties have a crop cycle of some 65 days and intermediate varieties of some ten days more. In the extreme south of Colombia (Ipiales) early varieties have a cycle of 210 days and traditional varieties of 245 days.

Earliness is also a relative concept in a breeding context. In the search for yield and resistance, earliness has often been neglected. Consequently many improved varieties were less early than the traditional varieties. This brought problems with adoption of these varieties. For many breeders earliness implies reducing the crop cycle of improved varieties back to those of traditional ones, not so much the reduction of crop cycles to shorter times than for the traditional varieties.

Earliness and Farmer Objectives

Earliness can only be understood in a farm systems context. The first question to be asked is on the objectives of the farmer. These vary widely, but most often the following components are involved: Income, especially in Latin America; adequate nutrition, especially in Africa; security and family welfare, important on both continents.

To fulfil these objectives the farmer makes use of certain resources. Traditionally four major resources are distinguished: land, labor, capital and management. The farmer can not freely use these resources. His farm only has a certain size, his family and neighbors only provide a certain amount of labor, his savings and credit-room at the bank are limited, as is his education. On top of these constraints, climatic, soil and market conditions further limit the options of the farmer.

The farmer tries to satisfy his objectives by the employment of his available resources in different activities. Bean production, and production of other annual crops, production of perennial crops and cattle holding are among the agricultural activities. As well the farmer might work as a day-laborer, or use his time and capital in trading activities.

Earliness obtains many dimensions if we consider how farmers balance their objectives with their available resources and alternative activities. At least five areas where earliness can make a difference in farm operation should be distinguished. These are: crop management; the efficient use of resources; the availability of food through the year; the opportunities to sell his produce and the area of risk and uncertainty in agricultural production.

Risk and Uncertainty

One of the most wide-spread ideas on earliness is that it serves as a drought-escape mechanism. In areas where the rainy season is short and irregular, early varieties have more chance to have passed the flowering stage before the dry season starts. Farmers are aware that with sufficient rain late varieties outyield early varieties, but are willing to accept a reduction in yield potential for a bigger chance of obtaining a successful crop. In a 1985 survey in the Southeast of Guatemala 43% of farmers planted early varieties to escape drought. In the same survey 66% of the farmers planted only early varieties, 26% planted early and late varieties and 8% planted only late varieties.

The evidence on the stability of early varieties is not very convincing in the case of Guatemala. Table 1 shows the outcome of a survey in the first semester (A) and the second semester (B) of 1985. In the first semester survey a distinction was made according to crop cycle. Yields per hectare were equal for early, intermediate and late varieties. There is no clear pattern in the adaptation to different cropping systems, with the exception of the low yields of the late varieties in monoculture. In such a situation early varieties are preferable. They yield as well as late varieties in less time.

The second survey made a distinction between traditional varieties and improved varieties. Most traditional varieties (but not all) were early, while all improved varieties were late. In this survey the improved (late) varieties considerably outyielded traditional varieties. THe resistance to Bean Golden Mosaic Virus, for which the improved varieties were developed and introduced could explain these yield differences. The yield difference per day, however, is minimal and the relative performance of improved varieties in associations was less than in monoculture. Questions that could not be appropriately answered were on the effect of earliness on the yield of the associated crop; on the comparability of production conditions; and on the value of time and timing by the farmer.

It appears that in 1985 earliness did not imply an advantage for traditional varieties in terms of yield potential. For the improved varieties a yield advantage was clearly present in the second season. The question for the farmer then becomes whether yield potential could not be introduced in earlier varieties. This is a particularly challenging question since it appeared that the traditional early varieties were grown on poor soils (hill sides), while the improved varieties were grown on more fertile and more humid flat soils (Viana et al., 1986). Earliness was not only associated with drought escape but also with water and nutrient efficiency and possibly with yields of the associated crop.

Furthermore, the superiority of improved varieties depended on the criteria used. If yields per hectare were used, they were better, but if yields per hectare per day were used they performed equal to the traditional early varieties.

A final remark with respect to risk and uncertainty concerns replanting. Many farmers purchase their seed in common grocery stores or store it for almost a year at the farm. Germination of this seed is very variable. With early varieties the possibility to replant, without facing drought problems, is greater than with late varieties.

ICTA has been aware of the value of earliness, especially after the introduction of the first BGMV resistant lines. Their efforts to produce more early varieties are indeed a very appropriate response to these needs (Ruiz et al., 1988).

Crop management

Early varieties provide four obvious advantages in crop management. In rotations, an early variety will provide more time to prepare and plant the next crop. The benefits of such earliness will be expressed in the yields of the next crop, as well as in the monetary costs of production (less need to hire labor).

Early varieties, many of which are of type III growth havit, may cover the field more rapidly and will need less weed control. This advantage might be expressed in the yield of the bean crop, but more probably will impact on the cost of production per hectare.

In crop associations the early variety will be harvested more quickly and provide less competition. This will result in increased yields for the associated crop. One must note that earliness in associations might also impact negatively, if the early bean variety is more competitive with other crops shortly after planting than a late variety would be.

Finally earliness might help to escape the build-up of insects and diseases to economic damage levels. In this case bean yields might increase and the cost of insect and disease control might be reduced.

A salient observation with respect to earliness for crop management is that it impacts mainly on costs of production and yields of other crops. Organizing research along commodity lines is beneficial in many aspects, but might incorrectly reduce the attention for the interaction with the rest of the farm system.

Capital and labor use

For almost all small farmers in the developing world capital is extremely scarce. Banking services (credit and savings) are insufficiently provided. Early varieties partially resolve these problems. Since they can be harvested earlier, they provide a higher rate of return and make borrowing more feasible. As well they allow the farmer to pay back his loans rapidly and reduce the costs of interest. Thirdly the income from an early bean crop might be an intermediate source of financing, for example to pay for fitosanitary control in other crops. Finally it provides cash to the farmer at an early moment in the production cycle. This allows the farmer's family to make consumer spending earlier in the year and facilitates cash flow management.

Labor is a resource that small farmers appear to possess abundantly. Although the overall ratio of labor to land is high, farmers often face periods in which labor is needed in many activities. These are almost always the periods of the year when other farmers are also occupied, so it is difficult to hire labor. For bean production, planting and harvesting are peak periods in the year. Early varieties that can be planted later in the year allow the farmer to grow a larger area of beans, by extending the planting season. If the planting period is extended the harvest period will be extended as well.

Earliness also affects labor in another way. Farmers might be active in employment outside their farms, for example as a day laborer or a rural assembly agent. For example in Brazil it appears that small farmers obtain up to 65% of their income from off-farm activities (Schuh, 1988). In many regions small farmers immigrate temporarily to other areas, to earn an income in the harvest of other crops. It is clear that each day saved in the production of his crops is an extra day of income in the alternative employment.

For Latin American agriculture labor productivity has critical value. The ratio of urban consumers to rural producers has grown rapidly over the last 30 years. Farmers now need to be more productive to supply sufficient food to the urban markets. As well, labor productivity influences strongly the agricultural income. If this income does not increase enough, migration of farm labor to the urban areas will continue and might make the continent more dependent on imports.

Land use

In Asia early maturing rice crops allowed the inclusion of a third crop in the production cycle. In many rainfed areas such intense cropping might be impossible, but early varieties might still allow a double crop instead of a single.

As is the case with labor and capital productivity, increasing land use is complex. An example from Ipiales, the extreme south of Colombia, will be used to illustrate such complexity.

Table 2 shows two traditional crop systems and two experimental crop systems for this region. In order to intensify bean production (system 2), a new system (3) was developed in which the climbing bean is replaced by an earlier bush bean. Since it was not possible to find a maize variety that was compatible in duration and quality, the bush bean was grown in monoculture. After the bush bean is harvested a second crop can be planted of barley or potato. Alternatively a production system, in which promising climbing beans and maize are intercropped, was designed (4).

The production system which includes the bush bean (3) occupies the land for more time. It is effective in increasing the land use through the year. Its benefits are higher than for the traditional production system, on a per hectare as well as a per day basis. The alternative production system (4), however, produces even higher net benefits per hectare and per day. As well it has lower cash costs than the system with the bush bean.

What is the chance of success of the land use increasing production system? For several reasons, this does not look promising. Cash costs are higher (risk!) and benefits per day increase only marginally. On the other hand, the system needs harvest and planting labor when farmers are harvesting potato and planting barley (Production system 1). While production system (1) provides the barley with the residual fertility of the potato crop, bush beans will not provide such residual fertility, since they are not as heavily fertilized as potato. Finally farmers use the bean/maize field for animal grazing during the remainder of the year. This could be practiced for some 120 days in the traditional system and only 40 to 70 days in the new system.

Besides, there is an alternative beans/maize production system that has higher expected benefits. Although this system does not increase land use through the year, it makes more intensive use of it during the crop cycle by means of an association. Not only land use through the year but also intensity of use matters.

Earliness has imminent potential to increase land use by intensifying the crop cycle. To understand this potential the farm system needs to be analyzed as a whole, and advantages for specific crop systems need to be compared with what happens to the other crop systems in the farm. Of course such analysis is highly location specific.

Food availability through the year

The importance of earliness for food availability through the year can be demonstrated with an example from Africa (Bittenbender et al., 1984). When the crop is in its vegetative growth stage, farmers eat bean leaves. Later on, when pods are being filled, green pods are consumed. When the crop reaches maturity, green shelled beans are eaten. Finally when the dry beans are harvested and dried, dry beans are eaten.

In a system where people rely on beans for part of their food needs from so early on, the importance of early varieties is obvious. It should be stated that for food availability purposes it is very advantageous if the early materials are complemented with late materials that provide food after the harvest period.

Sales opportunities

Earliness improves the sales possibilities for the individual farmer. This can be appreciated in figure 1, that shows average monthly bean prices at wholesale level in Bucaramanga, Colombia from 1982 to 1987 for the variety Radical). The harvest concentrates around July (first cycle) and December (second cycle). At both harvest periods, prices at wholesale level tend to drop. For a farmer it is advantageous to sell his beans early, since this might cause a 20% difference in the price he receives. Not only the higher price matters to the farmer. If he offers his beans before the majority of farmers offers beans, he will need less effort to sell, will face less quality restrictions and will have a higher chance of cash payment, because traders still have money instead of beans.

Earliness as a means to improve sales opportunities is a doubtful strategy. If only a limited group of farmers have access to early materials, they will sell at higher prices. Nevertheless, if all farmers will have obtained access to the early materials, a demand for even more early materials will arise. This might eventually lead to an "early to market" trap, where yield potential is continuously sacrificed for marketability. Furthermore, early materials appear to have smaller grain size on average than late materials, which further affects the viability of earliness as a means to improve sales opportunities (Kornegay, 1988). However, to increase the feasibility of a new varietal introduction, earliness is very important. If farmers are market oriented they will not quickly accept a variety that delays their market access.

Alternatives to earliness

Earliness is appreciated by farmers for many reasons, as described in the previous sections. Farmers are willing to sacrifice yield potential or nitrogen fixation capacity in order to obtain their harvests at an earlier stage. Why is earliness so appreciated? To a large extent this can be understood by studying the alternatives to earliness.

With respect to risk, alternatives to earliness are: a better root systems (drought); a crop insurance system; a high quality seed distribution system to avoid replanting.

With respect to the crop management aspects of earliness, one might consider protective inputs, education and to some extent other crops.

Efficient resource use was treated as a major reason for preferring early varieties. As an alternative to efficient land use one might consider improved fertilizer availability or land reform programs. For more efficient labor use, mechanization can be considered. Earliness to reduce capital needs can be substituted by improved credit availability and by the existence of loans at reasonable interest rates.

Food availability through the year can be improved with storage methods or with food distribution and credit (for food purchases) schemes. Finally the wish of the farmer for early varieties in order to sell at better prices could be substituted with market support schemes.

Earliness forms an alternative to many different things, from mechanization to crop insurance. Earliness is attractive to many farmers because it combines different alternatives in one trait. The various alternatives to earliness are probably more difficult both to manage and to understand. As well many of the alternatives fall outside the scope of the individual farmer and need to be supplied at the community level.

In total fourteen alternatives to earliness were mentioned, nine of which have a large or almost complete institutional dimension. Market support programs for example are absent in many countries or function badly. In conclusion, for the individual small farmer earliness is the alternative to a great range of institutional solutions. It is the answer of the small farmer to the underdeveloped agricultural sector in which he operates. This also suggests that if institutional arrangements improve, the farmers demands for earliness will probably be reduced.

Measuring the Value of Earliness

The author of this paper is not aware of studies that explicitly try to measure the economic value of earliness. Three reasons come to mind to explain the absence. Firstly, economic methodologies are often developed in the temperate zones and afterwards applied in the tropics. Since earliness is less important in temperate zones, there methods were probably never developed. Secondly, measuring the benefits of earliness is very difficult, because it has so many different dimensions. Thirdly, as described in the previous section, earliness is the poor farmers answer to deficient institutional arrangements. This means it is a "second-best solution". Most economists are more interested in studying well-functioning markets and institutions than in studying a "second-best solution".

Some suggestions on measuring the value of earliness can be made. One can study the evidence of adoption. How many kilograms per hectare extra needs to be harvested to compensate for a certain lack of earliness? For example, ICTA-Quetzal in Guatemala is an improved variety with reasonable diffusion, however without replacing the traditional varieties. It yields some 320 kg more per hectare but is 25 days later. It then appears that in Guatemala a day earliness has a value of some 13 kg.

The problem with this method is that aside from length of growth cycle and yield, other differences (grain size, resistance) might be involved in the comparison. This can be avoided by the use of elicitation methods, which are also often used in risk analysis (Binswanger, 1980). In these methods farmers opinions on the relative value of earliness versus yield are elicited. This is done for hypothetical situations. This brings the advantage that other differences are not involved but the disadvantage that the comparison is artificial.

A completely different way to measure the value of earliness is by studying and questioning farmers on objectives, activities, attitudes, resources and constraints. On the basis of this information a farm model can be built which represents farmer behavior. In this model the effect of early varieties can be simulated. In comparison with the previously described methods, this method offers more understanding of why farmers like early materials. However, the methodological procedure is more complex; the procedure is normative (it includes a decision-rule); and it is very difficult to specify a complete farm model.

Conclusions

Earliness has many dimensions. It can improve labor, land and capital use, limit risk and insecurity, facilitate crop management, supply food shortly after planting and improve market prospects. In breeding for earliness it is very important to know what dimension is being aimed at, in order to make a rigorous assessment of (breeding or institutional) alternatives. It should be very clear that it is much more than a drought escape mechanism.

To understand earliness, it is not enough to study the bean crop, not even the bean association. Earliness often is valued because it improves the organization of the farm system and it facilitates farm management. In an equal way, studying the farm system might help to understand why earliness is not needed.

Earliness can be usefully combined with "lateness". If early varieties are used to spread the planting period, to obtain food rapidly, or to have access to intermediate capital for production purposes, it is not necessary that all beans planted are early. Also a farmer might have plots with different water retention capacity. He could plant early varieties on the dry land and late ones on the humid land.

From a socio-economic perspective earliness appears, more than a drought escape mechanism, an "institutional deficiency" escape mechanism. For many farmers earliness is a way to deal with badly functioning markets, credit input and mechanization services. This suggests that crop improvement should be integrated in more comprehensive development plans. The institutional components of such plans could focus on credit use and mechanization, reducing the objectives and the constraints for the crop improvement component.

Earliness has a price. Most clearly this is appreciated in the reduced yield potential. Where the institutional deficiencies are big and the need for earliness great, farmers are willing to pay a high price for earliness. Unfortunately, the author is not aware of economic studies that have tried in a systematic manner to estimate the price of earliness.

In Latin America earliness has large potential to increase labor productivity. Even on small farms productivity is constrained by seasonal peaks in the labor film. If earliness can contribute to the reduction of these seasonal peaks by spreading agricultural activities through a larger part of the crop season, this will have strategic value in the struggle to increase small farm income.

Finally, earliness has to be associated with poverty. Poor people live from day to day and will not wait until next week, if they can obtain something tomorrow. It is well known that the inability to save and invest is strongly correlated with poverty. The ultimate conclusion is that earliness does not correspond with the expression "time is money" nor with "haste makes waste". It corresponds with both at the same moment. Often it helps people to survive from day to day and year to year. However if they could do without earliness, this might well imply that they had reached substantially better living conditions.

References

Binswanger, H.P. 1980. Attitudes towards risk; Experimental measurement in Rural India. American Journal of Agricultural Economics, vol 62 (3) pp. 395-407.

Bittenbender, H.C., R.P. Barret, B.M. Indire-Lavasa. 1984. Beans and cowpeas as leaf vegetables and grain legumes. East Lansing, Michigan State University, Bean/Cowpea CRSP, monograph No.1.

CECORA, 1988. Internal price data, Bogota, Colombia.

Kornegay, J. 1988. Personal communication, CIAT, Cali, Colombia.

Ruiz, M., A. Viana and S.H. Orozco. 1988: Aceptacion y pronostico de impacto en Guatemala con la variedad de frijol ICTA-Ostua, paper presented at the PCCMCA-meetings, 21-25 March, San Jose, Costa Rica.

Schuh, G.E. 1988. Agricultural Development and Technology Demand in Latin America towards the year 2000: some issues presented to NARDS think tank, CIAT, Cali, Colombia. October 3-7, 1988. Mimeograph.

Viana, A., S.H. Orozco and D. Pachico. 1986. El impacto tecnologico y economico de las nuevas variedades de frijol generadas y transferidas para agricultores del sur-oriente de Guatemala, Centro America. Mimeograph, CIAT, Cali, Colombia.

Zandstra, H.G., E.C. Price, J.A. Litsinger and R.A. Morris. 1981. A methodology for on-farm cropping systems research. IRRI, Los Baños, The Philippines.

Acknowledgments

To Abelardo Viana, CIAT-Guatemala, who has been emphasizing earliness since 1984 and who provided valuable suggestions for this paper.

Table 1. Yields per hectare of different bean types in different cropping systems. In Southeast of Guatemala, 1985.

	A (first semester)[1]			B (second semester)	
	Early varieties	Intermediate varieties	Late varieties	Traditional varieties	Improved varieties
Monoculture	1350	1818	1038	976	1464
Association with maize	1364	909	1402	864	1135
Association with sorghum and maize	1122	1364	1243	694	990
Association with sorghum	1092	779	1266	841	1179
Average yield	1232	1218	1237	844	1192
Average yield per day	19.0	15.6	13.7	13.0	13.2

[1] No specific reference to traditional or improved varieties.

Source: Internal data, Bean Economics, CIAT.

Table 2. Traditional and experimental production systems, Ipiales, Colombia 1988.

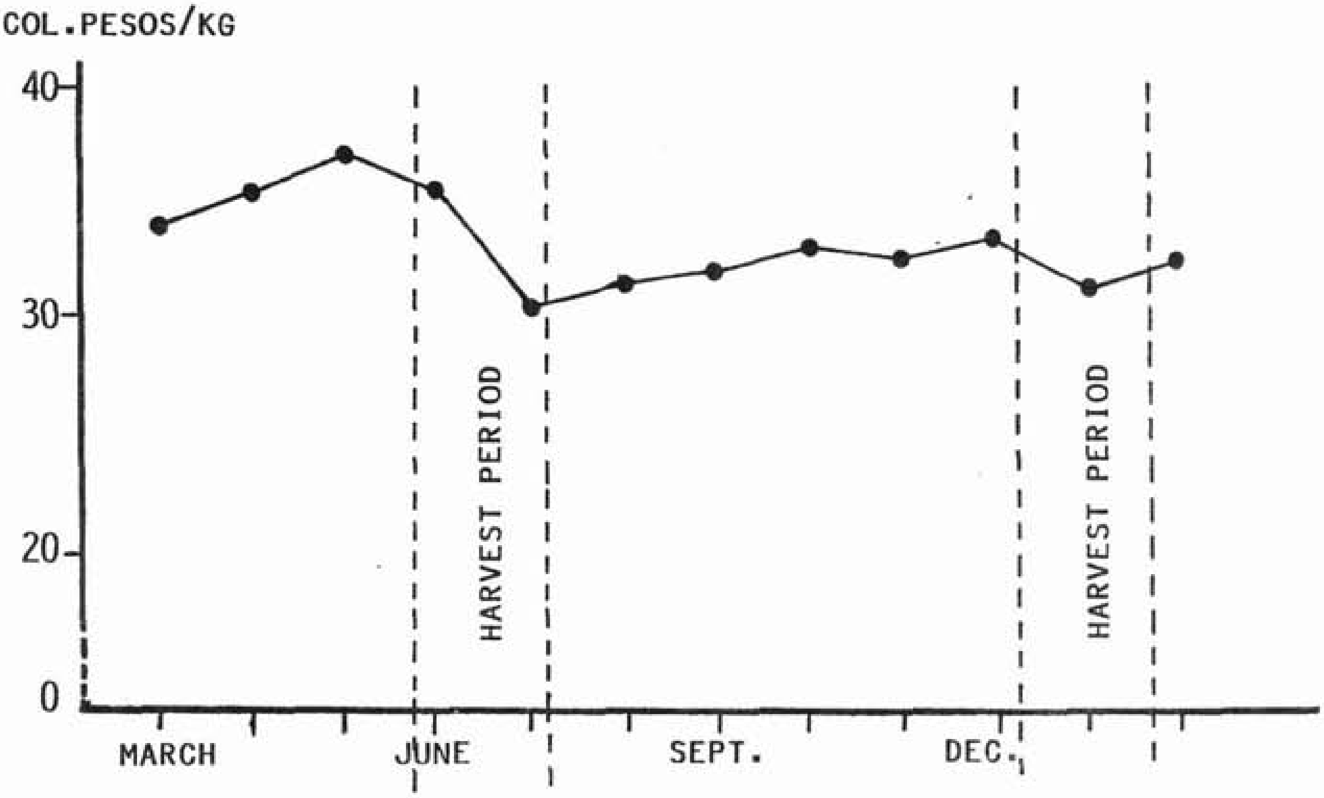
	Traditional		Experimental	
	(1) Potato followed by barley	(2) Beans associated with maize	(3) Bush beans followed by barley or potato	(4) Improved beans associated with improved maize
Duration (days)	150 + 120	245	165 + 135	220
Net benefit (US$/ha)	n.a.	703	970	1046
Cash costs/ Total costs	n.a.	0.32	>0.45	0.32
Net benefit/day (US$/ha/day)	n.a.	2.87	3.23	4.75
Residual fertility	yes	--	no	--
Period available for cattle grazing (days)	70	120	40 - 70	145

Source: Internal data, Bean Cropping Systems, CIAT.

Figures

Fig. 1. Colombia: average prices per month 1982-1987. Radical, Bucaramanga.

FIGURE 1. COLOMBIA: AVERAGE PRICES PER MONTH 1982-1987
RADICAL, BUCARAMANGA



SOURCE: CECORA, BOGOTA

35667

PHYSIOLOGICAL ASPECTS OF EARLINESS IN COMMON BEAN

Jeffrey W. White*

Introduction

Recent interest in developing early maturing bean cultivars has raised many questions related to the physiology of bean crops. Foremost is whether earliness really offers advantages which offset the apparently inherent loss of yield potential associated with short growth cycles. Accepting that earliness is desirable, one can ask how to breed cultivars which combine the desired level of earliness with acceptable yield potential. This problem has two facets where physiology research might help. The first concerns genetic and environmental effects on bean phenology. Given that beans are typically short day crops, effects of photoperiod are of particular concern. The second facet is whether certain morphological or physiological characteristics can be identified which breeders can use as selection criteria for yield in early maturing materials. This paper reviews available information on these physiological questions.

The Relation Between Yield and Maturity

In the absence of marked seasonal variations in stresses, notably drought or low temperatures, late maturing bean genotypes typically out yield similar, but earlier maturing materials by substantial amounts. As an example, Figure 1 presents data from a yield trial of 42 genotypes varying in maturity from 52 to 83 days at CIAT Palmira. This difference in maturities was associated with a yield difference of nearly 2000 kg ha^{-1},

---

* Crop physiologist, CIAT, A.A. 6713, Cali, Colombia.

giving a linear correlation of r = 0.80 (p = 0.01).

Another illustration of the same trend is found in the review of Laing and co-workers (1984). Using photoperiod treatments to delay flowering of Porrillo Sintetico, they found that a 10 day delay in maturity was associated with a 1000 kg ha^{-1} increase in yield. Further examples are discussed by White and Izquierdo (in press), and the phenomenon is well known in other crops (Charles-Edwards, 1982).

Given the strong evidence for the loss of yield potential with earliness, it is imperative to seek evidence for benefits of earliness which would compensate for the expected loss of yield potential. One situation where early maturing genotypes can out yield later maturing ones is when a major stress increases in strength during the crop cycle, and early maturity results in at least partial "escape" of the stress. Drought and freezing temperatures are the most obvious examples, but for any disease or pest problem which increases in severity over time, early maturity also might permit escape.

Circumstantial evidence for drought escape in beans is found in drought screening nurseries (White and Castillo, 1988). When yield and maturity are compared, a negative relation is frequently found although many exceptions occur. As a single example, Figure 2 shows a significant negative correlation between yield and maturity for 72 genotypes evaluated under drought at Palmira. A simple analysis of precipitation and potential evapotranspiration for five day periods during the growth cycle indicated that starting approximately 25 days after planting, there was a 40 day period with only 22 mm of precipitation but a potential evapotranspiration of 193 mm.

A particularly interesting case of drought escape is shown by P. acutifolius. Independent studies conducted in Honduras and at CIAT have found that some genotypes of P. acutifolius are much earlier than typical lines of P. vulgaris, and that this may explain some of the drought adaptation associated with P. acutifolius (Zuluaga et al., 1988; White and Castillo, 1988).

Rather than ask whether drought escape through earliness is a useful characteristic, a more productive approach is to ask under what conditions drought escape is useful. Unfortunately, the response to this question is very site specific since it depends on such variables as rainfall distribution, soil moisture retention, and willingness of farmers to take risks.

Instead of attributing usefulness to earliness based on escape from a single stress, it can also be argued that earliness permits escape from a wide range of stresses which may vary in importance from season to season. One approach for studying such an effect is through analysis of multilocation yield trials. Using a Finlay and Wilkinson (1963) type analysis one would expect early maturing cultivars to show lower regression responses (B) and smaller deviations from regression (D).

In a review of date from seven years of International Bean Yield and Adaptation Nurseries (IBYANs), only the 1975 IBYAN produced a significant relation between mean days to maturity and B (White, 1984; Fig. 4), and no significant correlations were found for D. This apparent lack of relations between earliness and stability was attributed to the typically very narrow range of maturities found among genotypes of individual IBYANs.

This question has only received limited attention in other crops. Working with 54 sorghum genotypes in 48 environments, Saeed and Francis (1983) found that more than half of the variation in B was attributed to maturity effects, and D was also affected by maturity.

Control of Earliness

If it is accepted that earliness is a desirable character to seek in common beans, the question arises of how to breed for earliness for a given region. Although such work could be done on a strictly empirical basis, information on the genetic control of earliness and on effects of photoperiod and temperature could improve efficiency of breeding.

Studies on the inheritance of earliness in common bean are few. However, only two or three major genes seem to be of concern. One or two genes have a direct effect on maturity, while another appears to modify phenology indirectly through effects on growth habit.

Masaya et al. (1986) reported that for the cross ICTA Quetzal x Rabia de Gato, earliness was dominant and controlled by a single gene when evaluated at a site with a mean temperature of $29^{o}C$. Recent work at CIAT (White et al., in preparation) with 19 early maturing indeterminate genotypes seems to confirm this. Using test crosses of the early genotypes with A 301 (as the female parent), all 19 F1 populations flowered and matured almost as early as the respective early parent. The F2 populations were slightly less early, but were still much earlier than the mean of the two parents (Table 1). Further studies are needed to determine whether the same pattern of inheritance is found in determinate genotypes, and whether the different early parents share the same dominant allele.

Another gene known to have a major effect on phenology is the one governing the shift between indeterminate to determinate growth habit. Most studies have suggested that the determinate habit is recessive, showing a 3 to 1 segregation ratio, and is associated with a 5 to 8 day increase in earliness (e.g. Bliss, 1971). However, recent work suggests that exceptions to the pattern of inheritance of stem type do occur (O. Ortiz, 1988, personal communication).

Understanding the basic control of earliness is an important step in predicting how early the progeny of a cross will be. However, given known effects of temperature and photoperiod on phenology in common bean, it is easily anticipated that identifying the basic genes controlling earliness will prove insufficient, particularly when materials are grown under different photoperiod or temperature regimes. For example, Figure 4 presents data for evaluations of time to maturity for 25 early genotypes grown at Cotaxtla, Veracruz, Mexico (E. Lopez S., 1988, personal communication) and at CIAT Palmira. Although the overall correlation is highly significant (r = 0.68, p = 0.01), some genotypes shifted their maturity as much as eight to ten days relative to other materials. Furthermore, in this case, photoperiod response does not appear to have an obvious association with these shifts. Further examples are found in Masaya et al. (1986) where segregation ratios were found to vary when populations were grown at two sites differing in mean temperature.

Our knowledge of effects of photoperiod and temperature on phenology is not yet at the stage where one can predict phenology for any genotype under a given set of environmental conditions (Masaya and White, in press). However four principles provide some guidance:

1. Each genotype has a characteristic minimum time to flowering ("tendency to flower", "maximum flowering rate"). This is expressed under short photoperiods and, typically, warm temperatures. Problems with instability of earliness tend to occur as delayed flowering, not excessive earliness.

2. For photoperiod sensitive genotypes, if daylengths are greater than a critical minimum length, flowering will be delayed.

3. Higher temperatures increase sensitivity to photoperiod. This effect is most dramatically expressed in Andean materials adapted to cooler regions.

4. Independent of the effect on photoperiod sensitivity, rate of development increases with temperature. Thus, if no confounding photoperiod effect occurs, warmer temperatures hasten flowering and maturity.

In selecting for earliness, the worst problems with instability would probably occur when materials are selected under short photoperiods (low latitudes or winter cropping seasons) and then moved to long ones. However, in some cases temperature effects will certainly be an additional confounding factor.

Inheritance of photoperiod response in beans requires further study, but most evidence suggests that two genes are involved (Wallace and Masaya, 1987, personal communication). Considerable variation in photoperiod sensitivity occurs within early maturing materials (Table 1).

Selection Criteria for Yield in Early Materials

Given that early maturity implies loss of yield potential, the need to find efficient ways to select for yield under earliness is even stronger than for when maturity is not a factor. If precautions are not taken, selection for yield will undoubtedly lead to loss of the desired earliness.

Following suggestions for ways to increase yield potential in genotypes with normal maturity, one approach is to suggest specific plant characteristics which partially determine the potential of yield of early maturing genotypes. To date, the only attempt to formulate a list of hypotheses relating yield to characteristics of early maturing lines appears to be that of Rodriguez (1986) who compared growth of 13 early genotypes and 3 normal ones in two semesters at CIAT Palmira. Testing such hypotheses is not as simple as one might think because they implicitly contain the sub-hypothesis that not only does a characteristic affect yield, but that this effect varies with length of the growth cycle of individual genotypes. For example, it is insufficient to say that a high harvest index is desirable; it must be decided whether harvest index should be relatively greater in early or late maturing genotypes. The simplest way to test such hypotheses is through multiple regressions. Using yield as the dependant variable, a test for significant effects of maturity, of the characteristic in question, and of the maturity by characteristic interaction should suggest whether the characteristic is of special importance in early materials. Significance of the interaction with maturity is the critical test since it indicates whether the effect of the characteristic varies with length of growth cycle.

To illustrate this approach, five hypotheses were examined using data from the same trial of 42 genotypes presented in Fig. 1. The hypotheses were:

1. Relatively long podfilling: Since yield is highly correlated with length of podfilling period, but early maturity implies a shortening of the podfilling period, the relative proportion of the growth cycle allocated to podfilling should be increased in earlier maturing genotypes. (The proportion of the growth cycle represented by the podfilling period is defined as length of the podfilling period divided by days to maturity).

2. High growth rate: The short growth cycle places a strong limit on overall growth, so a high growth rate is imperative. One rough index of the growth rate is biomass at maturity.

3. Higher harvests index: Again, since growth is limited, what growth does occur must be converted efficiently into yield, and the harvest index should be especially high. Furthermore, with a smaller plant size, less structural support is needed. This should also permit a higher harvest index in early genotypes.

4. Larger seeds: Early maturity implies a reduced period for vegetative establishment. Since large seed size should permit a greater initial crop growth rate, large seeds might be particularly desirable in early maturing genotypes.

5. Fewer seeds per pod: With a shortened podfilling period, the rate with which individual pods can be filled might be limiting. Thus it would be desirable to have smaller, but more numerous, pods. Since it was already argued that larger seeds are desirable, the only alternative is to have fewer seeds per pod.

The analyses of variance for variables associated with these five hypotheses are presented in Table 2. In all cases, the maturity effect is very large. The only hypothesis where a significant effect of other variables was found was for crop dry weight. No interaction with maturity was found for any of the five characteristics. Taking these results at face value, one would conclude that all of the hypotheses have to be rejected. A more generous conclusion is that such analyses should be attempted for a wider range of trials.

The related problem of how to select directly for yield in early materials when higher yields will be associated with later maturity is also approachable through regression analysis. This approach seems superior to the more conventional one of calculating yield per day (yield divided by days to maturity) or yield accumulation during podfilling (yield divided by length of the podfilling period) not withstanding the apparent popularity of such indices (e.g. Wallace and Masaya, 1988; CIAT, 1987).

Yield per day suffers from an important bias which frequently favors late maturing genotypes, but depending on the actual relation between yield and maturity in a given trial, can also favor early or intermediate genotypes. This bias is best illustrated by considering a line representing a constant level of yield per day on a graph of yield vs days to maturity. Such a line is exactly equivalent to defining a fixed limit for selection based on yield per day. In Fig. 5 the data from Fig. 1 are replotted including the origin on the two axes, and a line for yield per day = 25 kg ha^{-1} is drawn. This line passes through the origin, as will any line for a constant yield per day. This is shown by rearranging the definition of yield per day (YPD) as a function of yield (Y) and days to maturity (M).

$$YPD = Y/M,$$

thus becomes

$$Y = YPD * M,$$

which is the equation of a line through the origin and with slope of YPD. Cultivars lying above the line in Figure 5 thus have yields per day greater than 25 kg ha^{-1} day^{-1} (e.g. RAB 60), and those lying below, less than 25 (e.g. G 2923). For this set of data, if we imagine successive lower limits of yield per day, it is clear that all of the late maturing genotypes will be selected first.

The type and seriousness of the bias varies from trial to trial, according to the actual relation found between yield and days to maturity. Replotting the two semesters of data from Rodriguez (1986), one finds that in the first semester use of yield per day would again favor late maturing lines (Fig. 6a), while in the second semester, little bias would occur because the relation between yield and days to maturity would define a line similar to that of constant yield per day (Fig. 6b). For the case where no relation between yield and days to maturity is found, here illustrated by data from Masaya and co-workers (1988), selection based on yield per day would probably favor early maturing lines (Fig. 7).

Fortunately, regression analysis offers a simple and more robust alternative. If the regression for yield as a function of days to maturity is calculated (Fig. 1), the residual values for each genotype (deviations from the regression) are equivalent to yields corrected for a maturity effect. Thus, superior genotypes will simply be those with the largest positive residuals. The results of using different criteria for selection are evident in Table 3, where very different sets of genotypes would be selected depending on whether yield per day, yield in podfill, or deviations from regression are used.

In most trials, a linear model should be adequate, but where both early and late genotypes are disadvantageous (as may happen at higher latitudes), addition of a quadratic term to the model may be necessary. Analogous arguments hold for selection based on yield accumulation during podfilling. In this case though, days to maturity is replaced by duration of podfilling.

Conclusion

Breeding for earliness is an important and exciting opportunity for bean breeders. Although physiological studies of earliness are few (due in part to the paucity of early genotypes with minimal levels of disease resistance), existing physiological information should help breeders achieve their goals more efficiently.

There seems no question that drought escape through earliness is a useful characteristic. However, studies are needed to indicate what levels of earliness are needed for a given production area. Arguments for the value of earliness as a more generalized escape mechanisms seem plausible, but hard data are lacking.

The basic genetic control of earliness seems relatively simple, and many early genotypes are already known. Perhaps more problematic than achieving earliness at a given site will be the task of unravelling effects of temperature and photoperiod when early materials are planted in environments different from those they were selected under. It should be born in mind that many materials which are early at CIAT show intermediate to high photoperiod sensitivity.

We are still regrettably far from being able to suggest an ideotype for early maturing genotypes. Hypotheses are easy to generate, but correct testing is more problematic. One promising approach is to use a multiple regression, permitting testing for the desired interactions with maturity.

Finally, bean breeders should not underestimate the problem inherent in breeding for yield in early genotypes due to the fact that yield usually varies directly with maturity. The traditional use of yield per day seems of dubious value, but again, regression analyses or use of maturity as a covariate in ANOVAs show promise.

References

Bliss, F.A. 1971. Inheritance of growth habit and time of flowering in beans, *Phaseolus vulgaris* L. J. Am. Soc. Hortic. Sci. 96:715-717.

Charles-Edwards, D.A. 1982. Physiological determinants of crop growth. Academic Press; Sydney. 161 pp.

CIAT. 1987. Annual Report 1986 Bean Program. Working Document No. 27. CIAT; Cali, Colombia.

Finlay, K.W. and G.N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res. 14:742-754.

Laing, D.R.L., P.G. Jones and J.H.C. Davis. 1984. Common bean (*Phaseolus vulgaris* L.) p. 305-351. In P.R. Goldsworthy and N.M. Fisher (eds.). The physiology of tropical field crops. John Wiley & Sons; New York.

Masaya, P.M., D.H. Wallace and J.W. White. 1986. Genetic control of flowering behavior of tropical bean cultivars under two subtropical temperature regimes. Annu. Rept. Bean Improv. Coop. 29:54-55.

Masaya S., P.M., R. Rodriguez C., G. Galvez, S.H. Orozco and C. Orellana. 1988. Potencial de rendimiento y estabilidad de precocidad de algunas variedades tradicionales y poblaciones de frijol en Centroamerica. Paper presented at the XXXIV Reunion Anual del PCCMCA, San Jose; Costa Rica.

Masaya, P.M. and J.W. White. Adaptation to photoperiod and temperature. In A. van Schoonhoven and O.V. Voysest (eds.). Bean (Phaseolus vulgaris L.) production and improvement in the tropics. CIAT; Cali, Colombia. (In press).

Rodriguez C., R.R. 1986. Caracterizacion morfo-fisiologica e identificacion de caracteres para mayor rendimiento en genotipos precoces de frijol comun (Phaseolus vulgaris L.). M.Sc. Thesis. Colegio de Postgraduados; Chapingo, Mexico. 178 pp.

Saeed, M. and C.A. Francia. 1983. Yield stability in relation to maturity in grain sorghum. Crop Sci. 23:683-687.

Wallace, D.H. 1985. Physiological genetics of plant maturity, adaptation and yield. Plant Breed. Rev. 3:21-167.

Wallace, D.H. and P.N. Masaya. 1988. Using yield trial data to analyze the physiological genetics of yield accumulation and the genotype x environment interaction effects on yield. Annu. Rept. Bean Improv. Coop. 31:vii-xxiv.

White, J.W. 1984. Associations among yield, yield stability and duration of growth cycle in IBYAN trials. p. 380-400. In International bean trials workshop. CIAT; Cali, Colombia.

White, J.W. and J. Castillo. 1988. Studies at CIAT on mechanisms of drought tolerance in bean. p. 146-164. In J.W. White, G. Hoogenboom, F. Ibarra and S. Singh (eds). Research on drought tolerance in common bean. Documento de Trabajo No. 41. CIAT; Cali, Colombia.

White, J.W. and J. Izquierdo. Physiology of yield potential and stress tolerance. In A. van Schoonhoven and O.V. Voysest (eds.). Bean (Phaseolus vulgaris L.) production and improvement in the tropics. CIAT; Cali, Colombia. (In press).

White, J.W. and P. Masaya. Adaptation to photoperiod and temperature. In A. van Schoonhoven and O.V. Voysest (eds.). Bean (Phaseolus vulgaris L.) production and improvement in the tropics. CIAT; Cali, Colombia. (In press).

White, J.W., S. Singh and C. Pino A. Inheritance of earliness in indeterminate bush common bean (Phaseolus vulgaris L.). (In preparation).

Zuluaga, S., C.M. Elvir, C. Rodriguez S. and J.D. Erazo. 1988. Investigaciones sobre tolerancia a sequia en frijol en Honduras. p. 69-90. In J.W. White, G. Hoogenboom, F. Ibarra and S. Singh (eds). Research on drought tolerance in common bean. Documento de Trabajo No. 41. CIAT; Cali, Colombia.

Table 1. Days to maturity of 19 early genotypes, A 301, and respective F_1 and F_2 populations from crosses with A 301 grown at CIAT-Palmira (White et al., in preparation).

					Days to maturity			
Early genotypes	Origin	Growth habit	Seed weight	Photo. resp.[1]	Early geno.	A 301	F_1	F_2
			mg					
Aguascal. 11 4	Mexico	3	250	S	56	70	58	60
G 2923	El Salvador	2	260	N	55	70	63	60
G 3017	Guatemala	3	220	N	56	70	60	62
Orgulloso	Nicaragua	3	280	N	56	70	61	62
O.C. Sta. Rita	Mexico	3	350	S	56	70	58	60
G 1345	Nicaragua	3	220	N	57	69	59	62
G 1344	Nicaragua	3	200	N	58	69	62	66
Zacaticano	Mexico	3	300	S	58	71	58	60
O.C. 24 MV	Mexico	3	350	S	59	69	59	62
Pata de Zope	Guatemala	3	230	N	59	72	66	66
Chile 20	Chile	3	270	S	59	72	62	61
A 59	CIAT	2	270	I	60	71	62	64
G 1965	Guatemala	2	290	I	60	75	63	64
Dilmason	Turkey	3	330	S	61	71	61	65
BAT 304	CIAT	3	200	I	61	72	63	65
RAB 60	CIAT	3	230	N	61	71	61	66
Rabia de Gato	Guatemala	3	200	N	61	72	64	66
Cuarenteno	Nicaragua	3	350	I	62	71	63	65
Favinha	Brazil	3	410	S	64	71	62	65
Mean					59	71	61	63

[1] Photoperiod response summarized from CIAT scale of 1 to 8, where N (1 or 2) is day neutral, I (3 or 4) is intermediate in sensitivity, and S (5 to 8) is photoperiod sensitive. Scores are based on delay in flowering under 18 hour, artificially extended photoperiod at CIAT Palmira.

Table 2. Results of multiple regressions on yield for five variables hypothesized to have interactions with days to maturity. Based on data for 42 genotypes at CIAT-Palmira.

Source of variation	DF	Mean square	F
Proportion of cycle as podfilling (PROPOD)			
Days to maturity	1	6054347	67.5**
PROPOD	1	4923	0.1
PROPOD x maturity	1	7550	0.1
Residual	38	89638	
Crop dry weight at maturity			
Days to maturity	1	6054347	124.3**
Crop dry weight	1	1519564	31.2**
Crop dry weight x maturity	1	7721	0.2
Residual	38	48696	
Harvest Index			
Days to maturity	1	6054347	76.8**
Harvest index	1	267308	3.4
Harvest index x maturity	1	154261	2.0
Residual	38	78872	
Seed Weight			
Days to maturity	1	6054347	71.5**
Seed weight	1	1	0.0
Seeds weight x maturity	1	203214	2.4
Residual	38	84619	
Seeds per Pod			
Days to maturity	1	6054347	70.4**
Seeds per pod	1	90822	1.0
Seeds per pod x maturity	1	60480	0.7
Residual	38	85985	

** Significant at the $p = 0.01$ level.

Table 3. Comparison of days to flower and maturity, yield, and three parameters used to correct for effects of length of growth cycle on yield. Yield in podfill is yield divided by duration of podfilling. Deviation from regression is the residual from regression of yield as a function of days to maturity.

Genotype	Days to		Yield	Yield per day	Yield in podfill	Deviations regression
	Flower	Maturity				
			kg ha-1	--kg ha-1 day-1-		kg ha-1
G 4524	40	82	2351	28.6*	55.5x	-272
PVAD 1028	34	73	1785	24.7	46.4	-80
BAT 304	33	72	1794	25.1*	46.5	16
BAT 37	38	71	1888	26.5*	55.9x	132
G 3807	38	71	1860	26.1*	56.1x	120
NAG 30	36	71	1847	26.0*	52.0x	109
XAN 141	34	71	1802	25.3*	49.2	73
XAN 145	38	71	1920	27.3*	58.2x	217+
A 260	35	70	1986	28.0*	55.8x	302+
XAN 146	35	70	1970	27.9*	56.4x	294+
RAO 14	35	70	1416	20.2	40.5	-253
PVAR 1479	32	70	1325	18.9	34.8	-343
RAB 60	34	70	2135	30.5*	59.6x	470+
G 6416	32	70	1447	20.8	38.5	-185
G 1965	31	69	1248	18.0	32.7	-364
A 496	30	69	1466	21.3	37.4	-139
DOR 200	36	69	1663	23.9	50.5x	72
G 12494	30	69	1452	20.9	37.3	-137
PVAR 1474	33	69	1317	18.9	36.6	-271
BAT 41	35	69	1867	27.0*	55.3x	286+
BAT 1388	32	69	2007	29.2*	53.6x	433+
G 577	31	69	977	14.3	26.1	-562
PVBZ 1776	33	68	1686	24.7	48.0	151
A 59	32	68	1293	19.0	36.4	-205
G 2858	31	68	1811	26.7*	48.6	324+
A 186	31	67	1441	21.4	39.8	1
PVAD 823	32	67	1357	20.4	38.8	-63
PVMX 1604	31	67	1959	29.3*	55.1x	561+
G 1344	31	67	1181	17.6	33.3	-209
G 4450	31	65	1300	19.8	38.5	20
G 1621	31	65	611	9.6	18.0	-619
G 274	31	64	716	11.1	21.6	-472
G 7121	30	64	1270	19.8	37.9	92
G 51	30	64	1565	24.4	46.5	391+
G 57	31	64	1192	18.8	36.4	22
G 1345	31	63	1461	23.0	45.5	327+
G 122	30	63	1112	17.6	34.0	8
G 4965	32	60	594	9.9	21.1	-315
G 2923	30	60	1222	20.3	40.7	344+
G 3017	29	59	890	15.4	30.0	116
G 3255	31	59	372	6.5	13.4	-394
G 2883	27	52	263	4.9	10.4	-1

* Genotypes selected using yield per day over 25 as criterion.

x Genotypes selected using yield in podfill over 50 as criterion.

\+ Genotypes selected using deviation from regression over 200 as criterion.

Figures

Fig. 1. Relation between yield and days to maturity for 42 genotypes grown at CIAT Palmira.

Fig. 2. Relation between yield and days to maturity for 72 genotpes grown under drought conditions at CIAT Palmira. A. Yield vs days to maturity. B. Distribution of rainfall during the cropping season.

Fig. 3. Relation between regression coefficient for yield and days to maturity for the 20 genotypes of the 1975 IBYAN.

Fig. 4. Comparison of days to maturity for 25 early maturing genotypes grown at Cotaxtla, Ver., Mexico and CIAT Palmira. The symbols N, I, and S indicate day neutral, intermediate, and sensitive photoperiod response as described in Table 1.

Fig. 5. Relation between yield and days to maturity illustrating the bias introduced by using yield per day as a selection criterion. The line corresponds to a constant yield per day of 25 kg ha^{-1} day^{-1}. Data are for 42 genotypes grown at CIAT Palmira.

Fig. 6. Relation between yield and days to maturity illustrating the bias introduced by using yield per day as a selection criterion. Lines are for constant yield per day as indicated. Data are for 16 genotypes grown at CIAT Palmira grown two semesters in 1985, and are from work of Rodriguez (1986). A. Semester A. B. Semester B.

Fig. 7. Relation between yield and days to maturity illustrating the bias introduced by using yield per day as a selection criterion. The line is for a constant yield per day of 20 kg ha^{-1} day^{-1}. Data are for 122 genotypes grown at Jutiapa, Guatemala as described by Masaya el al. (1988).

Figure 1.
Relation between yield and days to maturity for 42 genotypes grown at CIAT Palmira.

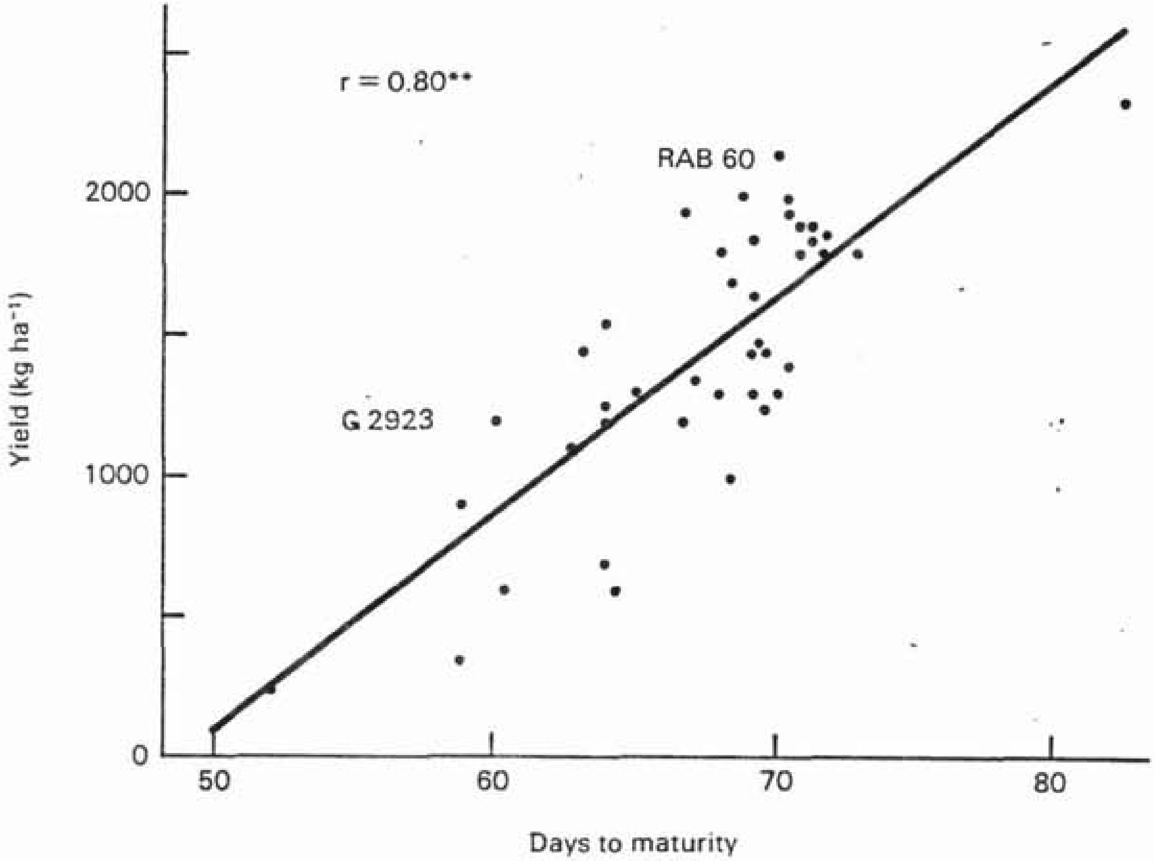


Figure 2A.
Relation between yield and days to maturity for 72 genotypes grown under drought conditions at CIAT Palmira.

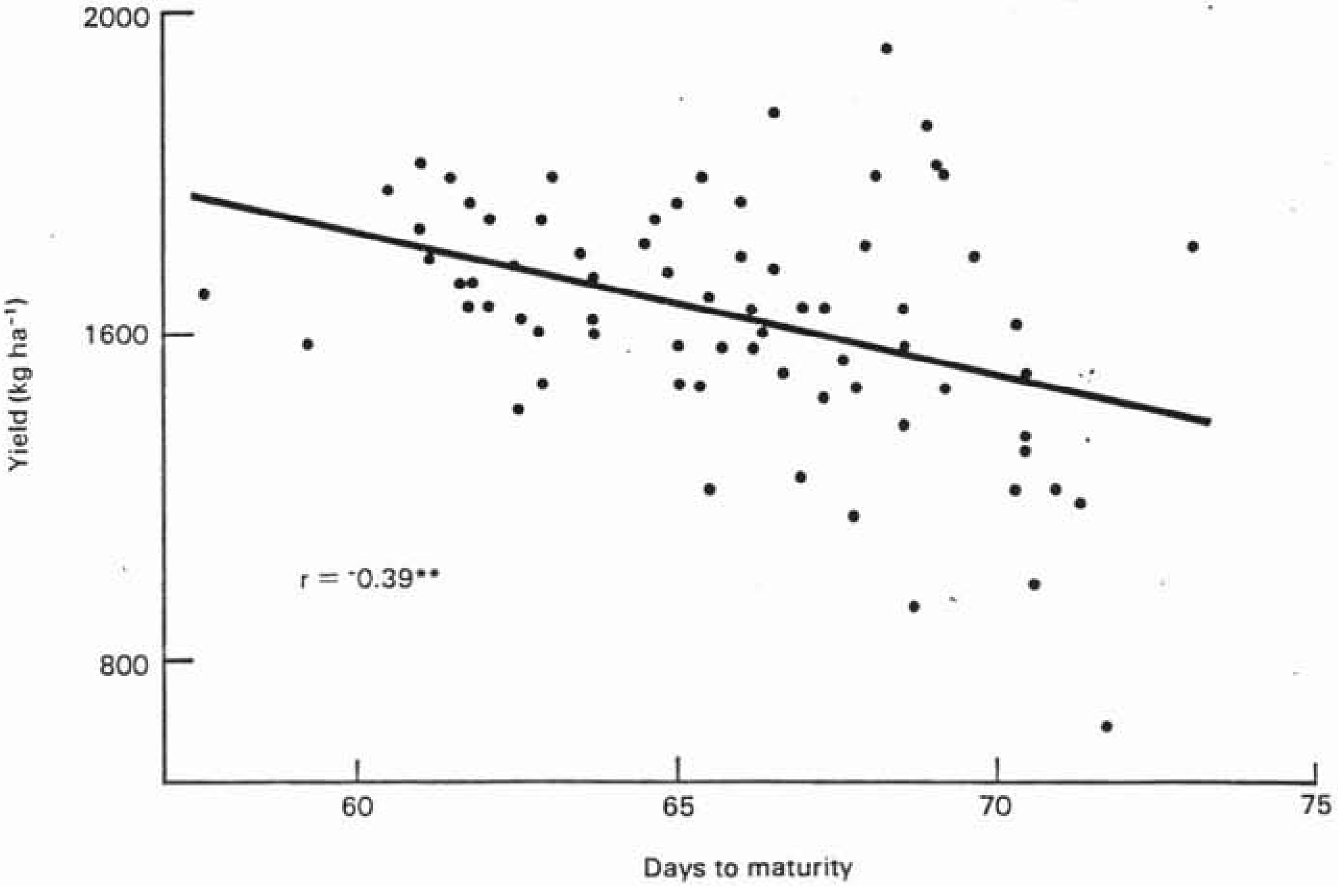


Figure 2B.
Total potential evapotranspiration and actual precipitation for the drought trial with 72 genotypes at CIAT Palmira.

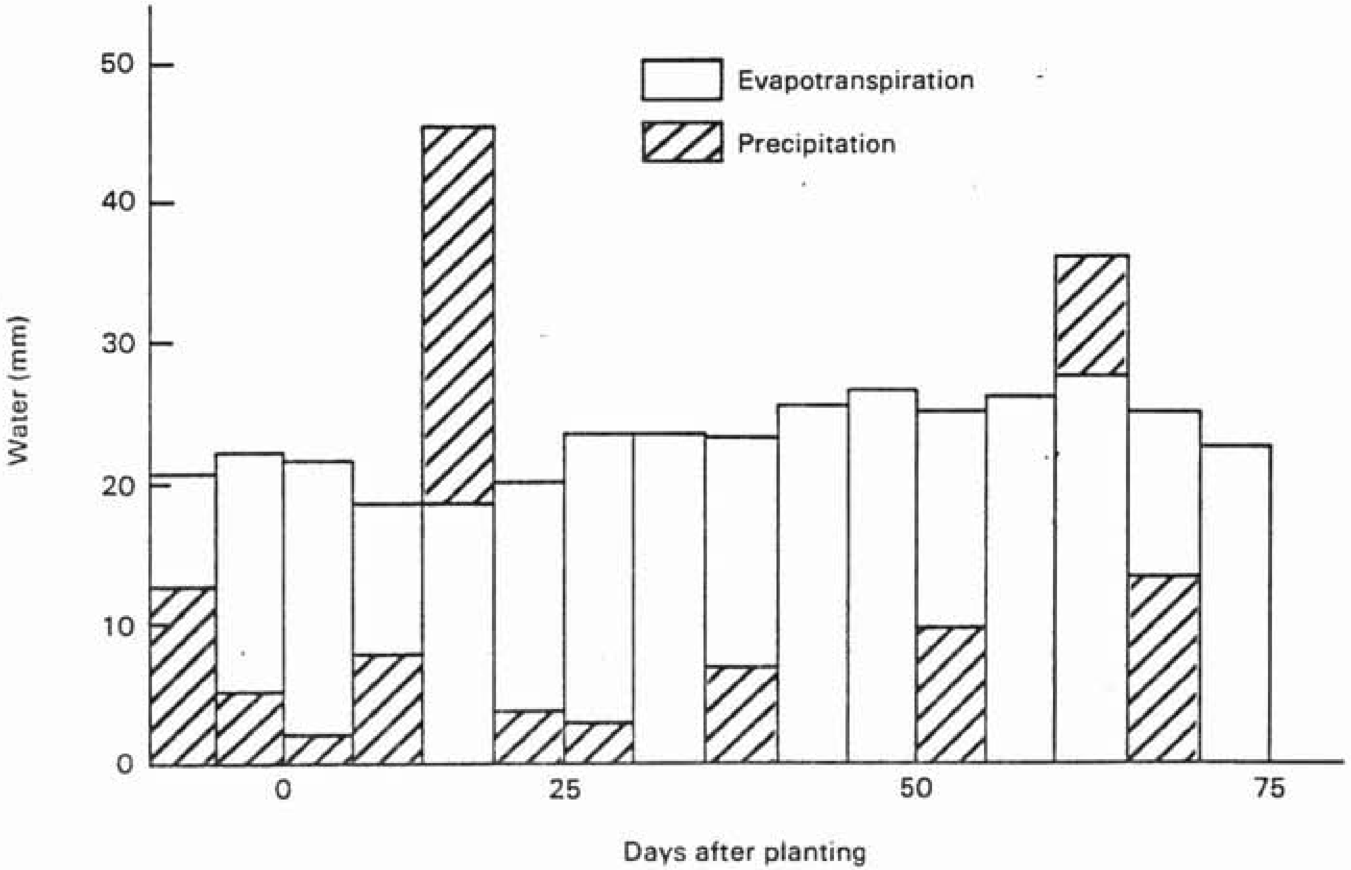


Figure 3.
Relation between regression coefficient for yield and days to maturity for genotypes of the 1975 IBYAN.

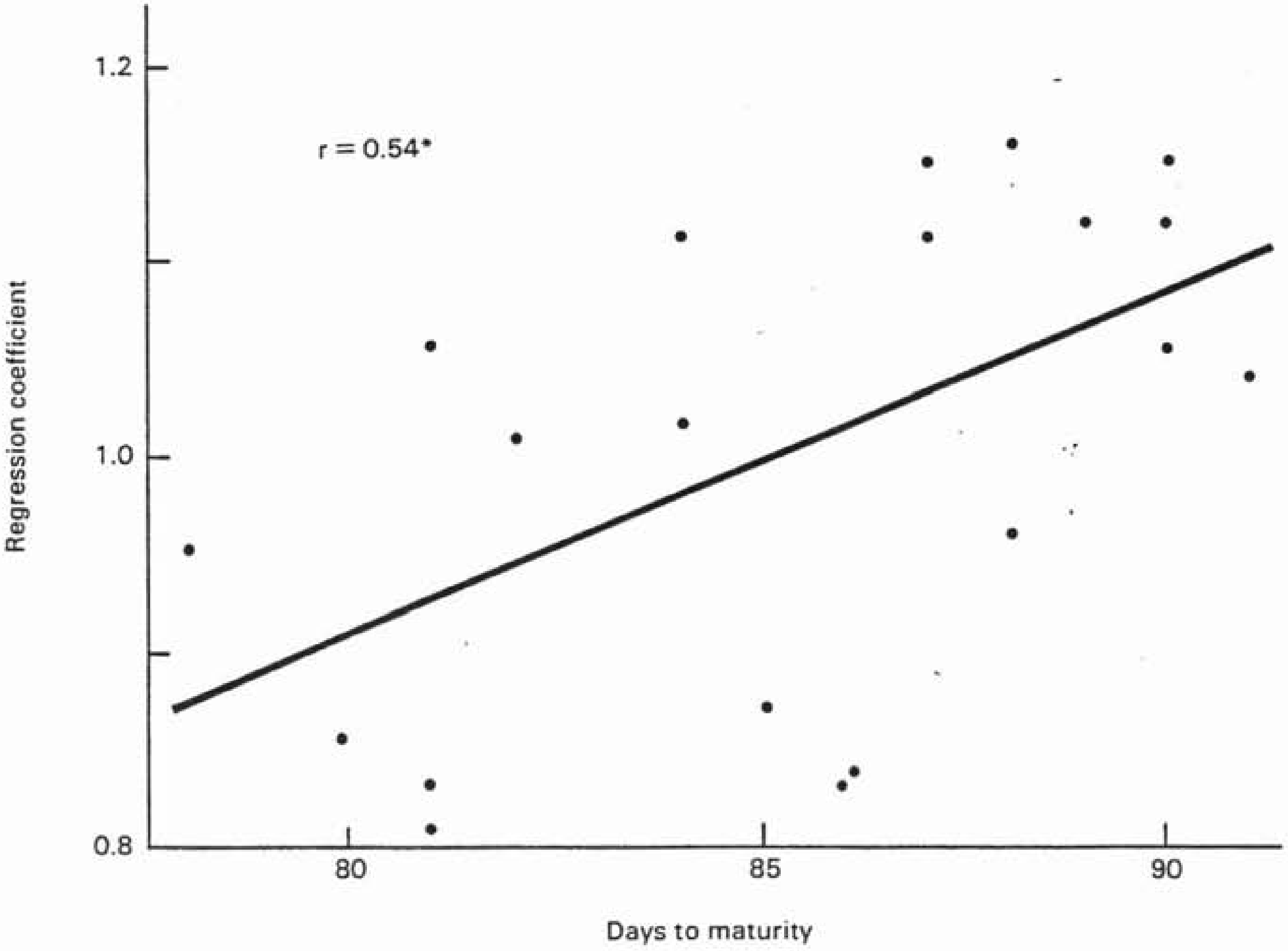


Figure 4.
Comparison of days to maturity for 25 genotypes grown at Cotaxtla, Veracruz, Mex. and at CIAT Palmira.

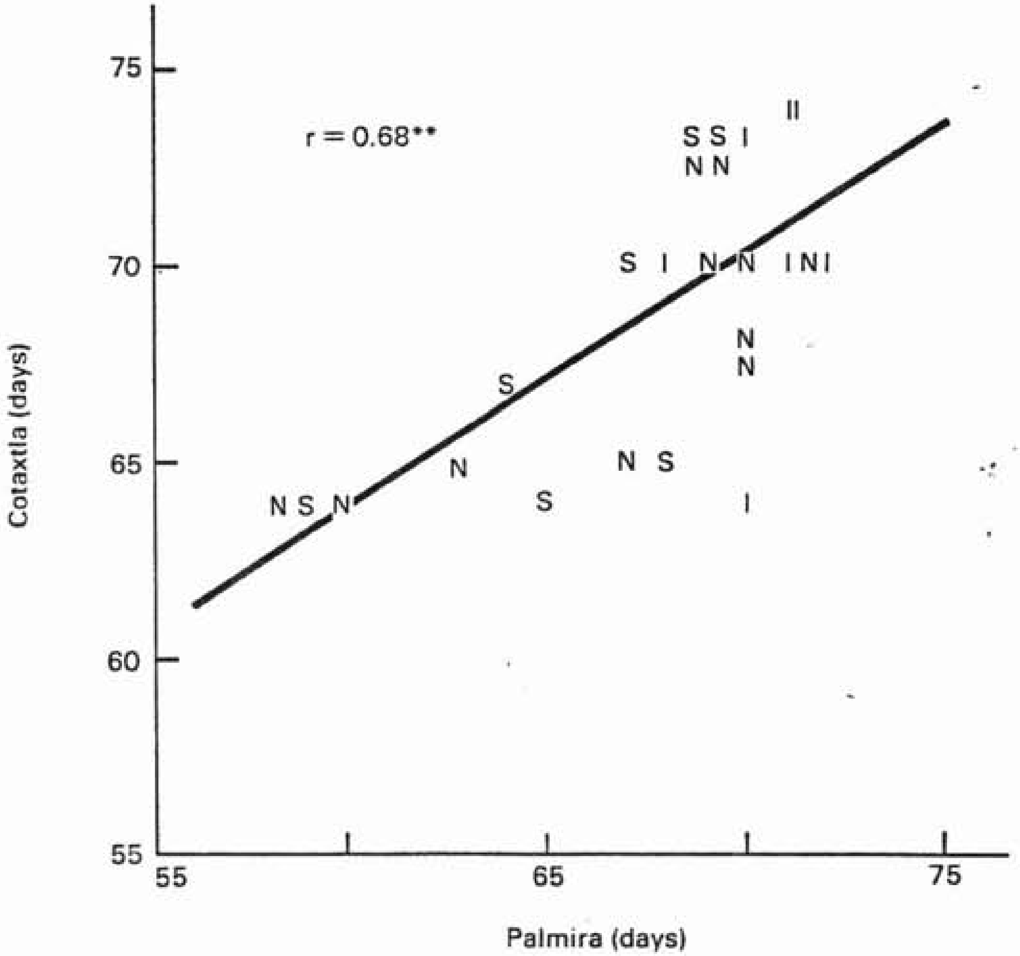


Figure 5.

Relation between yield and days to maturity illustrating the bias introduced by using yield per day as a selection criterion. 42 genotypes at CIAT Palmira.

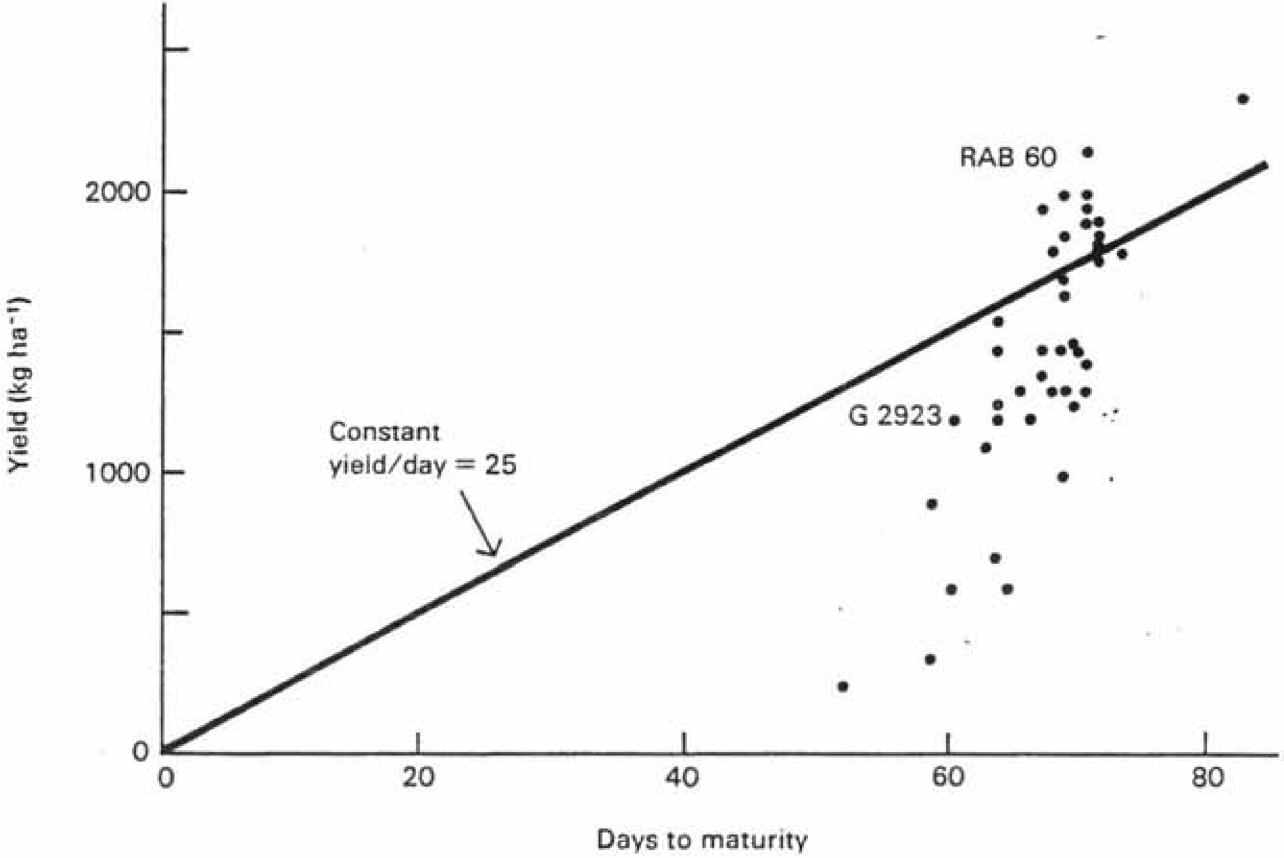


Figure 6A.
Relation between yield and days to maturity for 16 genotypes grown at CIAT-Palmira, 1985a. From Rodríguez (1986).

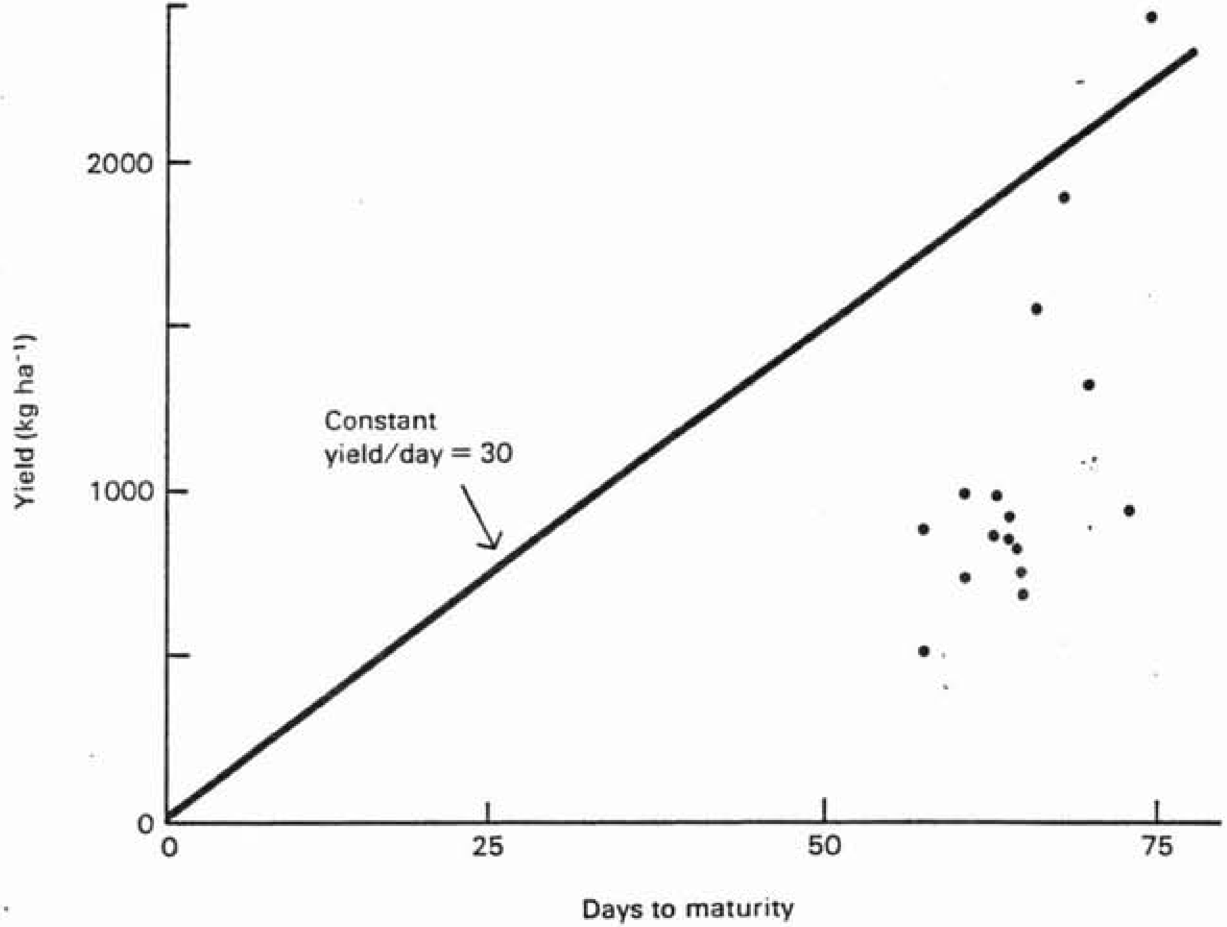


Figure 6B.
Relation between yield and days to maturity for 16 genotypes grown at CIAT-Palmira, 1985b. From Rodríguez (1986).

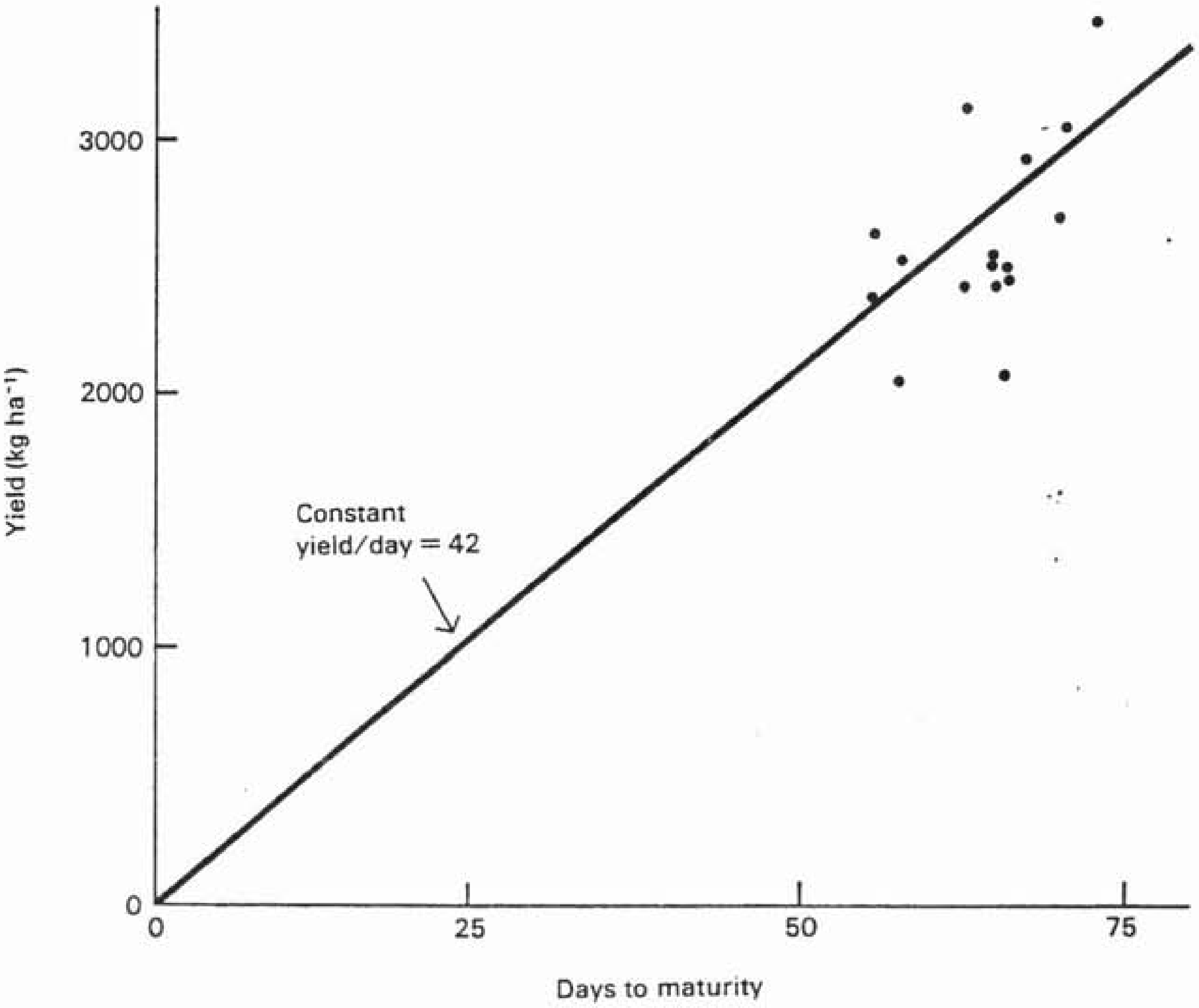
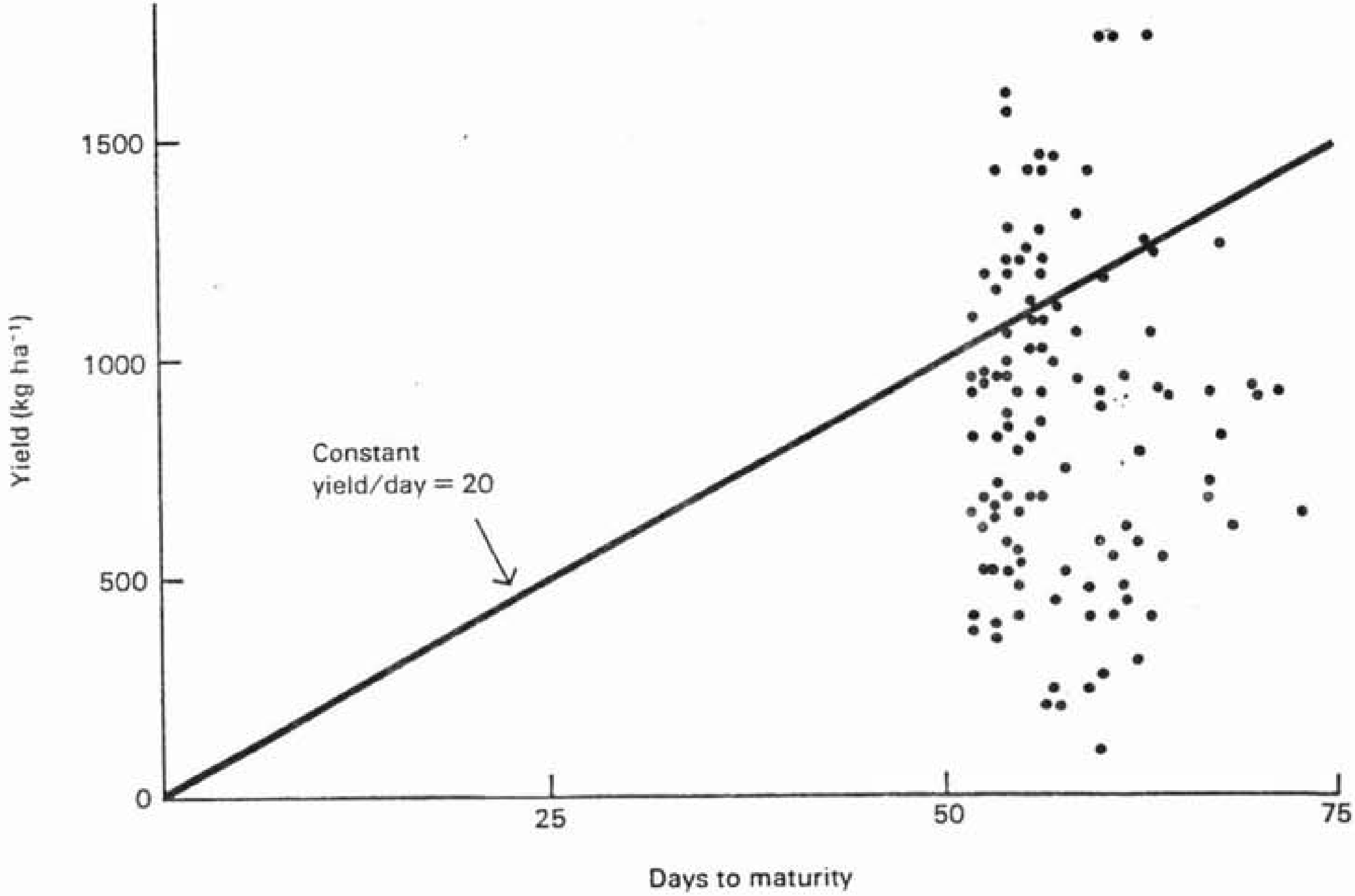


Figure 7.
Relation between yield and days to maturity for 112 genotypes grown at Jutiapa, Guatemala. Based on data from Masaya et al. (1988).



35668

THE DEVELOPMENT OF EARLY-MATURING VARIETIES FOR CENTRAL AMERICAN AGRICULTURAL SYSTEMS

Porfirio Masaya*

1. Introduction

Bean production in Central America has certain traits in common throughout the five countries.

a. The majority of production occurs from April to November.
b. Small grain types II and III of the Mesoamerican class ("S" phaseolin group gene pool) are predominantly grown.
c. It is a crop for small farms.
d. Production in mixed systems or in sequential crops is common.
e. Frequently, the family which produces bean at the same time consumes a significant portion of the volume produced.

In the Dominican Republic, Cuba, and, in a recent period, Guatemala, an appreciable quantity of production comes from plantings that are made during the dry season under irrigation, which begins in October, taking advantage of some rains in climates under the influence of winds which move from north to south during the Northern Hemisphere's winter.

In all the Central American countries and the Caribbean, governments are facing the dilemma of maintaining food prices, at levels low enough for poor people in urban centers, and at the same time of improving living conditions for producers of these low-cost foods, who are poor farmers.

---

* Breeder, Bean Program, ICTA, Apartado Postal 231 "A", Zona 10, Guatemala, Guatemala.

This situation and growing pressure on tillable land stimulate the development of intensive production systems in which a crop cycle limits options, so that another relay crop can occupy the same land area during the favorable climatic season.

In the case of common bean, current varieties are adapted to zones with average temperatures around 23°C. These temperatures occur in the American tropics at elevations between 800 and 1400 meters above sea level. These are zones of small valleys surrounded by mountains, in which mechanization that permits a lowering in cost of food production has not been able to extend itself. The coastal plains or lowlands that can be mechanized are too hot and humid, or too frequently lack roadways or present deficiencies or excesses of some mineral element, or they have an inadequate pH. In these zones, weed control and adequate drainage are also problematic.

As a consequence of this situation, the necessity of developing early-maturing varieties with resistance to the principal diseases and pests in the region, an erect architecture, and high yield potential has been suggested. The Regional Bean Cooperative Program of Central America, Mexico, and the Caribbean began a project to help resolve the urgency of this varietal problem in 1987.

2. Phenology, Adaptation, and Yield

The agricultural value of a bean variety is defined by the harmony between the two most integral physiological processes in the plant: growth and development. Growth has been defined as the irreversible increase in cell, organ, or plant size. Development is the irreversible change in functions or form of a cell or group of plant cells.

In the testing of crop varieties, we often talk about adaptation, understanding for adaptation the capacity of the plant to achieve its vital functions in a given environment. When we consider common bean, an annual senescent plant which we grow from its seeds, we should understand adaptation as the ability of the plant to germinate, grow, flower, and form fruits and seeds.

On the other hand, the farmer defines adaptation of bean varieties by their capacity to grow, flower, and produce seeds within the limits of his agricultural system. These limits are defined by climate, soil, and socioeconomic characteristics of the farm.

In Central America and the Caribbean, the necessity has arisen for bean varieties that can be adapted to crop rotations or to short rainy periods, giving origin to the search for early varieties. It also happens that the bean plant type that adjusts itself to such requirements is more efficient but will require improved agronomic management for being a noncompetitive type visualized as a high-yielding ideotype (Donald, 1968).

3. Genetic Control of Flowering Time and Maturity

Maturity time in *Phaseolus vulgaris* is determined by a tendency to flower, with a basic development pattern as follows.

3.1 Determinate growth versus indeterminate growth

3.1.1 *Determinate varieties*. In determinate varieties, the recessive gene *fin* determines differentiation of the apical meristem in an inflorescence. The dominate allele *Fin* codifies for vegetative growth in the apical meristem. It is possible that there exists a reproductive terminal meristem which is never produced under normal cropping conditions in indeterminate cultivars. The stimulus codified by the *fin* gene is probably necessary for differentiation of the terminal meristem as a reproductive structure but not sufficient for ulterior differentiation of different floral structures, such as sepals, petals, anthers, and stigma

(Bidwell, 1974).

3.2.1 Indeterminate varieties. Indeterminate varieties lack a gene for differentiation of an apical floral meristem. The *Fin* gene present in these plants permits the maintainence of apical dominance for vegetative growth. Therefore these varieties continue growing and forming nodes on the main stem in a prolonged manner.

3.2 Modulation of flowering by photoperiod and temperature

Multiple research work that has been carried out on photoperiodness in several species (Bidwell, 1974; Ojehomon, 1966) and that which has been carried out on *Phaseolus vulgaris* (Vince-Prue, 1975) allows us to draw some conclusions.

There exist at least two *loci* in the plant which codify for the response to conditions of photoperiod and temperature. At least one allele in each locus provokes delay in the development of the floral meristem which normally is differentiated first. In determinate varieties (Type 1), said floral meristem occurs in the axil of the highest node in the main stem (Evans, 1975). In indeterminate varieties, said floral meristem occurs in the axil of the first trifoliolate leaf of the main stem (Masaya and Wallace, 1984), when the average temperature is from 16-18°C.

According to results for other vegetable species, we can imagine that in the bean plant, in indeterminate varieties, an unknown substance which acts as a floral stimulus activates genes for differentiation of a meristem in the axil of the first trifoliolate leaf. This floral stimulus is synthesized in the leaves and is transported to the meristem. Once the synthesis and transfer process is initiated, its effects are permanent and irreversible (Bidwell, 1974). Nevertheless, the subsequent activation of the same genes, or perhaps different genes for the ulterior differentiation of the different floral structures, seems necessary. There are indications that the interaction of sugars and hormones is needed for the complete setting in motion of the initiation of flowering (Bidwell, 1974).

There are also indications that the optimum of temperature for development of floral structures and fruit growth is lower than the optimum for growth of stems and leaves in all the plant species. Probably as a result, when the bean plants grow in temperature regimes higher than 16-18°C, branches are developed in the axils of the first trifoliolate leaf and the subsequent leaves instead of floral racemes. This is presented in Table 1, with data taken from a study carried out in Guatemala in 1983.

According to this hypothesis, nondifferentiation of the axillary meristem of the first leaf in the main stem owes itself to the increase in net photosynthesis without a corresponding increase in the number of nocturnal inductive cycles having occurred. It should be noted that this is an effect of temperature on growth and development.

Photoperiod also has a similar effect. Long days are in reality short nights. According to what is known about the action mechanism of the photoperiod and the phenomena associated with photoperiodicity, we can interpret the experimental results observed as an interaction between higher photosynthesis during the day and a shorter, and therefore weaker, inductive cycle.

The effect of long days thus has a double mechanism. On one hand, the most prolonged light period produces a larger quantity of products of photosynthesis accumulated during the day. On the other, a short night (associated with a longer day) reduces the quantity of synthesized floral stimulus (see Table 3). The participation of the products of photosynthesis in the induction and differentiation processes is well known (Bidwell, 1974). In the case of bean, the effect of photosynthesis on floral induction can also be noted by the effects of any treatment or cultural practice which might increase photosynthesis over the position of the first inflorescence in the main stem. For example, the use of supports in comparison with growth as a prostrate plant increases net photosynthesis measured as an accumulation of biomass and also results in the appearance of the first inflorescence in the main stem in a higher node, indicating a delay in floral induction (Table 2). The most intense photosynthesis produced a physiological delay, in induction and/or differentiation of the inflorescences, but not a delay in time, since the number of days to the first flower was essentially equal.

We can then conclude that average temperatures higher than 16-18°C, as well as daylength duration beyond 12 hours, delay induction physiologically toward floral meristems and differentiation of floral structures. This process takes place in so-called "sensitive" as well as insensitive varieties. Unfortunately, these processes have remained ignored by breeders and emphasis of research in previous years has been centered almost exclusively in phenology of the crop.

The number of days required for anthesis will then be the result of the number of day-night cycles required (inductive cycles) and the growth rate of the floral primordia. The alleles present in "sensitive" varieties require a larger number of inductive cycles and/or longer and hotter nights.

Insensitive varieties are a synonym for early varieties. These varieties flower in approximately 28 days under temperature conditions around 24°C. Under regimes of average temperature lower than that, flowering is delayed.

4. Earliness and Yield

Improved bean varieties produce maximum yields if they combine a spatial distribution of the leaves which allows taking maximum advantage of light and CO_2 in the spaces between the different leaves or levels of leaves, with an optimal duration of growth and a maximum efficiency of accumulation of photosynthesis toward seeds. Early varieties have high efficiency but small size. Plant size is strongly defined by the number of nodes in the plant, and this is defined by the number of days between germination and flowering and by temperature.

Central American farmers prefer an early variety, but perhaps they are not aware that yield is reduced, in comparison with late varieties, unless planting distances are changed, possibly along with the quantities of fertilizer applied.

The term "earliness" has been used freely, being necessary to define for each production area the number of days which define the time of maturity.

The different alleles that surely exist for the at least two loci that are influenced by long days produce profound changes in the size and morphology of a plant, even when corresponding changes in phenology may not be profound. In bean, genetic effects on the rate of development of floral structures are associated with effects on the size and distribution of biomass in the plant. The use of simulation models, testing variations in rates of development, has confirmed this (Wallace, 1985).

5. Priorities of Future Research

Researchers and bean breeders can have a better understanding of necessities in each production region if they agree on defining production environments or, better yet, adaptation environments, and if at the same time types of maturity in common bean are defined.

Genetic effects would be visualized better if we knew the principal effects of genes with response to photoperiod and temperature. Taking into account the principle in biological systems toward simpleness and saving of energy, it does not seem probable that genes which carry out equal functions in the plant may have been duplicated. Although superficial observation of the effects on phenology might give the impression that the different genes with response to photoperiod and temperature have similar vital functions (from a point of view of their usefulness to survival of the species), surely they differ in their functions or in environmental factors to which they respond.

There is evidence that different genes exist, with effects of different intensities on phenology, but whose effects on distribution of biomass and morphology we can exploit in breeding. This means, for example, that we can select early cultivars, but ones that are sensitive to photoperiod with local adaptation to each adaptation region. Some examples can be cited. The variety Pata de Zope (G 37) is an early type in southeastern Guatemala ($23^{O}C$ - 13.5 hours), but late (sensitive) in the United States, and it seems to respond more to longer days than to high temperatures.

The variety San Martín is an early type in the highland of Guatemala ($16\text{-}19^{O}C$ - 13.5 hours), but late and unadapted in low coastal zones, and it seems to respond more to high temperature than to longer days. The important thing to point out in this case is that both varieties are considered early types in the zone of their adaptation and commercial cropping.

For some breeders, the early-maturing types are also the most efficient and therefore the ideotype for high yield. The reduced number of leaves allows better light interception even in the lower leaves and better development of pods. Nevertheless, the majority of early Central American varieties are of growth habit type II or III, and their architecture is rather poor. One of the immediate high-priority objectives should be the development of a significant number of lines with erect architecture and early maturity. There is evidence that the combination of both characters is feasible. These lines should show some kind of delay in flowering so that pods can develop from the third node of the main stem, and they should avoid losses through rotting.

Once this group of early erect lines exists, it is necessary to investigate planting density, mainly varying the distance betweeen rows to compensate for yield loss caused by a shorter growth period. These studies should include the study of fertilizing options.

References

Bidwell, R.G.S. 1974. Plant Physiology. McMillan; New York.

Donald, C.M. 1968. The breeding of crop ideotypes. Euphytica 17:385-403.

Evans, L.T. 1975. Crop Physiology. Cambridge Univ. Press; London.

Masaya, P. and D.H. Wallace. 1984. Effect of elevation (temperature) on number of days to and node of flowering in beans. Bean Improv. Coop. 27:199-202.

Ojehomon, O.O. 1966. The development of flower primordia of Phaseolus vulgaris. Ann. Bot. 30:487-492.

Vince-Prue, D. 1975. Photoperiodism in plants. McGraw-Hill; New York.

Wallace, D.H. 1985. Physiological genetics of plant maturity, adaptation and yield. Plant Breed. Reviews 3:21-166.

Table 1. Insertion node of the first flower in plants of three bean varieties grown under various average temperature regimes in Guatemala.

Place	Average Temp. °C	Variety Rabia de Gato	 San Martín	 JU-80-11
Tecpán	15	2.0	2.1	2.8
Chimaltenango	19	2.0	3.8	4.7
Guatemala	21	3.6	4.2	5.5
Jutiapa	24	3.6	4.2	5.6
Mita	26	3.7	6.8	6.9
Cuyuta	29	6.0	10.9	7.7

Masaya, P. y Wallace, D.H. 1984.

Table 2. Accumulated biomass at the end of the life cycle, node where the first inflorescence in the main stem appears, and number of days to flowering in bean cultivars, sensitive and insensitive to long days under two growth conditions in Palmira, Colombia.

Cultivar	Flowering	Total g/plant	Node of the first flower
JU-78-12 (insensitive)			
No support	43.0	101	8.7
With support	43.0	180	8.7
GI7648 (sensitive)			
No support	42.0	87	9.3
With support	42.0	151	11.0
XAN 112 (sensitive)			
No support	41.3	106	8.0
With support	42.0	174	8.7

P. Masaya and J.W. White, 1985. Unpublished data.

Table 3. Position of the first raceme on the main stem in three varieites of bean plant under three photoperiod treatments.

Cultivar	12.5h (a)	13.5h (b)	14.5h (b)
JU-18-12	7.7	8.3	8.7
G17648	6.7	9.0	11.0
XAN 112	6.3	6.7	8.7

(a) Natural photoperiod.

(b) Natural photoperiod and extension with artificial lighting.

P. Masaya and J.W. White, 1985. Unpublished data.

BASIC CONCEPTS IN QUANTITATIVE GENETICS RELEVANT TO COMMON BEAN BREEDING

Julia Kornegay*

Introduction

Bean breeders are well aware that many of the traits they are trying to improve are of a complex nature and that the inheritance of these traits depends on genes at may loci. A recent review of bean genetics by Singh (1988) summarizes the information available to date on the genetic mechanisms in beans. It is obvious, when compared with other crops such as maize and soybeans, that the information available on bean genetics is limited and that investigation on the genetic mechanisms controlling many important bean traits is incomplete or non existing.

The bulk of the quantitative genetic studies reported have been on yield and yield components of beans (Coyne, 1968; Chung and Stevenson, 1933; Hamblin and Morton, 1977; Sarafe, 1978; Fooland and Bassiri, 1983; Zimmermann et al., 1984; Conti, 1985; Nienhuis and Singh, 1986, 1987; and others). Other studies, however, have also shown that resistance to Common Bacterial Blight (review of Beebe, 1988), *Fusarium* (Boomstra and Bliss, 1977), *Phythium* (York et al., 1977), and *Rhizoctonia* Root Rots (Dickson and Boettger, 1977), *Empoasca* leafhoppers (Kornegay and Temple, 1986), tolerance to low soil phosphorus (Fawole et al., 1982), seed protein quantity and quality (Bliss and Brown, 1984), seed tannins (Ma and Bliss, 1978) and cooking time (Wassimi, 1986) are also quantitatively inherited; though in some cases, conflicting evidence does exist as to the genetic mechanisms responsible for the inheritance of the trait and the results

---

[1] Plant Breeder, CIAT, A.A. 6713, Cali, Colombia.

should be taken in context to the parental lines chosen to study, the genetic analysis employed, and the environmental conditions occurring during the study.

For many other traits of interest no formal genetic studies have been published, although empirical evidence in breeder's nurseries suggests that resistance to Ascochyta Blight, Bean Golden Mosaic Virus, Web Blight, Apion Pod Borers, African Bean Fly, as well as bean nitrogen fixation and drought tolerance genetic mechanisms may also be controlled poligenically with low to moderately high levels of heritability.

For breeders to design successful programs for improving traits that are quantitatively inherited, it is important that a basic knowledge of the genetic mechanism controlling a trait be understood. The purpose of this report is to define in broad terms the science of quantitative genetics and its usefulness in bean breeding.

Quantitative Genetics - Definitions and Terminology

Quantitative genetics deals with those differences between individuals in a population which are of a continuous nature, grading imperceptibly from one extreme to another. The inheritance of quantitative differences often depends on gene differences at many loci, the effects of which are not individually distinguishable (Falconer, 1960; Sprague, 1966). The traits are usually expressed in terms of metric units such a length, weight, time, or proportions, and because of this require a greater use of statistics in the data analysis.

The science of quantitative genetics is based on the principles of classical (or Mendialian) genetics (such as segregation, gene interaction, linkage, and recombination) and extends the principles revealed through the study of discrete categories, which are relatively insensitive to environment, to the study of continuous variation that is highly responsive to environmental variation (Sprague, 1966; Mather and Jinks, 1977). Stated more simply, each of the genes that control a quantitatively inherited trait follow the same laws of transmission as genes that affect qualitative (or single gene) traits. However, we are usually dealing with many genes that have small individual effects and only when the complete set of genes controlling a trait are present in an individual can the maximum expression of a trait be obtained.

Gene and Genotypic Frequencies

Through the studies of population genetics we know that the genetic properties of a population of plants are theoretically expressible in terms of gene frequencies and genotypic frequencies.

Gene frequencies. The specification of all the alleles present at every locus, and the numbers (or proportions) of the different alleles at each locus.

Genotypic frequencies. The frequency of a particular genotype among the individuals in a population.

In real life, however, we do not know the gene frequencies of a quantitatively inherited trait in a plant population (e.g. an F_2 generation), and genotypic differences are only measurable when we are concerned with a single locus when the genotypes are phenotypically distinguishable (i.e. AA vs aa) or when we are measuring the differences between highly inbred lines (Falconer, 1960). So, one may ask, how is it possible to determine the genetic mechanism of a quantitatively inherited trait when the two basic genetic properties of a population are not measurable? The answer to this question lies in the science of applied quantitative genetics.

Means and Variances

A quantitatively inherited trait can be described through the use of metric units. The frequency distribution of the metric units used to describe the trait will approximate more or less a normal curve, where discrete categories are not discernible. In studying metric traits it is therefore possible to make use of the normal distribution of the units and apply appropriate statistical analysis. It should be noted, however, that when the curve is not normally distributed (skewed to one side or the other), then the data should be transformed so that the distribution becomes approximately normal (Steel and Torrie, 1980) in order to fulfill one of the basic assumptions of the analyses of variance.

The data taken as metric units can then be analyzed and three properties describing a population can be found: the means, variances and covariances. Through the partitioning of means, variances, and covariances, information can be obtained as to the amount of genetic variability in a population and the type of gene action involved.

To interpret the results generated through the analysis of metric units, a basic understanding of gene action is needed. To do this several quantitative genetic terms need to be defined.

Phenotypic and genotypic values

A value is the measurement of a trait and is expressed in metric units.

Phenotypic value, therefore, is the value observed when the trait is measured on an individual plant family or line. All observations (whether means, variances, or covariances) must be clearly based on measurements of phenotypic value.

To analyze the genetic properties of a population, the phenotypic value has to be divided into its component parts attributable to different causes.

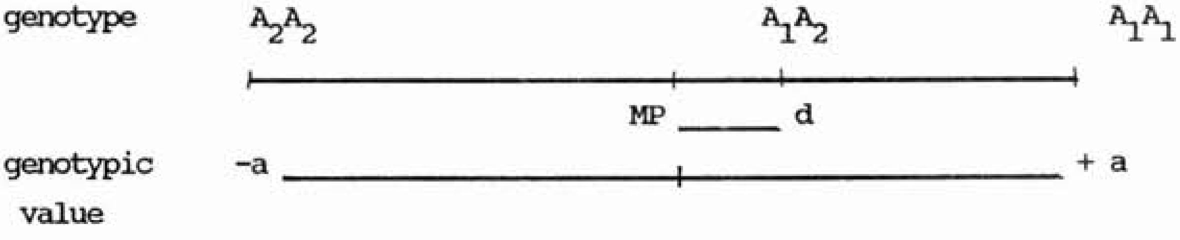
$$P = G + E$$

where P = phenotypic value
G = genotypic value
E = environmental deviation

The genotype is the particular assemblage of genes possessed by the individual plant.

The genotypic value then is the metric expression of the genotype. The genotypic value = phenotypic value when the environmental deviations (positive and negative) sum to zero through the use of appropriate experimental design and replication.

In the F_2 generation of a cross between two inbred lines, each locus may exhibit one of three states



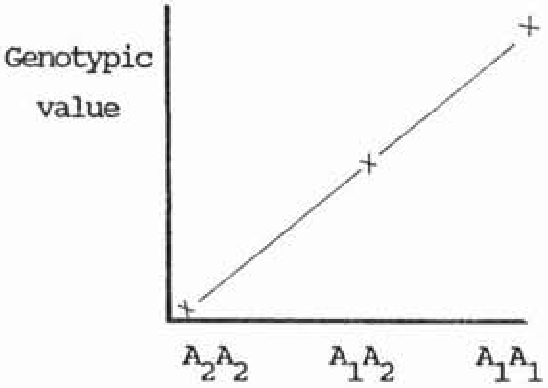
In this case, the allele A_1 increases the expression of a trait. (It does not imply dominance like in Medelian genetics). The genotypic values are +a and -a for the homozygotes and d for the heterozygote. The value of d depends on the degree of dominance. (Falconer, 1960; note, Mather and Jinks, 1977, use a slightly different system of nomenclature for the genotypic values).

Keeping this simple diagram in mind, we can use it to help explain the total gene action of a quantitatively inherited trait. The genotypic value can be subdivided into 3 basic groups of gene action.

$$G = A + D + I$$

where G = genotypic value
A = additive gene effects
D = dominance deviations
I = interaction or epistatic deviations

Additive gene effects are those due to gene action whereby the effects on a genetic trait are enhanced by each additional gene, either an allele at the same locus or genes at different loci. First we consider additive gene effects and deviations from additivity at individual loci.

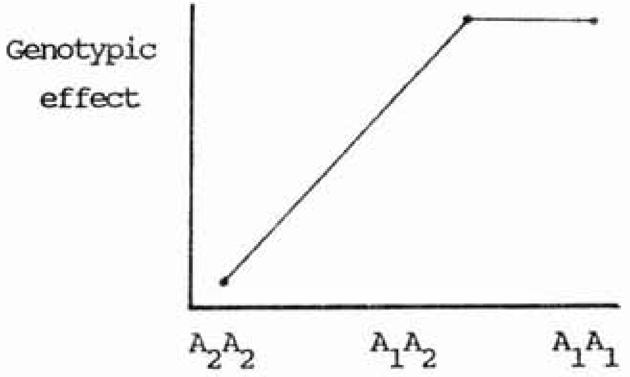


In this case each additional allele adds an equal increment to genotypic value and the result forms a linear relationship. In other words, what is present at one allelic position has no effect on the expression at another allelic position. Therefore, at a given locus, genes that show no dominance are said to act additively.

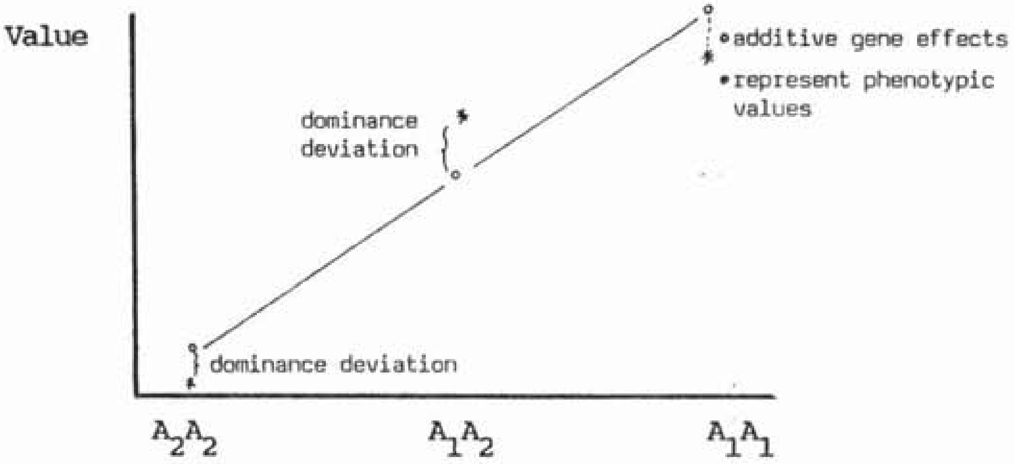
Now, with respect to continuous variation, we can not distinguish individually the genes contributing to the expression of a quantitative trait. If we consider two homozygous lines, the departure of each of them from the mid-parent value will reflect the simultaneous action of all the genes affecting the trait by which the lines differ. If we assume that the effects of these genes are simply additive, the departure from the mid-parent will be the sum of a's, one from each of the genes, taking the sign into account.

When these two individuals are crossed, the genes of the two individuals are passed on to their offspring. Thus, the transmission of value from parent to offspring can not be determined by genotypic value alone, since parents pass on their genes and not their genotypes to the next generation, with new genotypes being created each generation. To measure the value of the genes, a new concept is needed. This is called the breeding value. The breeding value is the value of the genes of an individual, judged by the mean value of its progeny. Therefore, when we estimate the breeding value of an individual (i.e. parental line) we are estimating the average effect of a group of genes that the progeny received from a parent. Or in other words, the sum of the average effects of genes over all alleles and loci.

Dominance deviation is the gene action which deviates from additive effects such that the heterozygote is more like one parent than the other. It is a property of dominance among alleles at a locus, and in statistical terms represents interactions between alleles, or within -locus interactions. If dominant gene action occurs, then the relationship at a single locus would be quadratic:



Or viewed as deviation from additive gene effects:



Dominance gene effects in self pollinating crops like beans are of little use. Only those crops where hybrids are readily made and show significant heterosis can dominance gene effects be exploited. In beans, the only genetic effects we can use are additive (and additive x additive) gene effects because the genetic state of an inbred line is homozygocity at all loci. Therefore, in breeding we look for the best combination of genes that combine additively to improve quantitatively inherited traits. The parental lines with the best breeding value, therefore, are those which can pass on to their offspring a superior complement of genes.

<u>Interaction or epistatic deviation</u> occurs when the genotypic value may contain an additional deviation due to non-additive combination when the alleles at one locus influence the expression of alleles at one or more other loci. Three kinds of interaction are known:

additive x additive
additive x dominance
dominance x dominance

Plant breeding and selection of a self pollinating crop can capitalize only on additive x additive types of gene action.

For the sake of brevity, those interested in more in depth explanation of interaction deviations are referred to Falconer (1960) and Mather and Jinks (1977).

Interpretation of gene action through means and variances

The development of an effective plant breeding program is dependent upon the existence of genetic variability. The amount of variation is measured and expressed in means and variances. The components of variance are those described for gene action, where:

$$\sigma^2 P = \sigma^2 G + \sigma^2 E$$

and $\sigma^2 G = \sigma^2 A + \sigma^2 D + \sigma^2 I$

VA, additive genetic variance results from the additive effects of the genes at all segregating loci. It is also described as the variance of breeding values, and is considered the most important component of genetic variance since it is the chief cause of resemblance between relatives. Therefore, it is the main cause of the observable genetic properties of a population that can be selected. (Falconer, 1960).

For bean breeders, the most important component of genetic variance is additive genetic variance, with all the rest (non-additive genetic variance and environmental variance) being unfixable. This partitioning gives us the ratio of

$$\frac{\sigma^2 A}{\sigma^2 P}$$

which is the heritability of a character defined in the narrow sense (h^2NS) which considers only the additive genetic effects relative to the phenotypic value. Heritabilities can also be defined in the broad sense (h^2BS)

$$\frac{\sigma^2 G}{\sigma^2 P}$$

Though here, other properties of the genotypic variance may also be expressed in the calculated heritability figure which are not utilizable by bean breeders.

The subject of heritability will be reviewed in the report on the inheritance of Common Bacterial Blight, and therefore, will not be detailed here. However, it is important to note that heritability is a property not only of a trait, but also of the population and the environmental circumstances to which individuals are subjected. Since the calculated value of heritability depends on the magnitude of all the components of genetic variance, a change in any one of these will affect the estimate. Therefore, whenever a value is stated for heritability of a given trait it must be understood to refer to a particular population under a particular set of conditions.

Mating Designs to Estimate Genetic Mechanisms in Quantitative Traits

Parent-offspring regression

Parent-offspring regressions are also used to determine the heritability of a trait. Beginning with a reference population (i.e., F_2 generation), one makes individual plant measurements for the trait of interest (i.e., yield, disease resistance). The seed is harvested from the measured plants in the population and then the measurements are repeated in the offspring (i.e., F_3 plants) of each parent (the F_2 individual).

Using this procedure the degree of association between the traits measured in the parents and their respective offspring can be determined using a regression analysis. The Y (or dependent value) is the progeny measurement, and the X (or independent value) the parental plant measurement. The standard regression model of $Yi = a + bXi + e_i$ is used.

We want to find the calculated value of b, which is the regression of Yi on Xi. This gives us a measure of the covariance of parent-offspring.

To determine the heritability (h^2NS), we can calculate it using two methods:

one parent-offspring | mid-parent-offspring

$$h^2NS = 2b = \frac{\sigma^2 A}{\sigma^2 P} \quad \text{or} \quad h^2NS = b = \frac{\sigma^2 A}{\sigma^2 P}$$

In the case of mid-parent-offspring analysis, we record the measurements of traits in each parent used in crosses and regress offspring measurement Y on those of the means of the pairs of parents, X. This method is more commonly used in cross pollinating plants.

In self pollinating crops, the b value must be corrected to account for the measure of relationship (rXY) between the parent Y and its offspring X. The corrections were outlined by Smith and Kenman (1965).

Parent-offspring generation	rXY	$h^2NS = b(2rXY)$
F_1, F_2	1/2	b F_2, F_1
F_2, F_3	3/4	(2/3)b F_3, F_2
F_3, F_4	7/8	(4/7)b F_4, F_3
F_4, F_6	15/16	(8/15)b F_5, F_6
F_5, F_6	31/32	(16/32)b F_6, F_5

Thus, the estimates of heritability become more conservative when we have continuous self-fertilization. The major limitation is that large numbers of parents and offspring are needed to give estimates of even modest precision (Falconer, 1960).

Generation means analysis (Gamble, 1962)

Estimates of genetic parameters can be obtained using a minimum of six generations derived from the cross of two homozygous lines. The generation means used are:

$$\overline{P_1} \quad \overline{P_2} \quad \overline{F_1} \quad \overline{F_2} \quad \overline{BCP_1} \quad \overline{BCP_2}$$

Estimates of mean (m), additive (a), dominance (d), add x add (aa), add x dom (ad), and dom x dom (dd) gene effects can be calculated from the means.

The advantages of the Generation Means Analysis are 1) generation means are used which can be measured with more precision than variances; 2) the generations are relatively easy to prepare in self pollinating crops; 3) the model can be extended to more complex inheritance patterns; and 4) linkage does not bias additive and dominance effects as it does in estimates of variances.

The disadvantages are 1) cancellation of positive and negative additive effects may occur; 2) potential sampling problems in the segregating generations; 3) possible border effects when the generations have different levels of vigor, and 4) information about the means does not allow estimation of heritability.

In order to estimate heritability values, modifications of the generation means analysis have been designed (Warner, 1952; Mather and

Jinks, 1977).

Diallel analysis

Diallel crosses are used to describe a procedure in which a set of inbred lines are intercrossed in a diallel fashion. The diallel can include or exclude the use of parents, F_1 or F_2 generations; nor do the reciprocal F_1 hybrids need be included depending on the method of analysis chosen to be performed (Griffing, 1956). Gene action can be inferred from the results of the analysis with several restrictions imposed on the interpretation.

The interpretation depends on whether a random or fixed model was used. In fixed models, the parents utilized are the only genotypes under consideration and estimates of genetic parameters apply only to the genotypes included in the study and cannot be extended to a hypothetical reference population. The random model includes parents that are a random sample of genotypes from a reference population and the interpretation of the results can be extended to the reference population (Hallauer and Miranda, 1981).

In bean breeding, we are usually interested in studying a specific set of parents, and therefore, the genetic interpretations we can make are limited to the estimate of general combining ability effects (GCA) and specific combining ability effects (SCA).

GCA is the average performance of parents in hybrid combination and is primarily a measure of additive and/or digenic variance (which may also include some dominance and epistatic variance).

SCA is the deviation (both positive and negative) of individual crosses from the average performance of their parental lines and are considered to be the result of dominance and epistatic effects.

In the fixed model, the diallel analysis gives considerable information about the fixed set of parents used in the study - information that can be useful for the selection of parents that have good general combining ability in a series of crosses and good specific combining ability for specific pairs of parents.

The disadvantage of the diallel mating design is that it is difficult to evaluate a large number of parental lines due to the number of crosses required, and that no direct estimate of gene effects can be made.

Design II

The Design II was developed by Comstock and Robinson (1948) to estimate components of genetic variance from covariances of relatives. It is often called a factorial crossing arrangement, and approximately twice as many parents can be use, compared to the diallel cross, to make the same number of crosses.

The Design II crossing arrangement can be visualized this way:

		females			
		f1	f2	f3	fn
m	m1	P11	P12	P13	P1n
a	m2	P21	P22	P23	P2n
l	m3	P31	P32	P33	P3n
e	m4	P41	P42	P43	P4n
s	mm	Pm1	Pm2	Pm3	Pmn

Estimates of GCA and SCA can be made from the data as well as estimates of σ^2A and σ^2D.

By calculating the expected covariance of paternal half sets and maternal half sets two formulas can be derived when inbred parental lines are used:

$$\mathrm{COV(FHS)} = \sigma^2 M = (1/2)\ \sigma^2 A$$

$$\mathrm{COV(MHS)} = \sigma^2 f = (1/2)\ \sigma^2 A$$
$$\sigma^2 mf = \sigma^2 D$$

Because we have two sets of parents in design II, we have two independent estimates of $\sigma^2 A$, and an independent estimate of $\sigma^2 D$.

Other designs

Other mating designs can also be used to estimate the genetic mechanisms in quantitatively inherited traits. However, many of the other designs (for example Design I and III) have not yet been used for beans. Estimates of genetic variances can also be obtained from triple and double crosses, and from the use of unselected inbred lines. Hallauer and Miranda (1981) give indepth descriptions of mating designs for quantitative traits. Although their examples are with maize, the ideas in most cases can be adjusted to self pollinators.

Gain from selection

The primary purpose for obtaining estimates of genetic parameters is to provide guidelines in developing breeding programs, and to predict future gain from selection. The gain from selection can be calculated using the calculated h^2NS value, where:

$$\Delta = (\bar{X}s - \bar{X})\ \frac{\sigma^2 A}{\sigma^2 p}$$

where: $\bar{X}s$ = mean of the individuals selected

and $\bar{X}$ = is the simple mean of the population

When selection is practiced among families rather than among individuals some modification in the formula is needed.

$$\triangle FS = (\bar{X}s - \bar{X}) \frac{\sigma^2 A}{2\sigma^2 p}$$

Selection changes gene frequencies and genotypic frequencies in a population. However, for complex traits, such as those influenced by many loci with small effects, genetic variances would probably change very slowly with selection. If this is the case, especially for traits of low heritability, drastic changes in variances with selection are unlikely, and variances estimates in the original populations may serve for predictions over several selection cycles.

Conclusion

This report has attempted to give a brief summary of the basic concepts in quantitative genetics. The main emphasis has been on explaining gene action that can be interpreted through the statistical manipulation of means, variances, and covariances. Several mating designs are described that have been used by bean breeders to study quantitative traits. The science of quantitative genetics, however, is much more complex than this report can hope to summarize. Important subjects such as heterosis, genotype x environmental interactions, and the effects of linkage have not been covered, and those persons interested in exploring these areas should refer to the references cited at the end of the report.

The ultimate objective of a bean breeder is to produce varieties that are superior in some way to those already in commercial production. To accomplish this, the breeder must devise a breeding program which will allow him to produce and reproduce genotypes that represent, as best as possible, the optimum combination of genes for a particular area. Information concerning the variation that exists in the breeding population is of fundamental importance in planning such a program. The study of genetic variance and heritability can help the breeders answer these questions:

1. Is there sufficient variability present to allow for improvement ?

2. How extensive must testing be to identify superior parents or superior populations ?

3. Which populations or lines in the germplasm are the most promising ?

4. What breeding procedure will most rapidly and efficiently produce acceptable levels of improvement ?

For traits with high heritability, pedigree breeding schemes may be effective in identification and selection of superior progeny. For traits with low heritability, however, selection in early generation will probably be inefficient, and the breeder risks losing the few superior progeny that may be in the tail end of the distribution curve. For low heritability traits, bulk breeding strategies are recommended, with individual selections made in relatively advanced generations when the genotype of the individuals are in a more homozygous states and variance due to additive gene effects being the principal cause of difference among the genotypes.

References

Beebe, S. 1988. Quantitative genetics in Phaseolus vulgaris: the example of resistance to Xanthomonas campestris pv. phaseoli. Proceedings of the International Workshop on Breeding Common Beans, Nov. 7-12, 1988. Cali, Colombia, 1988.

Bliss, F.A. and J.W.S. Brown. 1984. Breeding common bean for improvement quantity and quality of seed protein. Plant Breeding Rev. 1984 pp 59-96.

Boomstra, A.G. and F.A. Bliss. 1977. Inheritance of resistance to Fusarium solani f. sp. phaseoli in beans (Phaseolus vulgaris L.) and breeding strategies to transfer resistance. J. Am. Soc. Hortic. Sci. 102: 186-188.

Chung, J.H. and E. Stevenson. 1973. Diallel analysis of the genetic variation in some quantitative traits in dry beans. N.Z.J. Agric. Res. 16:223-231.

Comstock, R.E. and H.F. Robinson. 1948. The components of genetic variation in populations of biparental progenies and their use in estimating average degree of dominance. Biometrics 4:254-266.

Conti, L. 1985. Conclusive results of a selection programme for obtaining a dwarf bean (Ph. vulgaris) resistant to some viruses and characterized by agronomic qualities. Genet. Agr. 39:51-63.

Coyne, D.P. 1968. Correlation, heritability, and selection of yield components in field beans, Phaseolus vulgaris L. Proc. Am. Soc. Hort. Sci. 93:388-396.

Dickson, M.H. and M.A. Boettger. 1977. Breeding for multiple root rot resistance in snap beans. J. Am. Soc. Hortic. Sci. 102:373-377.

Falconer, D.S. 1960. Introduction to Quantitative Genetics. Longman House, UK. p. 340.

Fawole, I; W.H. Gabelman; G.C. Gerloff; and E.V. Nordheim. 1982. Heritability of efficiency in phosphorus utilization in beans (Phaseolus vulgaris L.) grown under phosphorus stress. J. Am. Soc. Hort. Sci. 107:94-97.

Foolad, M.R. and A. Bassiri. 1983. Estimates of combining ability, reciprocal effects and heterosis for yield and yield components in a common bean diallel cross. J. Agric. Sci., Camb. 100:103-108.

Gamble, E.E. 1962. Gene effects in corn (Zea mays L.) 1. Separation and relative importance of gene effects for yield. Canad. J. Plant Sci. 42:339-347.

Griffing, B. 1956. Concept of general and specific combining ability in relation to diallel crossing systems. Austral. J. Biol. Sci. 9: 463-493.

Hamblin, J. and J.R. Morton. 1977. Genetic interpretations of the effects of bulk breeding on four populations of beans (Phaseolus vulgaris L.). Euphytica 26:75-83.

Hallaver, A.R. and J.B. Miranda. 1981. Quantitative genetics in maize breeding. Iowa State Univ. Press, Ames, Iowa. p. 468.

Kornegay, J.L. and S.R. Temple. 1986. Inheritance and combining ability of leafhopper defense mechanisms in common bean. Crop Sci. 26:1153-1158.

Ma, Y. and F.A. Bliss. 1978. Tannin content and inheritance in common bean. Crop Sci. 18:201-204.

Mather, K. and J.L. Jinks. 1977. Introduction to Biometrical Genetics. Cornell Univ. Press. p. 231.

Nienhuis, J. and S.P. Singh. 1986. Combining ability analyses and relationships among yield, yield components, and architectural traits in dry bean. Crop Sci. 26:21-27.

Nienhuis, J. and S.P. Singh. 1988. Genetics of seed yield and its components in common bean (Phaseolus vulgaris L.) of middle-American origin. I. General combining ability. Plant Breeding 101:143-154.

Nienhuis, J. and S.P. Singh. 1988. Genetics of seed yield and its components in common bean (Phaseolus vulgaris L.) of middle-American origin. II. Genetic variance, heritability and expected response from selection. Plant Breeding 101:155-163.

Sarafi, A. 1978. A yield-component selection experiment involving American and Iranian cultivars of the common bean. Crop Sci. 18:5-7.

Singh, S.P. 1988. Bean Genetics. In Common Beans: Crop Improvement for Sustainable Productivity. (Eds. A. v. Schoonhoven and O. Voysest). CIAT, Cali, Colombia. In press.

Smith, J.D. and M.L. Kinman. 1965. The use of parent-offspring regression as an estimator of heritability. Crop Sci. 5:595-596.

Sprague, G.F. 1966. Quantitative genetics in plant improvement. In Plant Breeding (ed. K.J. Frey) Iowa State Univ. Press, Iowa. pp 315-354.

Steel, R.G.D and J.H. Torrie. 1980. Principles and Procedures of Statistics. 2nd ed. McGraw-Hill Book. Co, N.Y. p. 633.

Warner, J.N. 1952. A method for estimating heritability. Agron. J. 44:427-430.

Wassimi, N.N. 1986. Genetic analyses of cooking time, nutritional and culinary quality in dry beans (Phaseolus vulgaris L.). Diss. Abstr. 46:2137B.

York, D.W; M.H. Dickson; and G.S. Abawi. 1977. Inheritance of resistance to seed decay and pre-emergence damping-off in snap beans caused by Phythium ultimum. Plant Dis. Rep. 61:285-289.

Zimmermann, M.J.O.; A.A. Rosielli; J.W. Waines; and K.J. Foster. 1984. A heritability and correlation study of grain yield, yield components and harvest index of common bean in sole crop and intercrop. Field Crops Res. 9:109-118.

35670

QUANTITATIVE GENETICS IN *Phaseolus vulgaris*: THE EXAMPLE OF RESISTANCE TO *Xanthomonas campestris* pv. *phaseoli*

Steve Beebe*

Introduction

Although the science of quantitative genetics has not had wide application to the breeding of common bean (*Phaseolus vulgaris*), several authors have published studies on quantitative analysis of resistance to *Xanthomonas campestris* pv. *phaseoli* (Xcp), the pathogenic agent of common bacterial blight. Therefore, the case of resistance to Xcp is unique in bean, since it allows us, to a certain degree, to compare results with different statistical methods and the interpretations that different authors give to these. Of course, such a comparison is possible in other crops and with other characters. The purpose of this article is, first, to review studies carried out, and second, to consider the application of their results and progress in breeding beans for resistance to Xcp..

Summary of Studies Carried Out

Quantitative genetic studies on resistance to Xcp are summarized in Table 1. Parameters studied include heritability, the number of genes controlling the character, and variances which indicate whether genes act in an additive manner, by dominance, or interact (through epistasis).

The results are not altogether comparable, since the same resistance sources were not used in all the trials. Nevertheless, the majority worked with genes derived from two principal sources: Great Northern #1

---

* Bean plant breeder, CIAT, A.A. 6713, Cali, Colombia.

Sel. 27 and P.I. 207262. This is the case for the studies by Borges (1987), Faure (unpublished data), Oliveira (1987), Coyne and Schuster (1974), Webster (1980), Valladares et al. (1983), and in part for Rava et al. (1987).

Another group of researchers worked with P. acutifolius. McElroy (1985) and Drijfhout (1987) reported on results with P.I. 319443 and Ochoa (unpublished data) worked with genes of this species already introduced in P. vulgaris. Scott and Michaels (1988) worked with three unspecified accessions of P. acutifolius.

Also, different authors have studied the reaction to Xcp in different parts of the plant: in the unifoliolate, in the trifoliolates, and in the canopy (Table 1).

These facts limit possible conclusions; however, several studies have enough in common to be able to emphasize some important points. Also, some authors have reported results obtained by more than one method, which permits a comparison among methods.

Heritability

Heritability should represent the degree of a character, expressed in the parent, which is expressed in the offspring. That is, it is the part of the character which the offspring inherits from the parent.

Estimates of heritability values (represented as h^2) are calculated in two general ways: in a broad sense and in a narrow sense.

Heritability in a broad sense (h^2bs) is a very general concept which relates genetic variability of a given character with total variability (genetic plus environmental):

$$h^2bs = \frac{\sigma^2g}{\sigma^2g + \sigma^2e} = \frac{\sigma^2g}{\sigma^2T}$$

where σ^2g is the genetic variability, σ^2e is the environmental variability and σ^2T is total variability.

If there is much environmental variability, and σ^2g is relatively small, h^2bs is lower. In terms of selecting lines or individual plants in the field, if there is much environmental variability, one doesn't know if a line or plant is expressing its own genetic potential or if its reaction is merely an effect of the environment, and therefore, it will not be inherited by the offspring. Thus it is said that heritability is low.

It is necessary to point out that h^2bs is not based on a comparison of parents and offspring and the degree of a character that the offspring inherit. Therefore it is a general or broad concept of heritability. It presupposes that the reason for which an offspring is not like its parent is because of the environmental effect and thus, if the range of the environmental effect is quantified, it will be possible to predict that so much of the phenotype of the parent will be maintained in the offspring.

Heritability in a narrow sense (h^2ns) is calculated in two very different ways, which in this article will be dealt with separately. The first way requires an estimate of the additive variance. That is, the total genetic variance is to be separated into various components in order to arrive at an estimate of the additive part. This requires a plan of crosses and backcrosses and the solving of certain equations that will not be listed in detail here. It is sufficient to point out that h^2ns is defined as the relationship between additive variance and total variance:

$$h^2ns = \frac{\sigma^2a}{\sigma^2T}$$

Since σ^2a has to be equal to or less than σ^2g, h^2ns has to be equal to or less than h^2bs.

The calculation of h^2ns is based on a comparison of variances of different generations (parents, F_2, and backcrosses), but it is not based strictly on the relationship between a given parent and its offspring. That is, it is calculated in an artificial context, supposing that it is possible to define and measure the causal factors of the parent-offspring relationship, in order to extrapolate these results to selection work in the field.

The other way to calculate heritability in the narrow sense is by the regression of the value of the offspring over the value of the parent: βph. This method involves a comparison of parents and offspring, and it has the advantage of being calculated in the context of selection, which the breeder is practicing. It is rather empirical and therefore practical.

It is interesting to note that when Galton developed the concept of regression--which has had an application in all branches of science--he did it in the context of heritability.

For discussion purposes in this article, h^2ns will refer only to h^2 calculated on genetic variances derived in the described manner. Heritability calculated as parent-offspring regression will be represented as βph.

With these introductory comments about methods of calculating heritability in mind, let us refer to Table 1. Here we see relatively low heritability values (.14, .15, and even .00!), intermediate values (.28, .34, and .54), and high values (.69, .87, and .98). With such results, it is difficult to say if heritability is high or low! Even recognizing the limitations cited previously, we are going to explore what effect the statistical method can have on the results.

Let's concentrate on the results of Faure (unpublished data) reproduced in Table 2. Faure found an average value of h^2bs of .44, and an average value of βph of .75, applying two different methods to the same data taken from six populations. These figures represent a moderately large difference in the estimate of h^2, from intermediate to high. In addition, looking at the values of each population, there isn't a constant relationship between the two methods. For example, the population of DOR 60 x XAN 112 has the highest h^2bs (.59) but the lowest βph (.52).

Oliveira (1987) has also presented estimates of heritability calculated by different methods, and of evaluations of disease made on trifoliolates and on all the canopy (Table 3). He also compared the βph calculated on parents and offspring planted in successive semesters, or in the same semester. In general, results with trifoliolates and with the entire canopy are similar. The planting of parents in the previous season, or in the same season with the offspring seems to have influenced the value of βph but not dramatically. The biggest effect was the effect of the statistical method, and it wasn't a constant effect. In one population (Rio Doce x XAN 112) h^2ns gave values a little bit above the βph. In the other two populations, values of h^2ns were less than the βph. The widest difference is observed in the population Ouro x XAN 112, where h^2ns was .34 and the βph had an average value of .62.

From these two examples it is evident that the statistical method used has a great effect on the values obtained and on the evaluation of heritability as high, medium, or low. There is not necessarily a good correlation between the methods. Given this situation, each researcher should choose the method that most approximates the real situation in which the researcher wishes to apply results. In this sense, this author prefers the βph.

The other point to be mentioned in relation to heritability (in whatever sense) is that it is always reduced by environmental variability. Good techniques at the field level (that is, an appropriate and uniform agronomic management) will always result in greater heritability. Also, an improved method to distinguish genotypes will serve to increase heritability. In the case of resistance to Xcp, the inoculation method has a big effect on h^2. We see this effect in the results of Faure (unpublished data) and Coyne (1974). These two calculated βph of F_3 families on F_2 plants, and the two worked with the same resistance genes derived from P.I. 207262 (in the work of Faure, represented in XAN 19). Nevertheless, Faure reported a βph = .90 and Coyne a βph = .14. The difference in heritability is explained by the manner of inoculation and evaluation. Coyne used an aspersion method which allows more escapes in the field and a diffuse development of symptoms. Faure inoculated trifoliolates plant by plant with razor blades, thus eliminating escapes and creating a discrete lesion and one easy to quantify. The result was a more precise evaluation of the genetic potential of each plant and a greater heritability.

Inheritance: Number of Genes

Of the various authors who have published on resistance to Xcp derived from P.I. 207262 and GN #1 Sel. 27, only Oliveira (1987) has attempted to determine the number of genes which control reaction to Xcp. Applying the appropriate equations to the respective variances, Oliveira concluded that there was a single gene acting on the reaction of trifoliolates, canopy, and pods, in cases where it was possible to apply the equations. Nevertheless, there were other cases where analysis indicated that epistasis existed. The existence of epistatic interaction does not allow the application of equations to determine the number of genes. Nevertheless, the existence of epistasis in some cases implies the action of more than one gene.

In a population of Ouro x XAN 112, Oliveira observed transgressive segregation. In addition, XAN 112 in itself represents transgressive segregation since it combines resistance of GN #1 Sel. 27 and P.I. 207262 and is more resistant than any of its progenitors. The existence of transgressive segregation also implies the action of more than one gene. Coyne and Schuster (1974) had also noted evidence of different genes in these two sources.

In this case, quantitative genetics tells us one thing and biological knowledge tells us something else.

In the case of P. acutifolius resistance, several authors have reported on its inheritance (Table 1). McElroy (1985) interpreted his segregation data by two methods: forming discrete classes and applying Mendelian genetics; and through the application of equations from Mathers and Jinks (1977) to the appropriate variances. Through the Mendelian method, McElroy concluded that there was a single dominant gene. The method of Mathers and Jinks suggested three genes. McElroy reconciled these results saying that there existed a major dominant gene and two minor genes. An alternative interpretation would be that one or the other method is correct, but not the two. Where a Mendelian interpretation seems to explain the facts, this can be less theoretical and closer to the biological reality and therefore preferable. Indeed, Drijfhout (1987), working with the same source of resistance, concluded that a single gene controlled the reaction.

These two examples are offered here to illustrate the following point. Quantitative genetics is a statistical description of biology. It may or may not be a true description. We should not expect it to be precise but recognize that it offers estimates. Since quantitative genetics is not precise, we should compare its conclusions with biological facts. Moreover, we should always look for a biological interpretation for statistical conclusions.

Manner of Genetic Action

Coyne et al. (1966) reported data suggesting that resistance of Great Northern #1 Sel. 27 was slightly recessive in the field. Afterward, Coyne and Schuster (1974) found that resistance of P.I. 207262 was slightly dominant in the field. Valladares et al. (1983), in a diallelic study including these two sources, found principally additive effects. All these studies were carried out in Nebraska, United States, under long summer days. Nevertheless, Webster (1980) demonstrated that resistance to Xcp can apparently be altered by a photoperiod response, long days favoring vegetative growth and reducing expression of symptoms. Therefore, segregation by maturity in the Nebraska studies, such as that described by Coyne and Schuster (1974), could be confused with segregation for reaction to bacteria. Being so, the data are difficult to interpret.

Oliveira (1987), as well as Rava et al. (1987), studied the manner of genetic action through the method of generation means. Although they worked with some of the same genes derived from G. N. Jules and P.I. 207262, Rava et al. studied the genes in crosses with the original genotypes, while Oliveira used advanced lines (XAN 40 and XAN 112) that combined genes from the two sources. In addition, Rava et al. included other sources of resistance. Nevertheless, the conlusions are not very different.

The two studies found that additive effects were the most common in foliage resistance, frequently being the greatest effect. Effects of dominance frequently were significant, especially in Oliveira's study. In the study of Rava et al., Jules presented principally additive effects, while P.I. 207262 as a source also presented dominance. Oliveira found dominance-dominance interaction in two crosses, while Rava et al. found all kinds of interaction.

Regarding reaction in pods, Oliveira reported only additive and dominance effects, while Rava et al. also found interactions.

McElroy carried out a study of means of generations on resistance of *P. acutifolius*, finding additive effects as well as dominance effects to be significant.

Ochoa (unpublished data), working with genes derived from PI 319443 but introduced into a *P. vulgaris* background, analyzed gene action using the model of Mather and Jinks (1977) and the modification of Cavalli (1983). He found that the additive-dominant model with three parameters definitely did not adjust, but with the inclusion of epistatic interactions the model adjusted well, which suggests a minimum of two genes with a high degree of interaction that control resistance. Nevertheless, there were certain values in the means of the backcross generations which were difficult to explain.

Application of Results of Quantitative Studies

How have quantitative studies served to improve resistance to common bacterial blight of beans?

The estimates of h^2 in general have been intermediate to high, confirming the possibility of selecting in segregating populations if the breeder desires. Nevertheless, good heritability depends on a good inoculation method. In the last ten years, there have been advances in developing effective and rapid methods that can be used at the field level. The values of h^2 (particularly those of βph) reflect the effectiveness of these methods.

The result that additive genetic action is the most important in the majority of cases confirms the possibility of selecting in early generations. Nevertheless, this is basically the same conclusion that we derive from βph estimates, and while βph is high, it is not critical to understand genetic action. In addition, less work is required to estimate the βph than to study genetic action through analysis of generation means, by diallelic studies, etc. In this situation, and given the imprecise nature of the information that one derives from studies on quantitative genetics, the breeder should consider if it is worthwhile to make such an analysis to study genetic action. There is more justification to study genetic action where problems exist in the selection which the breeder wishes to clarify.

Regarding the number of genes that control reaction to Xcp, there is little information even on the most used sources (P.I. 207262, Jules, and related genotypes). Nevertheless, all the studies reported are in agreement that inheritance is not complex, independent from the source used! (Table 1). This is slightly surprising in the case of a quantitative character.

All these facts (good heritability, additive genetic action, and relatively simple inheritance) should facilitate the incorporation of resistance, even more so since there is minimal or no interaction of resistance sources with isolates of pathogens. Nevertheless, progress has been slow, apparently because of genetic linkages to negative factors. The cases of apparent linkages are detailed as follows:

1. Resistance with seed brillance: it was consistently observed at CIAT and at IAPAR, Brazil (Dr. Tara Mohan, personal communication), that the resistant selections had brillinat seeds. Of course, this was a limitation only in the breeding of opaque grain varieties. Linkage probably occurred in Jules, which seemed to contribute the largest part of resistance. Nevertheless, it was possible to recover recombinants of opaque grain, so that this linkage was not limiting over the long term. The recombination rate was never quantified.

2. Resistance with color instability: many resistant selections with black grain and derived from Jules and/or P.I. 207262 suffered from a tendency to produce purple or "washed-out" grain. Since the penetrance of the purple grain was low, this character was difficult to eliminate, but it has been minimized through selection. In the case of bright red grain, it has been impossible up to now to recover resistance in genotypes of clear red grain (Central American type) from the mentioned sources, and although selections of dark red grain exist, many of these also suffer from "washing" of grain. On the other hand, it has been possible to recover resistance of XAN 159 (derived from P.I. 319442, P. acutifolius) with clear red grain, after two more cycles of crossing and selection.

3. Resistance with bad adaptation and/or instability of yield: while this is a difficult effect to quantify, it is probably a greater problem in black grained genotypes. The original sources, Jules and P.I. 207262, have very poor adaptation in the tropics. Nevertheless, it was possible in the first cycles of crossing and selection to overcome the majority of the bad adaptation and produce black grained lines such as XAN 87 and XAN 112. In subsequent selection cycles, resistant lines with even better adaptation at CIAT were recovered, and many of these have been widely distributed. Nevertheless, after three cycles of crossing and intensive selection starting from the original sources, the resistant lines still shown a certain tendency to be inferior to black grain commercial varieties under stress conditions. That is, the resistant lines do not show the rusticity that is typical of black grained varieties. This is a subjective observation. Until now, there has not been a statistical evaluation of stability of the lines, but soon these data may be available from trials in Cuba (Benito Faure, personal communication). It is possible that in certain environments the lines may have sufficient adaptation and stability to serve as varieties. Certainly in Cuba some of them have are very well adapted in preliminary trials and in Argentina, XAN 112 will be released as a

variety. Regarding reds, the dark grained resistant lines seem to be as productive and stable as the commercial varieties. But in this case, the red commercial varieties in themselves are not as stable as are the blacks. In the case of resistance derived from P. acutifolius, adaptation of the resistant selections continues being bad after three selection cycles.

There has not been any attempt to show in a formal study a genetic linkage between resistance and instability of yield or washing of grain. This would be very difficult, given the low penetrance of the washing, and the quantity of work which is implied in quantifying stability. Nevertheless, it is logical to suspect linkage problems (or pleiotropy) when the same problems continue to be associated with resistance after two or three selection cycles.

Search for New Sources of Resistance

As a response to problems mentioned, at CIAT we are looking for alternate sources of resistance. For a few years we have used G 4399 (Tamaulipas 9-B) and its progeny XAN 91 as sources. These have good resistance but they are also poorly adapted at CIAT. Until now there is not enough experience with them to indicate whether or not there are problems related to their resistance.

Since last year, a thorough evaluation of the Germplasm Bank has been initiated. The low frequency of resistance in bean germplasm has been surprising. Among the first 12,000 accessions evaluated, only three small-grain ones have shown an intermediate to high level of resistance in three confirmation tests: G 6700 (MSU 183), G 6708 (MSU 305), and G 6772 (Colima 9). The G 6700 and the G 6708 apparently come from Michigan State University, United States, and the origin of their resistance is unknown. The G 6772 is apparently a land race variety.

In a second group of 3,000 accessions of germplasm, several seemed promising, but there hasn't been a confirmation of their resistance yet.

Conclusions

This revision of quantitative genetic studies applied to resistance in common bean to the common bacterial blight pathogen has been developed to illustrate several points on quantitative genetics. Its conclusions are not original and it would be possible to repeat such a revision on other crops, with reference to other characters. Nevertheless, within the Phaseolus vulgaris species, there are more studies on resistance to Xcp than any other character.

It is evident that the results of the studies depend in a large part on the statistical methodologies used. Therefore, the researcher should carefully choose his/her methods, and use even more care in the interpretation of results. It is a mistake to give excessive credibility to any result in a very specific sense. Conclusions should be general: for example, that heritability is low, intermediate, or high, and not that it be a precise figure.

Above all, it is important to compare, whenever possible, the results of quantitative genetics with whatever other information of a biological nature is available. In the end, it is biology which should have the last word. Quantitative genetics is not perfect and it is subject to errors. But these can be minimized considering what they represent biologically.

Although information of a quantitative type is more complete for resistance to Xcp than for any other character of bean, unfortunately progress in developing resistant varieties has been delayed by the association of resistance with some negative characteristics. In this article, we have discussed principally problems of genetic linkage but the possibility of pleiotropy cannot be eliminated.

Thus, sources of resistance that do not suffer from such associations have been sought. While some alternate sources are available, it is still too early to know if they resolve the problems mentioned.

References

Adams, M.W., J.D. Kelly, and A.W. Saettler. 1988. A gene for resistance to common blight (Xanthomonas campestris pv. phaseoli). Ann. Rept. Bean Improv. Coop. 31:73-74.

Borges F., O.L. 1987. Selección para resistencia a la quemazón bacteriana (Xanthomonas campestris pv. phaseoli) y a la roya (Uromyces appendiculatus (Pers.) Unger) en caraota (Phaseolus vulgaris L.). U. Central de Venezuela, Maracay, Venezuela. 123 pp.

Coyne, D.P. and M.L. Schuster. 1974. Inheritance and linkage relations of reaction to Xanthomonas phaseoli (E.F. Smith) Dowson (common blight), stage of development and plant habit in Phaseolus vulgaris L. Euphytica 23:195-204.

Drijfhout, E. and W.J. Blok. 1987. Inheritance or resistance to Xanthomonas campestris pv. phaseoli in tepary bean (Phaseolus vulgaris). Euphytica 36:803-808.

Faure, B. Unpublished data.

Mather, K. and J.L. Jinks. 1977. Introduction to biometrical genetics. Cornell University Press; Ithaca, N.Y.

McElroy, J.B. 1985. Breeding for dry beans, Phaseolus vulgaris L., for common blight resistance derived from Phaseolus acutifolius A. Gray. Ph.D. Thesis. U. Cornell; Ithaca, N.Y. 45 pp.

Ochoa, I. Datos no publicados.

Oliveira e Silva, L. 1987. Método de inoculacao, heranca e ganho genético da resistencia a Xanthomonas campestris pv. phaseoli (Smith) Dye em cruzamentos de feijoerio comum (Phaseolus vulgaris L.). Tesis de M.Sc. U. Federal de Vicosa; Minas Gerais, Brazil. 91 pp.

Rava, C.A., M.J. de O. Zimmermann and R. da Silva Romeiro. 1987. Inheritance of resistance to *Xanthomonas campestris* pv. *phaseoli* (Smith) Dye in *Phaseolus vulgaris* L. Rev. Brasil. Genet. (Brazil. J. Genetics) X,4:709-727.

Scott, M.E. and T.E. Michaels. 1988. Inheritance of resistance to common bacterial blight in common bean. Annu. Rept. Bean Improv. Coop. 31:72.

Valladares-Sanchez, N.E., Coyne, D.P. and R.F. Mumm. 1983. Inheritance and associations of leaf, external and internal pod reactions to common blight bacterium in *Phaseolus vulgaris* L. J. Am. Soc. Hort. Sci. 108:272-278.

Webster, D.M., S.R. Temple, and H.F. Schwartz. 1980. Selection for resistance to *Xanthomonas phaseoli* in dry beans. Crop Sci. 20(4):519-522.

Table 1. Studies in quantitative genetics on the foliar resistance to *Xanthomonas campestris* pv. *phaseoli* in bean.

Author	Foliar unit	Heritability (h^2) Broad sense (bs)	Narrow sense (ns)	βph	Number of genes	Genetic action	Original source of genes
Adams et al (1988)	Trifoliate				1	Recessive	Co-60
Borges (1987)	Trifoliate	.39		$.15(F_3F_4)$			PI 207 262
Coyne y Schuster (1974)	Canopy			$.14(F_2F_3)$		Dominant	PI 207 262
Drijfhout (1987)					1	Dominant	PI 319 443
Faure (1988)	Trifoliate	.44		$.75(F_2F_3)$			PI 207 262, GN Neb. 1 Sel 27, G 4399
McElroy (1985)	Trifoliate				1 ó 3	Additive, dominant	PI 319 443
Ochoa	Trifolate					Reccesive	PI 319 443
Oliveira (1987)	Trifoliate Canopy		.18-.54 .34-.76	$.28\text{-}.87(F_3F_4)$ $.26\text{-}.69(F_3F_4)$	1	Additive > dominant, little interaction	PI 207 262, GN Neb 1 Sel 27
Rava et al (1987)	Unifoliate	$.63\text{-}.98^1$ $.41\text{-}.93^2$	0-.90 .09-.93			More additive than others	PI 207 262, GN Neb. 1 Sel 27 Mexico 168, Mexico 29
Scott y Michaels (1988)	Trifoliate				2	Dominant	P. acutifolius
Valladares (1983)						Additive	PI 207 262, GN Neb. 1 Sel 27
Webster (1980)	Unifoliate- Trifoliate- Canopy			$.16\text{-}.68(F_2F_3)$			PI 207 262, GN Neb. 1 Sel 27

[1] Calculated on maximum values among four inoculations on each plant.

[2] Calculated on the average of four inoculations on each plant.

Table 2. Heritability calculated by two statistical methods on the same data (Faure, 1988).

Population	Heritability	
	Broad sense	βph
DOR 41 x XAN 91	40	90
DOR 60 x XAN 112	59	52
BAT 58 x XAN 112	51	52
BAT 304 x XAN 112	42	88
XAN 19 x ICA Pijao	46	90
DOR 44 x XAN 87	25	75
$\bar{X}$	44	75

Table 3. Heritability calculated by two statistical methods for the same crosses (Oliveira, 1987).

Cross	Foliar unit	h^{2}ns (by variance)	βph	
			Over two seasons	Within the same season
Rio Doce x XAN 112	Trifoliate	.54	.51	.37
	Canopy	.76	.26	.46
Ouro x XAN 112	Trifoliate	.33	.87	.57
	Canopy	.34	.63	.41
Catu x XAN 40	Trifoliate	.18	.41	.28
	Canopy	.34	.69	.37

35671

DEVELOPMENT OF APPROPRIATE BREEDING STRATEGIES FOR RESISTANCE TO *Empoasca kraemeri* IN COMMON BEAN

Julia Kornegay and Cesar Cardona*

Introduction

The leafhopper *Empoasca kraemeri* (Homoptera: *Cicadellidae*) is generally considered to be the most important insect pest of common bean in many areas of Latin America and the Caribbean Islands with yield losses up to 96% being reported (Bonnefil, 1965; Gutierrez et al., 1975; Eskafi and Schoonhoven, 1981).

Feeding damage by *E. kraemeri* is most severe during hot, dry climatic conditions that occur during flowering and pod-setting growth periods (Schoonhoven et al. 1978). Symptoms of leafhopper feeding damage are yellowing and downward curling of the leaves, followed by necrosis at the leaf tip and margins. Plant growth is stunted, and pod number and seed weight are reduced. Under heavy infestations susceptible bean varieties may die.

Germplasm Evaluations for Sources of Resistance

Extensive screening of bean germplasm for resistance to *E. kraemeri* has been conducted at CIAT since 1974. Over 18,000 bean accessions from the world's *P. vulgaris* germplasm collection housed at CIAT have been systematically evaluated. The germplasm accessions are rated on the basis of a 1-9 visual damage score, where 1= no damage and 9= severe damage

---

* Plant breeder and Entomologist, respetively, CIAT, A.A. 6713, Cali, Colombia.

(leaves curled and yellowed, often accompanied by necrosis of leaf tissue, and stunted plant growth) (Kornegay and Cardona, 1988). Those accessions showing the least feeding damage are reevaluated in replicated nurseries using both feeding damage scores and a visual estimation of pod number as the selection criteria.

The results of the germplasm screening have shown that no high levels of resistance to *E. kraemeri* exist in these materials. Only low to moderate resistance levels have been identified (CIAT, 1983) with small-seeded black and cream colored bush bean lines of indeterminate growth habit and maturity showing the highest levels of resistance.

Mechanisms of Resistance

Tolerance to leafhopper feeding damage is the most predominant and, as to date, the most important mechanism of resistance in beans. Tolerant bean lines are able to withstand moderate population levels of the insect without a corresponding yield loss as compared to a susceptible check. However, when leafhopper populations are high, even the most resistant materials may suffer considerable yield loss (Kornegay and Temple, 1986).

Nonpreference (antixenosis) to leafhopper oviposition has also been identified in a few resistant bean lines in studies conducted under greenhouse and field conditions (Kornegay et al. 1986; Kornegay et al., 1988). In general, however, the bean lines containing antixenosis resistance to oviposition have smaller plant biomass and lower yields than bean lines tolerant to leafhopper feeding (Kornegay et al., 1988).

Inheritance of Resistance

Resistance to leafhoppers was shown to be quantitatively inherited in studies involving single and double crosses among 14 tolerant bean lines (CIAT, 1978). Further studies showed that the heritability of the tolerance resistance mechanism was low and that F_3 progeny from superior F_2 plants segregated widely, with few showing a uniform high tolerance level to leafhopper attack (Galwey and Evans, 1982). The low heritability estimates were concluded to be influenced by limited genetic variation for resistance and to the difficulties of adequately rating the resistance reaction of the plants.

Kornegay and Temple (1986) conducted inheritance and combining abilities studies with bean lines containing tolerance and antixenosis to oviposition resistance mechanisms. A generation means analysis using parental lines, F_1, F_2, and backcross generations was studied, with EMP 81 (a tolerant bean line) and EMP 89 and EMP 94 (nonpreferred for oviposition) crossed to a susceptible cultivar BAT 41. The results showed that the additive-dominance genetic model was sufficient to explain the inheritance of tolerance and nonpreference resistance (Table 1). These results indicated that epistatic effects had a minimal effect on the expression of the traits studied. Both additive [d] and dominance [h] gene effects were significant for damage scores and nonprotected yield, although dominance effects were more important in the inheritance of yield. For nymphal counts (a measure of nonpreference to oviposition) only additive gene effects were significant for the progeny of EMP 89 and EMP 94. The non-significant genetic variation for nymphal count in the tolerant by susceptible cross (EMP 81 x BAT 41) suggested that EMP 81 and BAT 41 were similar at all or most loci influencing their suitability for oviposition by E. kraemeri.

To determine whether overall resistance levels could be increased by combining different resistant mechanisms, a diallel study was conducted using the F_1 and F_2 progeny of crosses among five resistant bean lines: EMP 81 and EMP 82, tolerant to leafhopper feeding damage, and three lines EMP 89, EMP 94, and EMP 97, nonpreferred for oviposition (Kornegay and Temple, 1986).

General combining ability (GCA) which reflects the average performance of a genotype in hybrid combination and is primarily a measure of additive and/or digenic variance was significant for nymphal counts and damage scores in the F_1 and F_2 generations, and for protected F_1 yield (Table 2).

Specific combining ability (SCA), which is detected whenever specific hybrid combinations perform better or worse than what would be expected based on the average performance of the parental lines, and is a result of dominance and other nonadditive gene action, was *significant* for F_1 and F_2 damage scores and nonprotected yield, F_1 protected yield, and F_2 nymphal counts (Table 2).

For nymphal counts, damage scores, and protected F_1 yield, the GCA mean squares were greater than SCA (Table 2). For nonprotected yield, the large SCA mean squares indicated that dominance and other nonadditive gene effects were more important in the inheritance of this trait.

Estimates of GCA effects showed that the progeny of crosses involving the tolerant lines EMP 81 and EMP 82 tended to have higher nymphal populations, while progeny of lines resistant to leafhopper oviposition, EMP 89 and EMP 94 had lower nymphal populations (Table 3).

Estimates of SCA effects for nonprotected yield showed that certain cross combinations performed better (or worse) than what would have been expected on the bases of parental perfomance (Table 4). In the F_2 generation one cross combining tolerant and nonpreferred lines (EMP 81 x EMP 94) had significant positive SCA effects while another tolerant by antixenosis cross (EMP 82 x EMP 97) had significant negative SCA effects. The highest yielding cross under nonprotected conditions was between two nonpreferred lines (EMP 94 x EMP 97). These results indicated that transgressive segregation for higher levels of leafhopper resistance may be obtained in progeny of crosses among resistant lines.

Development of Appropriate Selection Strategy for Leafhopper Resistance

In 1976, a breeding program for increasing leafhopper resistance in beans was initiated at CIAT. The original parents used were germplasm accessions containing low to moderate levels of resistance. Pedigree selection procedures were used to advanced generations with the main selection criteria being low visual damage scores. Yield trials were conducted on the F_5 and later generations with the superior lines subsequently coded as EMP lines. These lines and other promising germplasm were then intercrossed to form the second cycle of a recurrent selection program.

After five cycles, progress had been made in diversifying resistance mechanisms (Kornegay et al., 1986) though the overall progress as measured by increased nonprotected yields compared to superior checks, was not significant (Pino and Kornegay, 1985). Several reasons could be given for the lack of overall progress:

1. low levels of resistance in P. vulgaris germplasm
2. resistance associated with specific bean types
3. dominance genetic effects more important in inheritance of resistance
4. significant genotype x environmental interaction make selection and evaluation results variable
5. only moderate correlation between feeding damage score (the principal selection criterion) and nonprotected yield
6. no correlation between insect counts and nonprotected yield

In 1985, the breeding strategy for Empoasca resistance was changed. The changes reflected a better understanding of the problems listed above and offered an alternative solution for overcoming the genetic limitations of leafhopper resistance.

The first objective of the new breeding program was to initiate a population improvement program to develop a core population of different bean lines with high levels of resistance to leafhoppers from which resistant varieties could be developed.

The strategy utilizes a modified recurrent selection and intermating program where nonprotected yield is the principal selection criteria for resistance (Table 4). Yield trials are conducted in the F_3, F_5, and F_6 generations under natural, dry season infestations of the leafhopper. The F_2 and F_3 generations are carried forward as single seed descent (actually one pod/plant) with some selection made among populations to eliminate inferior crosses as compared to the checks. The best materials (high nonprotected yield and low percent yield reduction) from the F_6 yield trial are crossed among themselves and also crossed with other leafhopper resistance sources, thus, beginning the next cycle in the recurrent selection program. For the first objective, little emphasis is placed on grain color, plant type or resistance to other diseases or pests.

The second objective of the breeding program is to develop leafhopper resistant bean varieties in a wide range of grain types and with acceptable agronomic traits. Selected lines coming out of the recurrent selection program which have commercially acceptable seed colors and growth habits can be increased immediately for varietal testing, or they can be crossed to other agronomically acceptable varieties that represent a wide range of bean types. These crosses can be handled in several ways. One way is to enter the crosses into a mainstream breeding program where the offspring are evaluated for overall agronomic value, including resistance to several diseases or other constraint factors, and acceptability of grain types. Generally, a dilution of resistance to leafhoppers occurs in this type of program, but varieties with lower levels of multiple resistance to several major constraint factors may be adequate in areas where several constraints occur together. A second way is to enter the crosses into the leafhopper breeding nursery and select for high levels of resistance in commercial types. Large populations may be needed to find the desired genotype, and again bulk or single seed descent practices of advancing generations are recommended. Yield trials need to be conducted over several seasons to detect possible genotype x environment interaction.

Preliminary results of new breeding strategy

The first F_6 materials originating from the new breeding strategy showed that positive progress was made in increasing overall resistance levels to leafhoppers. For the first time, resistant selections had higher nonprotected yield and lower percent yield reduction than the resistant check ICA PIJAO (Table 6). Progress was also made in transferring resistance into medium size determinate bush beans (Table 7), and F_3 populations of white seeded materials had higher nonprotected yields than the best white seeded check, EMP 175 (Table 8).

All three sets of materials indicate that the new breeding program is completing its objectives: first by increasing overall resistance and surpassing the resistance level of the best check, and second, by transferring resistance into determinate and white seeded types - two groups where little progress had been obtained in earlier breeding efforts.

Conclusion

The modified recurrent selection program begun in 1985, utilizes yield measurements as the criteria for selection of resistant offspring, and breeding lines with superior resistance levels have been obtained in a variety of bean grain types. The advantages of this breeding strategy are: 1) that selection for additive genetic effects conditioning resistance within families is enhanced by waiting until the F_4 and F_5 generations (when genotypes are relatively fixed) to make the majority of selections within families; 2) selection is made against inferior crosses in the F_2 and F_3 generations, thereby advancing only those populations with superior specific combining ability; 3) single seed descent practices are used to advance as many different potentially favorable genotypes as possible to a more homozygotic state in the minimum amount of space. This practice increases the chance of finding higher levels of resistant recombinants, especially with quantitatively inherited traits; 4) genotype x environment interactions are minimized by the repeated selection and yield testing of populations over time under natural infestations of the leafhoppers.

Although breeding for resistance to E. kraemeri is a long process of intermating and selection, acceptable progress can be obtained when breeders and entomologists work together to understand the interaction of the insect and the host plant. A thorough knowledge of the genetics of resistance is needed to design an appropriate resistance breeding strategy. Controlled field infestations are essential to identify small differences in resistance levels. The end product is the development of leafhopper resistant bean lines. Host plant resistance is considered the most reasonable approach for control of this pest by farmers who can not obtain or afford pesticides.

References

Bonnefil, L. 1965. Las plagas del fríjol en Centroamérica y su control. p. 95-103. In, XI Reunión Anual PCCMCA, Panamá.

CIAT. 1978. Annual Report 1977. Cali, Colombia, pp. B20-B28.

CIAT. 1983. Annual Report 1982. Cali, Colombia, pp. 54-63.

CIAT. 1985. Annual Report 1984. Cali, Colombia, 302 p.

CIAT. 1986. Annual Report 1985. Cali, Colombia, 372 p.

CIAT. 1987a. Annual Report 1986. Cali, Colombia (in press).

Eskafi, F.M. and A. van Schoonhoven. 1981. Interactions of leafhopper population, varietal resistance, insecticide treatment, and plant growth on bean yields in a tropical environment. J. Econ. Entom. 74:7-14.

Galwey, N.W. and A. M. Evans. 1982. The inheritance of resistance to Empoasca kraemeri Ross and Moore in the common bean, Phaseolus vulgaris L. Euphytica 31:933-952.

Gutiérrez, U.M.; M. Infante and A. Pinchinat. 1975. Situación del cultivo de fríjol en América Latina. Centro Internacional de Agricultura Tropical, CIAT. Series ES-19.33 p.

Kornegay, J.L.; C. Cardona and A. van Schoonhoven. 1986. The mechanisms of resistance in common beans to the leafhopper Empoasca kraemeri. Entom. Exp. Appl. 40:273-279.

Kornegay, J.L. and S.R. Temple. 1986. Inheritance and combining ability of leafhopper defense mechanisms in common bean. Crop Sci. 26:1153-1158.

Kornegay, J.L. and C. Cardona. 1988. Breeding for insect resistance in beans. CIAT publication (in press).

Kornegay, J.L.; C. Cardona J. van Esch and M. Alvarado. 1988. Identification of common bean lines with ovipositional resistance to Empoasca kraemeri (Homoptera: Cicadellidae). J. Econ. Entomol. (in press).

Pino, A. C. and J. Kornegay. 1985. Evaluación de líneas de fríjol (Phaseolus vulgaris L.) provenientes de cinco ciclos de fitomejoramiento por selección recurrente para obtener resistencia a Empoasca kraemeri Ross and Moore. In Congreso de la Sociedad Colombiana de Entomología, 12o, Medellín, Colombia, SOCOLEN, 1985. Resúmenes.

Schoonhoven, A. van; L.A. Gómez and F. Avalos. 1978. The influence of leafhopper (Empoasca kraemeri) attack during various bean (Phaseolus vulgaris) plant growth stages on seed yield. Ent. Exp. Appl. 23:115-120.

Table 1. Estimates of mean (m), additive (d) and dominance (h) gene effects from generation means analysis of leafhopper resistance[a].

Crosses (x BAT 41)	[m]	[d]	[h]	X^2[b]	P
Nymphs					
EMP 81	6.70**	0.72	0.72	0.72	0.90-0.75
EMP 89	5.25**	0.67**	0.59	0.16	0.99-0.97
EMP 94	7.01**	1.90*	-2.29	1.43	0.75-0.50
Damage scores					
EMP 81	3.78**	0.53**	-0.34*	0.94	0.90-0.75
EMP 89	3.67**	0.65**	-0.58**	0.71	0.90-0.79
EMP 94	3.67**	0.65**	-0.68**	0.13	0.99-0.90
Yield/plant					
EMP 81	14.25**	-5.04**	-7.06**	6.89	0.10-0.05
EMP 89	13.81**	-4.25**	8.39**	3.88	0.50-0.25
EMP 94	13.87**	-4.55**	9.53**	1.84	0.75-0.50

*,** Indicate significance at P = 0.05 or P = 0.01 lavels, respectively.

[a] Adapted from Kornegay and Temple (1986).

[b] X^2 denotes chi-square value for testing goodness of fit; P denotes probability level.

Table 2. Mean squares of the diallel analysis for leafhopper resistance in F_1 and F_2 generations[a].

Source of variation	df	Mean squares							
						g/plant			
		Nymphal count		Damage score		Non protected yield		Protected yield	
		F_1	F_2	F_1	F_2	F_1	F_2	F_1	F_2
Genotypes	14	5.96**	28.2**	0.47**	0.72**	3.23**	32.2**	4.44**	32.9
GCA	4	14.56**	65.4**	0.77**	1.24**	2.35	14.9	5.65**	-
SCA	10	2.52	13.3**	0.35**	0.51**	3.59**	39.2**	3.95**	-
Error	28	2.23	3.8	0.06	0.15	1.21	6.27	0.89	29.5

** Mean squares significant at P = 0.01 level.

[a] Adapted from Kornegay and Temple, 1986.

Table 3. Progeny means and estimates of general combining ability (GCA) effects for each parental line in F_1 and F_2 diallel analisys for leafhopper resistance[b].

	Nymphal count				Damage score			
	F_1		F_2		F_1		F_2	
Parent	Mean	GCA	Mean	GCA	Mean	GCA	Mean	GCA
EMP 81	7.9b[a]	0.74	13.2cd	1.38*	2.8b	0.33**	2.8b	0.30**
EMP 82	8.1b	1.06**	14.0d	2.23**	2.4a	-0.04	2.7b	0.11
EMP 89	6.2a	-0.92*	9.4a	-1.52**	2.3a	-0.12	2.2a	-0.34**
EMP 94	5.9a	-0.97*	11.2bc	-1.74**	2.4a	-0.05	2.3a	-0.12
EMP 97	7.1ab	0.04	10.7b	-0.34	2.3a	-0.12	2.6b	0.04

*,** Estimates of GCA effects significantly different from zero at P = 0.05 and P = 0.01 levels, respectively.

[a] Means within a column followed by the same letter are not significantly different (Waller-Duncan multiple comparison, K ratio = 100).

[b] Adapted from Kornegay and Temple, 1986.

Table 4. Cross means and estimates of specific combining ability (SCA) effects for nonprotected yield (g/plant) in F_1 and F_2 generations in a 5 parent diallel analysis[b].

	F_1		F_2	
Cross	Mean	SCA	Mean	SCA
EMP 81 X EMP 82	3.9 ab[a]	0.10	11.0 cde	0.93
EMP 81 X EMP 89	5.9 b	2.42**	13.9 def	2.40
EMP 81 X EMP 94	3.6 a	0.59	14.9 ef	3.44*
EMP 81 X EMP 97	3.0 a	-0.34	6.7 ab	-2.91
EMP 82 X EMP 89	3.1 a	-0.37	8.4 abc	-2.24
EMP 82 X EMP 94	3.3 a	0.36	10.2 bcd	-0.40
EMP 82 X EMP 97	4.0 ab	0.67	4.9 a	-3.86*
EMP 89 X EMP 94	2.5 a	-0.22	13.4 def	1.37
EMP 89 X EMP 97	3.3 a	0.23	7.0 abc	-3.18
EMP 94 x EMP 97	3.3 a	0.76	15.7 f	5.56**

*,** Estimates of SCA effects significantly different from zero at $P = 0.05$ and $P = 0.01$ levels, respectively

[a] Means within a column followed by same letter and not significantly different (Waller-Duncan multiple comparison, k-ratio = 100).

[b] Adapted from Kornegay and Temple, 1986.

Table 5. A modified recurrent selection program for *Empoasca* resistance in beans[a]

Generation	Procedures for population improvement
(Cycle 1) Parental lines	Intercrosses are made among germplasm accessions and bean lines previously shown to have resistance to *E*. *kraemeri*.
F_1	The hybrids are grown under protected conditions in order to obtain the maximum quantity and quality of seeds. F2 seed from each cross is bulked.
F_2	F2 seed (600-1000) from each cross are planted in a block in the field under natural leafhopper infestation.
	At harvest, the F2 populations that are visually inferior are eliminated. From the remaining populations, 1 pod (app. 3 seeds) is taken from each plant in a cross and the seed is bulked (app. 1500 seed/cross).
F_3	Each bulk is yield tested under leafhopper stress. Selection among F3 populations is made on the basis of yield data compared to resistant and susceptible checks. The F4 seed is bulked.
F_4	The bulked seed is space planted in the field under leafhopper stress. Individual plant selections with the highest visible yield are made within each F4 population.
F_5	Progeny rows of individual selections are planted under leafhopper stress. Selections are made among sister lines at harvest of the highest yielding lines and each selected line is bulk harvested.
F_6	A yield trial of the selected lines with nonprotected and protected field treatments is planted. Nonprotected yield and percentage yield reduction are used to select top lines with highest levels of resistance.
(Cycle 2) Parental lines	The second cycle of intermatings are made using resistant selections plus other germplasm.

[a] CIAT (1985)

Table 6. Yield of best F6 lines developed using the new breeding strategy to increase overall resistance levels to Empoasca kraemeri (CIAT, 1986)[c]

Lines	Color	Yield (kg/ha)		% yield reduction
		Nonprotected	Protected	
EMP 187	9	1711	3137	45.4
EMP 188	3	1335	2971	55.1
EMP 189	9	1276	2820	54.7
EMP 190	3	1238	2795	55.7
EMP 191	9	1233	3115	60.4
EMP 192	9	1151	3286	65.0
EMP 193	3	1109	2342	52.6
EMP 84[a]	9	1061	3010	64.7
EMP 135[a]	3	788	2841	72.3
ICA PIJAO[a]	9	1297	3863	66.4
BAT 41[b]	6	263	1786	85.3
LSD 5%			412.9	700.8
CV			29.9	17.0

[a] Resistant check

[b] Susceptible check

[c] Adapted from CIAT (1986)

Table 7. Best determinate bush bean lines developed using the new breeding strategy for resistance to *Empoasca kraemeri*[a]

Lines	Color	100-seed weight (g)	Nonprotected yield (kg/ha)		% yield reduction
			1986B	1987A	
EMP 177	6M	29	1114	385	29.8
EMP 178	6M	34	1102	596	35.5
EMP 179	7M	25	903	600	39.9
EMP 182	6M	33	807	495	39.9
EMP 184	7M	34	776	399	53.9
EMP 185	7M	30	749	488	50.4
EMP 186	6M	26	718	383	52.9
Checks:					
ICA P 11	6M	35	459	89	67.1
BAT 1366	6M	32	404	203	66.8
LINEA 24	6M	39	365	114	75.7
A 36	6M	30	-	200	63.2
LSD 5%			254	177	-
C.V.			22.6	25.6	-

[a] Adapted from CIAT (1987)

Table 8. Best F_3 populations developed using the new breeding strategy for resistance to *Empoasca kraemeri*[b]

Population	Color	Yield (kg/ha)		% yield reduction
		Nonprotected	Protected	
ER 13815-CM(V)	1	896	984	8.9
ER 13816-CM(V)	1	866	964	10.2
ER 13817-CM(V)	1	870	1027	15.3
ER 13861-CM(V)	1	967	1024	5.6
ER 13870-CM(V)	1	1085	1296	16.3
ER 13844-CM(V)	6	931	1134	17.9
ER 13848-CM(V)	6	756	894	15.4
EMP 175[a]	1	702	1058	33.6
BAT 41[a]	6	675	1325	49.0
LSD 5%		287	393	-
C.V.		20.6	20.1	-

[a] Checks

[b] Adapted from CIAT (1987)

BREEDING FOR YIELD IN COMMON BEAN OF MIDDLE-AMERICAN ORIGIN

Shree P. Singh*

Summary

Extreme care should be exercised in parental selection for hybridization for yield breeding in common bean, Phaseolus vulgaris L. For non-stress environments, high yielding parents and parents with positive general combining ability for yield should be crossed with other yield promoting traits. Under stress environments these must be combined with tolerance to factors causing yield losses.

Hybrid populations should be yield tested in replicated trials in F_2 and F_3 and all low yielding crosses should be discarded as soon as identified. Thus, selection for improved lines should be done only in large populations and among families of high yielding crosses.

Introduction

The purpose of most crop breeding programs is to increase and stabilize yield at a production cost which maximizes returns to the farmers. Where growing conditions are consistently favorable, yield increases by breeding can presumably be brought about by accumulation of genes which maximize biomass production and efficient partitioning of assimilates. Under unfavorable environments, initial yield increases, also stabilizing yield and reducing production costs, can be obtained by breeding for tolerance to factors causing crop losses (e.g., diseases, genes which maximize biomass production and efficient partitioning of

---

* Bean Breeder, CIAT, A.A. 6713, Cali, Colombia.

genes which maximize biomass production and efficient partitioning of assimilates. Under unfavorable environments, initial yield increases, also stabilizing yield and reducing production costs, can be obtained by breeding for tolerance to factors causing crop losses (e.g., diseases, insects, drought, and low soil fertility). However, subsequent increases in yield can be brought about only by simultaneous accumulation of favorable genes for yield and tolerance to adverse biotic and abiotic factors.

Most dry bean (Phaseolus vulgaris L.) production occurs under stress conditions where average dry bean yields are low (≤ 600 kg/ha). These production regions occur in tropical and sub-tropical Latin America and Africa where farm sizes are small, bean is often intercropped for subsistence, and farmers rarely apply inputs. Severe yield losses are caused by diseases, insects, adverse climatic and edaphic factors, and other problems.

Singh (1988, 1989) described 12 gene pools for dry cultivated common bean and their association with yielding ability, cropping systems, and growing environments to facilitate breeding work and germplasm resource management. Six of these belonged each to Middle and South American center of domestication. Germplasm representing each of the 12 gene pools of dry bean is presently grown commercially, although they vary greatly in their yield potential and relative global economic importance. The objective of this paper is to discuss breeding for maximum yield, in favorable environments, for common bean of Middle-America.

Selection Criteria

Morphological, physiological and yield components are often suggested as selection criteria for maximizing yield. The usefulness of these traits will be discussed here with reference to bean yield improvement.

Physiological traits

Physiological traits have often been suggested as selection criteria (Wallace, 1973; Wallace et al., 1972; Wallace and Munger, 1966; Laing et al., 1984; Vieira et al. 1973) but rarely have proven their worth (Wallace et al., 1976; Kueneman et al., 1979) and utilized in selection programs to maximize productivity potential of common bean.

Morphological characters

In common bean node and leaf number and plant height are positively associated with pod number, and consequently, with seed yield (Adams, 1982; Aggarwal and Singh, 1973; Coyne, 1968; Denis and Adams, 1978; Duarte and Adams, 1972; Laing et al., 1984; Nienhuis and Singh, 1985; Prakash and Ram, 1981). Adams (1973, 1982) advocated the utilization of morphological traits as selection criteria and provided a description of an ideotype for sole crop to maximize yield of Navy bean in Michigan. Moreover, due to larger additive genetic control (Nienhuis and Singh, 1986), their higher heritability (Paniagua and Pinchinat, 1976), and ease of visualization, selection for architectural traits is much easier than selection for physiological traits, yield and yield components. For example, selection for high node number to develop small-and medium-seeded lines of growth habits I and II such as 'A 132', 'A 156', 'A 157', 'A 475', and others (Singh and Gutiérrez, 1982) was accomplished by selecting tall, upright plants with small leaves. Some of these were compared at 16 plant density-environment combinations under high inputs (Nienhuis and Singh, 1985). However, none of the improved architectural lines yielded significantly more than their respective check cultivars. Component compensation (Adams, 1967), deficient agronomic management, and limitations of the growing environment could be among possible causes for low yield. Moreover, contrary to our above results, some improved architypes of Navy bean outyielded classic type check cultivars of similar growth habit II in comparative yield trials in Michigan (Adams, 1982; Izquierdo and Hosfield, 1983). The increase in yield was thought to be due to improved lodging resistance due to reduced branching and a narrowing of the plant canopy.

Yield and its components

In dry bean, some attempts to improve seed yield have been ineffective (Coyne, 1968; Duarte, 1966; McFerson, 1983; Patiño and Singh, 1989; Sarafi, 1978; Singh et al., 1989b; Sullivan and Bliss, 1983; Tolla, 1978). Failure to increase seed yield in bean is attributed to (1) the lack of desirable alleles in the base population (Singh et al., 1989b; Tolla, 1978), (2) low narrow sense heritability of yield (Chung and Stevenson, 1973; Coyne, 1968; Mutschler and Bliss, 1981; Nienhuis and Singh, 1988b; Paniagua and Pinchinat, 1976; Zimmermann et al., 1984), (3) large genotype x environment interaction (Coyne, 1968), (4) negative compensatory effect of yield promoting traits (Adams, 1982, 1967; Nienhuis and Singh, 1985), (5) zero or negative general combining ability of high yielding small-seeded commercial cultivars (Nienhuis and Singh, 1988a), and (6) dependance on visual selection for seed yield in early segregating generations.

Parental Performance and Combining Ability

Seed yield and its components in common bean are quantitatively inherited. Hamblin and Evans (1976) and Nienhuis and Singh (1988b) provided evidence for the importance of additive genetic variance in the inheritance of yield and its components. This suggested that high, stable yielding parents should result in good progenies (provided these do not carry complementary genes for hybrid disgenesis), and that poorly performing crosses could be discarded in early generations without hesitation. In a subsequent study of the general combining ability (GCA) of a large number of mostly small-seeded bean lines and cultivars it was found that the high yielding bean cultivars of growth habits II and III in Latin America (e.g., 'ICA Pijao', 'Porrillo Sintetico', 'Jamapa', 'Carioca', 'Rio Tibagi', etc.) possessed either zero or negative GCA for yield and most yield components (Nienhuis and Singh, 1988a).Moreover, crosses among such parents did not produce lines yielding higher than the best parent (Singh et al. 1989b). Nonetheles, from quantitative genetic analyses, it was evident that in order to increase yield in common bean, among yield and its components, yield per se should be utilized as primary selection criterion (Nienhuis and Singh, 1988b). Thus it became necessary to consider simulataneously (1) parental performance per se, (2) parental general combining ability, and (3) early generation yield testing in any selection program designed to improve yield of bean cultivars of Middle-America. Some data supporting these conclusions were obtained from selection experiments (Singh et al., 1989a).

Heterosis and Inbreeding Depression

While heterosis for yield cannot be commercially exploited in bean at the moment (Gutiérrez and Singh, 1985; Nienhuis and Singh, 1986), crosses with high positive heterotic values should result in greater recombinational variability in F_2 and subsequent generations and would, therefore, provide greater opportunities for effective selection for yield factors (Ghaderi et al., 1984). Such crosses would be of special value if their yields were more than the highest yielding check cultivars and did not exhibit inbreeding depression in the subsequent generation. In Table 1, examples of four kinds of single crosses of bush bean, based on their F_1 and F_2 yields, are given. High yielding heterotic crosses with minimal inbreeding depression and exhibiting transgressive segregation in the F_2 generation (the bottom two groups in Table 1) ought to be elected for further evaluation and selection, since these should carry a high proportion of high yielding genotypes.

Selection Methods

Recurrent selection

After repeated cycles of phenotypic recurrent selection based on F_2 testing, it was possible to combine strong, erect, upright plant types (growth habit IIA and IIB) of small-seeded cultivars in pinto bean which, traditionally, have medium-sized seeds and a sprawling growth habit III with weak stems (Kelly and Adams, 1987). Comparative yield data are not available yet to indicate whether recombinant lines yield equal or better than either pinto or small-seeded architypes used as the source of stem erectness in this program. Duarte (1966), after two cycles of recurrent selection in cross of 'Algarrobo' x 'Michelite' did not realize any increase in yield at any of the three locations in North or South America. Tolla (1978) failed to increase either bean yeild or protein content after two cycles of recurrent selection. Sullivan and Bliss (1983) were able to increase protein content but could not obtain yield gains from recurrent mass selection based on a desired gain index in common bean.

Inbred-backcrossing

St. Clair and Bliss (pers. comm., 1988) have successfully used inbred-backcross procedure to transfer and combine high N_2 fixation and high yield from bean cultivar 'Puebla 152' to 'Sanilac'. The cultivar 'Puebla 152' is an indeterminate type III from the highlands of Mexico. On the other hand, ''anilac' is a small-seeded (<25 g/100 seeds) Navy bean, determinate cultivar of growth habit I from Michigan. In their program two backcrosses to the recurrent parent followed by two or three generations of selfing often suffice.

Early generation yield test

Frey (1954) and Lupton and Whitehouse (1957) discussed limitations of conventional pedigree and bulk selection methods in the improvement of self-pollinating cereal crops and emphasized the value of quantitative yield data in the early generations for selection. The latter authors proposed two methods: F_2 progeny tests followed by yield trials without further selections in F_4, F_5, and F_6, and the pedigree trial method (i.e. conventional pedigree selection combined with yield test from F_4 onwards). Frey (1954) used only the first of the two methods in barley crosses and found it to be superior over conventional pedigree and bulk hybrid methods.

Harrington (1940) in wheat and Immer (1941) in barley reported that a reliable estimate of the value of a cross as a source of high yielding lines could be made from a study of the yields obtained in trials of unselected bulks in early generations. On the other hand, Atkins and Murphy (1949) in oats and Fowler and Heyne (1955) in wheat failed to find any such relation.

Use of any form of bulk or mass method of selection would be undesirable when it can significantly reduce frequency of some desirable genotypes. In studies of the effects of intergenotypic competition in mechanical mixtures of dry bean lines of different growth habits and seed sizes, generally high yielding lines in pure stand, characterized by small-seed and indeterminate growth habit were found to have a competitive advantage in mixtures over poor yielding determinate and large seeded genotypes (Dessert, 1987). The latter were eliminated when selection was practiced for seed yield in crosses of these with indeterminate small-seeded types (Singh et al., 1989a).

Hamblin (1977) and Hamblin and Morton (1977) observed that in common bean the bulk method of breeding did not alter the mean yield performance over generations in high yielding crosses but yield increased over generations in low yielding crosses.

Yield testing in replicated trials under high population density ($\leq$ 250,000 plants ha^{-1}) in the F_2 and F_3 was incorporated in our program in 1986 (Figure 1). At least 20% of the lower yielding crosses are eliminated in each successive generation, thus leaving only 60% of the initial F_2 populations for single plant selections in F_4.

For various reasons we are finding this method (Figure 1) useful in our program. It allows us to handle a relatively large number of crosses (200/year). In the F_2 and F_3 generations of hybrid populations, single pods from each plant (SPD) are harvested and bulked together on a cross basis before harvesting the plots for yield. After data analyses only the bulk of pods from selected crosses are saved for yield trials in the following generation. Also, yield testing of the F_2 and F_3 generations is done at different sites in order to minimize genotype x environment effect and seek relatively broader adaptation and stability of performance in experimental lines in advanced generations. SPD is preferred over single seed descent (SSD) (Brim, 1966); because it facilitates harvest, minimizes labor cost, and the probability of complete loss of favorable alleles (Sneep, 1977) are reduced as all seed is bulked together for yield testing in the field under some pressure of intergenotypic competition and natural selection (unlike advancing generations in SSD in separate hill-plot for each F_2 derived plant in glasshouse in temperate environments). In SSD, advanced experimental lines can easily be traced back to the original F_2 plants but not in the SPD method adopted in our program. In general, there is some increase (40-60%) in population size in successive generations of SPD.

References

Adams, M. W. 1967. Basis of yield component compensation with special reference to the field bean Phaseolus vulgaris. Crop Sci. 7:505-510.

Adams, M. W. 1973. Plant architecture and physiological efficiency in the field bean. p. 266-278. In: Potentials of field bean and other legumes in Latin America. Series Seminars No. 2E. Centro Internacional de Agricultura Tropical, Cali, Colombia.

Adams, M. W. 1982. Plant architecture and yield breeding. Iowa State J. Res. 56:225-254.

Aggarwal, V. D. and T. P. Singh. 1973. Genetic variability and interrelation in agronomic traits in kidney-bean (*Phaseolus vulgaris* L.). Indian J. Agric. Sci. 43:845-848.

Atkins, R. E. and H. C. Murphy. 1949. Evaluation of yield potentialities of oat crosses from bulk hybrid tests. J. Amer. Soc. Agron. 41:41-45.

Brim, C. A. 1966. A modified pedigree method of selection in soybeans. Crop Sci. 6:220.

Chung, J. H. and E. Stevenson. 1973. Diallel analysis of genetic variation in some quantitative traits in dry beans. N. Z. J. Agric. Res. 16:223-231.

Coyne, D. P. 1968. Correlation heritability and selection of yield components in field beans, *Phaseolus vulgaris* L. Proc. Am. Soc. Horticul. Sci.93:338-396.

Denis, J. C. and M. W. Adams. 1978. A factor analysis of plant variables realted to yield in dry beans. I. Morphological traits. Crop Sci. 18:74-78.

Dessert, J. M. 1987. Changes overtime in the proportion of beans in a varietal mixture. Annu. Rep. Bean Impr. Coop. 30:79-80.

Duarte, R. A. 1966. Responses in yield and yield components from recurrent selection practiced in a bean hybrid population at three locations in North and South America. Diss. Abstr. 27:1339B-1340B.

Duarte, R. A. and M. W. Adams. 1972. A path coefficient anaylisis of some yield component interaction in fields beans (*Phaseolus vulgaris* L.). Crop Sci. 12:579-582.

Fowler, W. L. and E. G. Heyne. 1955. Evaluation of bulk hybrid tests for predicting performance of pure line selections in hard red winter wheat. Agron. J. 47:430-434.

Frey, K. J. 1954. The use of F_2 lines in predicting the performance of F_3 selections in two barley crosses. Agron. J. 46:541-544.

Ghaderi, A., M. W. Adams and H. M. Nassib. 1984. Relationship between genetic distance and heterosis for yield and morphological traits in dry edible bean and faba bean. Crop Sci. 24:37-42.

Gutiérrez, J. A. and S. P. Singh. 1985. Heterosis and inbreeding depression in dry bush beans, Phaseolus vulgaris L. Can. J. Plant Sci. 65:243-250.

Hamblin, J. 1977. Plant breeding interpretations of the effects of bulk breeding on four populations of beans (Phaseolus vulgaris L.). Euphytica 26:157-168.

Hamblin, J. and A. M. Evans. 1976. The estimation of cross yield using early generation and parental yield in dry beans (Phaseolus vulgaris L.) Euphytica 25:515-520.

Hamblin, J. and J. R. Morton. 1977. Genetic interpretations of the effects of bulk breeding on four populations of beans (Phaseolus vulgaris L.). Euphytica 26:75-83.

Harrington, J. B. 1940. Yielding capacity of wheat crosses as indicated by bulk hybrid tests. Canad. J. Res. 18:578-584.

Immer, F. R. 1941. Relation between yielding ability and homozygosis in barley crosses. J. Amer. Soc. Agron. 33:200-206.

Izquierdo, J. A. and G. L. Hosfield. 1983. The relationship of seed filling to yield among dry beans with differing architectural forms. J. Amer. Sco. Hort. Sci. 108:106-111.

Kelly, J. D. and M. W. Adams. 1987. Phenotypic recurrent selection in ideotype breeding of pinto beans. Euphytica 36:69-80.

Kueneman, E. A., D. H. Wallace and P. M. Ludford. 1979. Photosynthetic measurements of field-grown dry beans and their relation to selection for yield. J. Amer. Soc. Hort. Sci. 104:480-482.

Laing, D. R., P. G. Jones and J. H. C. Davis. 1984. Common beans (Phaseolus vulgaris L.) p. 305-352. In: P. R. Goldsworthy and N. Fisher (eds.). The physiology of tropical field crops. John Wiley and Sons, New York.

Lupton, F. G. H. and R. N. H. Whitehouse. 1957. Studies on the breeding of self-pollinating cereals. I. Selection methods in breeding for yield. Euphytica 6:169-184.

McFerson, J. R. 1983. Genetic and breeding studies of dinitrogen fixation in common bean (Phaseolus vulgaris L.). Diss. Abstr. 44:701B.

Mutschler, M. A. and F. A. Bliss. 1981. Inheritance of bean seed globulin content and its relationship to protein content and quality. Crop Sci. 21:289-294.

Nienhuis, J. and S. P. Singh. 1985. Effect of location and plant density on yield and architectural traits in dry bush beans. Crop Sci. 25:579-584.

Nienhuis, J. and S. P. 1986. Combining ability analyses and relationships among yield, yield components, and architectural traits in dry bean. Crop Sci. 26:21-27.

Nienhuis, J. and S. P. Singh. 1988a. Genetics of seed yield in common bean of Middle-American origin. I. General combining ability. Plant Breed. 101:143-154.

Nienhuis, J. and S.P. Singh. 1988b. Genetics of seed yield in common bean of Middle-American origin. II. Genetic variance, heritability, and expected response from selection. Plant Breed. 101:155-163.

Paniagua, C. V. and A. M. Pinchinat. 1976. Criterios de selección para mejorar el rendimiento de grano de frijol (Phaseolus vulgaris L.). Turrialba 26:126-131.

Prakash, K. S. and H.H. Ram. 1981. Path coefficient analysis of morphological traits and developmental stages in frech bean. Indian J. Agric. Sci. 51:76-80.

Sarafi, A. 1978. A yield component selection experiment involving American and Iranian cultivars of common bean. Crop Sci. 18:5-7.

Singh, S.P. 1988. Gene pools in cultivated dry bean. Annu. Rept. Bean Improv. Coop. 31:180-182.

Singh, S. P. 1989. Patterns of variation in cultivated common bean (Phaseolus vulgaris, Fabaceae). Econ. Bot. 101:155-163.

Singh, S.P., C. Cajiao, J.A. Gutiérrez, J. García, M.A. Pastor-Corrales and F.J. Morales. 1989a. Response to selection for seed yield in high and low input environments in inter-gene pool crosses of common bean. Crop Sci. (In press).

Singh, S. P. and J. A. Gutiérrez. 1982. Sources of some architectural traits in dry bush beans, Phaseolus vulgaris L. Annu. Rep. Bean Impr. Coop. 25:6-8.

Singh, S. P., C. Urrea, J. A. Gutiérrez, and J. García. 1989b. Selection for yield at two fertilizer levels in small-seeded common bean. Can. J. Plant Sci. (submitted).

Sneep, J. 1977. Selection for yield in early generations of self-fertilizing crops. Euphytica 26:27-30.

Sullivan, J.G. and F. A. Bliss. 1983. Recurrent mass selection for increased seed yield and seed protein percentage in the common bean (Phaseolus vulgaris L.) using a selection index. J. Amer. Soc. Hort. Sci. 108:42-46.

Tolla, G. E. 1978. Effect of post-bloom nutrient applications and recurrent selection on seed yield and seed proteing in common bean (Phaseolus vulgaris L.). Ph.D. Thesis, Univ. of Wisconsin, Madison.

Vieira, C., F. C. Santa Cècilia and C. S. Sediyama. 1973. Indice de colheita de alguns cultivares de feijao. Rev. Ceres 20:120-128.

Wallace, D. H. 1973. Commentary upon plant architecture and physiological efficiency in the field bean. p. 287-294. In: Potentials of field beans and other food legumes in Latin America. Series Seminar 2E. Centro Internacional de Agricultura Tropical, Cali, Colombia.

Wallace, D. H. and H. M. Munger. 1966. Studies of the physiological basis for yield differences. II. Variations in dry matter distribution among areal organs for several dry bean varieties. Crop Sci. 6:503-507.

Wallace, D. H., J. L. Ozbun and H. M. Munger. 1972. Physiological genetics in crop yield. Adv. Agron. 24:97-146.

Wallace, D. H., M. M. Peet and J. L. Ozbun. 1976. Studies of CO_2 metabolism in Phaseolus vulgaris L. and applications in breeding. p. 43-58. In: R. H. Burris and C. C. Black (eds.). CO_2 metabolism and plant productivity, University Park Press, Baltimore, USA.

Zimmermann, M. J. O., A. A. Rosielle, and J. G. Waines. 1984. Heritabilities of grain yield of common bean in sole crop and in intercrop with maize. Crop Sci. 24:641-644.

Table 1. Mean Yield of the F_1 and F_2 generation of some dry bean single crosses grown in replicated trials at CIAT-Palmira, Colombia .

Cross	Generation	
	F_1	F_2
	kg ha^{-1}	
G 4770 X A 23	2030	2624
A 23 X G 7148	2329	2394
ICA L 23 X G 3807	3143	2702
ICA L 23 X A 30	3178	2418
A 23 X G 5066	3023	3103
A 21 X Carioca	3225	3384
G 3807 X Carioca	2875	3146
Carioca X G 7148	3089	3953

From: Gutiérrez and Singh, 1985.

Figures

Fig. 1. Use of early generation yield testing for yield breeding in dry beans at CIAT.

Figure 1. Use of early generation yielding test for yield breeding in dry beans at CIAT.

Month	Generation	Activities	Location*
March	Parent	Intermate among selected parents	C
June	Parent & F_1	Intermate among selected parents & crosses. Save F_2 seed from selected single crosses.	C
September	Parent & F_1	Grow out and save F_2 seeds from selected crosses.	Q
March	F_2	Yield test in replicated trials. Save bulk (single pod from each plant) seed from selected crosses.	P
September	F_3	Yield test and save bulk seeds from selected crosses.	Q
March	F_4	Space-plant selected crosses for maximun number of single plant harvests.	P
September	F_5	Grow plant-progeny-rows. Save bulk seeds from selected lines.	Q
March	F_6	Observation nursery	P
September	F_7	Yield test in replicated plots. Clean seed production at Vijes.	Q,P
January	F_8	Code selected lines for further evaluations.	VEF NAR

* C = CIAT - Palmira, P = Popayan, Q = Quilichao.

35673

BREEDING COMMON BEAN (Phaseolus vulgaris L.) FOR YIELD IN INTERCROP

María José de Oliveira Zimmermann*

Summary

Despite the growing industrialization, increasing modernization and technological sophistication of agriculture, and despite the fact that research has always been biased towards solecropping, intercropping will always represent a good proportion of bean production, especially in tropical areas, due to economical, technical and social reasons.

Among bean researchers, breeders have always been questioned on their work, because most breeding has been done in sole crop.

The present paper discusses some results from the literature on intercropping, addressed to answer the questions that are usually presented to breeders, with the following conclusions: 1 - Germplasm developed for sole crop may be good for intercropping, but this is not always true. 2 - The characteristics of bean plants that would be specifically adapted to intercropping are unknown, but disease resistance is important in all systems. 3 - Due to some conflicting objectives, special breeding programs for intercropping may not be a good option generally. 4 - A better approach might be a combined selection scheme, where early generation selection is made in sole crop, with testing of the best lines of each species as intercrops in all combinations of superior lines of the species,

---

* Bean Breeder, Centro Nacional de Pesquisa de Arroz e Feijao (CNPAF), Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA). Rod. GYN 12, Km. 10, Caixa Postal 179, 74000 Goiania, Goiás, Brasil.

with cultivar release decisions being made on the basis of average yields of all systems tested.

Introduction

Common bean (Phaseolus vulgaris L.) is an autogamous annual legume, often grown in intercrop with other plant species, particularly where subsistence farming is practiced (Wiley and Osiru, 1972). The species that are intercropped, the spacial arrangement and relative density among them, may vary with location and farmers. Beans are most commonly intercropped with maize, but are also found with coffee, sorghum, cassava, sugar cane and other crops.

Intercropping is understood as the growing of two or more crops simultaneously in the same field, where crop competition occurs during all or part of crop growth (Andrews and Kassam, 1976). The more general term "multiple cropping" refers to all systems that include the growing of two or more crops in the same field in a year.

There are not reliable statistics on how much of the bean area is in intercropping in any country, but it is estimated that about 70% of bean production in Latin America comes from intercroping and that the companion species is usually maize (Pinchinat et al., 1976).

With the increasing industrialization in the countries of the developing world, agricultural labor has been decreasing and agricultural practices are changing in order to increase the efficiency of agriculture as a whole. As a consequence, areas devoted to intercropping will tend to decrease. This system is one of intensive land and labour use. It is projected that the decrease will continue until an "equilibrium point" is reached. Although such a point is as yet unknown, in tropical areas intercropping will probably always be important for the production of common bean.

There are many reasons why this is so. Some of them are:

a) Intercropping is a very efficient soil preservation practice due to the exploitation of different soil layers by the different depths occupied by the root systems of the two or more crop species.

b) Where sun-light is not a limiting factor, temperature is high and water availability not always ideal, a taller crop such as maize or sorghum, can reduce the intensity of heat and water stress for a shorther crop such as beans, by the shading due to the taller crop and also by a wind breaking effect. Such effect may reduce transpiration losses of water for the shorter crop.

c) Intercropping is a safer and more stable system of agricultural exploitation than sole cropping, for small areas with low input and labor availability. If one crop fails, the other can still give some yield (Andrews, 1974, Willey and Osiru, 1972).

d) Intercropping makes possible the production of two or more crops at the same time and area which favors diversification of diets.

Although it is accepted that intercropping is important for common bean production in all countries where beans are an important agricultural product, research has always been centered on sole cropping and germplasm development has always been done in that system. Few attempts were made to select cultivars for intercrop (Francis et al., 1976) and in most cases they were on climbing bean-maize associations, that have obvious advantages because maize provides the necessary support for the bean plants, that should otherwise be provided by stakes (Davis et al., 1980). However, most farmers who grow beans with maize, prefer bushy plant types because they make harvesting easier.

For many years, plant breeders have been questioned about their work in relation to intercropping. The main questions are:

I - Will germplasm that was developed for sole crop, necessarily be good for intercropping?

II - How will germplasm that was selected for sole crop differ from germplasm developed for intercropping?

III - Is there a need for special breeding programs for intercropping?

IV - How could bean breeding programs approach the intercropping question?

I. Will Germplasm That Was Developed For Sole Crop Be Always Good For Intercrop?

Several articles report yields of bean cultivars in sole crop and in intercropping with maize. In most cases the correlation coefficients between yields in sole crop and in intercrop were positive, high and significant (Table 1). These positive correlations have led to the conclusion that cultivars that are good for sole crop may also be good for intercrop. However, significant genotype by cropping systems interactions have been reported (Francis et al., 1978a). Paniagua (1977) found that not all bean cultivars which where good in intercrop where also good in sole crop.

Hamblin and Zimmermann (1986) showed that it is possible to calculate how succesful selection in one system (sole crop or intercrop) would be for the other, by ranking the cultivars for yield in each system, applying a defined selection pressure (in their case 33%) in one system and observing how many of the selected genotypes were among the top 33% in the other environment. Selection efficiency (Se) in the alternate environment is defined as:

$$Se\% = \frac{\text{no. selected in alternate system} - \text{no. expected by chance}}{\text{no. chosen in selection system} - \text{no. expected by chance}} \times 100$$

The number expected by chance, is calculated assuming that there would be the same probability of randomly taking good genotypes for the alternate system among the selected ones, as the selection intensity. For example: the trial of Santa- Cecilia and Ramalho (1982) included 40 genotypes. With a selection pressure of 30% in sole crop, the 12 best genotypes were identified for that system. Following the rationale described, the probability of having taking the best ones by chance, was 0,30 x 12 = 3. Among the 12 that were selected for sole crop, there were 7 that were in the group of the top 12 in intercrop. The number expected by chance was again the same (3), because it was again calculated from the top 12. So selection efficiency in that case was:

$$Se\ \% = \frac{7 - 3}{12 - 3} \times 100 = 44\%$$

That means that only 44% of the genotypes that were consciously selected in one system were also consciously selected for the other system, although the percentage of selected material in one system that was good for the other (correlated response) was 58%. Those are low percentages considering that there was a highly significant correlation for bean yields between the two planting systems.

Table 2, taken from Hamblin and Zimmermann (1986), shows the selection efficiency for intercrop when a selection intensity of 33% was applied in sole crop. In only two cases, selection efficiency was greater than 50%, but this result may be due to the differential disease resistance of the cultivars. In the case of Vieira and Aidar (1984), yield data and anthracnose data in sole crop and in intercrop were correlated. Also, disease incidence data in sole crop were correlated to the same data in intercrop, and the levels of resistance to anthracnose for each genotype were similar across systems.

The results are very similar, in general terms, for relay cropping (beans planted between maize lines when maize reaches physiological maturity) and for simultaneous intercropping. Although crop competition is reduced in relay cropping, because maize plants are not actively growing when beans are planted, correlations between yields in relay crop and sole crop are positive and low, and selection efficiency accross systems was even lower than simultaneous intercrop (Table 3).

In conclusion, germplasm that was developed for sole crop will not always be good for intercrop, although performance in the two systems is often correlated. Selection for disease resistance may be practiced in the most convenient system for disease expression, but yield has to be measured in the same system that the germplasm is to be grown.

II. How Will Germplasm That Was Selected For Sole Crop Differ From Germplasm Developed For Intercrop?

Selection parameters in common bean vary with the program and region for which they are being selected. Generally for sole crop, beans are selected for resistance to the prevailing diseases and to some environmental stresses. Those resistances are useful in all planting systems and are considered of equal importance for intercrop and sole crop. It is the morphophysiological traits that will more often determine adaptation to intercropping. Some traits may be more important to one system than to the other, and generally some traits appear to be of particular importance when selecting for adaptation to intercropping but they are not really understood.

Zimmermann et al. (1984b) studied the relative importance of some traits in segregating populations in intercrop and in sole crop. It was reported that the same interactions noted for varieties also occurred in segregating populations. In those studies of segregating populations, harvest index of beans was negatively related to yield in sole crop and positively in intercrop and such correlations are not only phenotypic but also genotypic (Table 4). For all other traits studied the genotypic correlations with grain yield were in the same direction for both systems, although for the phenotypic correlations there were some changes of sign. Those correlations show that it is important, when selecting for yield in intercrop, to avoid a correlated reduction in harvest index in order not to obtain plants with excessive vegetative growth (Donald and Hamblin, 1976 and 1983).

A path coefficient analysis for yield components and grain yield of beans (Zimmermann et al., 1984b) showed that the importance of such components for grain yield varied with system (Table 5), with the direct effect of 100 seed weight being more important for intercrop than for sole crop and the direct effect of number of pods per plant being the opposite. Also, for grain yield of F2 derived F4 and F5 progenies, the genotypic correlations between cropping systems (Zimmermann et al., 1984a) were higher for the cross when Dark Red Kidney 2602, a larger seeded, determinate cultivar was one of the parents, than for the other crosses where both parents were small seeded and indeterminate (Table 6).

Larger seed size gives plants a competitive advantage because they have more reserves at the begining of the life cycle (Black, 1958; Donald, 1963). In highly competitive situations, Hamblin (1975) also found that seed size was positively related to competitive ability measured as grain yield. These highly competitive situations involved different cultivars from the same species (<u>Phaseolus</u> <u>vulgaris</u> L.). It appears that the same relationship of seed size x competitive ability exists when competition is imposed by another species (such as maize), as Zimmermann shows.

Guazzelli (1975) evaluated bean lines for their competitive ability in mixtures, and even among black, small seeded, indeterminate bean lines, differences could be detected. In a complementary work, the same author (1976), applied selection for high and low competitive ability in four bean varieties (populations), and obtained lines that differed from the others for their competitive ability. Later, those lines were tested in intercrop situations (Vieira and Aidar, 1984; Guazzelli and Kluthcouski, 1988), and some of the ones that gave the best results for intercrop where those that had been selected for high competitive ability in common bean mixtures, which is technically a sole crop because it involves only one species.

The advantage of a more competitive bean cultivar in intercrop, suggests that the environment is not fully exploited by the current cultivars, which means that short term gains may be expected by the enhancement of competitive ability of beans. In medium and long term this may not hold because beans are grown for their seed production (reproductive growth) and competitive ability is related to vegetative growth (Donald and Hamblin, 1983). Donald and Hamblin (1983) suggest that some features common to high yielding lines, adapted to sole crop, make plants poor competitors but the crop fully exploits the environment. Those features are:

. Ability to respond to high densities
. Lodging resistance
. Annual habit and determinant growth
. Improved canopy for efficient light interception
. High biological yield
. High grain yield
. Minimum competitive ability between plants
. Ability to respond to high nutrient levels
. Wide climatic adaptation

Some of those features may not prove as good as the others for beans, or very hard to combine, but generally they may prove valuable. Davis and Garcia (1983) also suggested that indeterminate bean cultivars with low competitive ability may also have an advantage for intercropping.

Therefore the answer to "how will germplasm selected for sole crop differ from that developed for intercrop" is still unclear. Since there is not a clearly defined ideotype for either situation, it is unknown for which caracters the cultivars should differ from one another. There are only some indications of traits to pay attention to, in order to avoid some undesirable side effects of selection (like decreased harvest index, or increased seed size when small seeds are preferred).

III. Is There A Need For Special Breeding Programs For Intercropping?

This question was addressed in Zimmermann's work (Zimmermann, 1983; Zimmermann et al., 1984a; Zimmermann et al., 1984b; Zimmermann et al., 1985) through studies of genetic effects, heritabilities, correlations and selection gains for beans under sole crop and intercrop with maize under constant conditions. A greater number of significant genetic effects (Zimmermann et al., 1985) was found for grain yield and harvest index of beans grown in intercrop with maize than as sole crop (Table 7). Hamblin and Evans (1976) had also found that epistatic effects decreased with increased sowing density.

Zimmermann et al. (1984a), reported standard unit heritabilities (Table 8) that were larger for grain yield of beans in intercrop than in sole crop. In the same paper (Table 9) it was shown that direct selection for each system was more efficient than indirect selection. Effects of indirect selection for intercrop based on selection practiced in sole crop were much smaller than either effects of direct selection or effects of selection on the mean of both systems. Effects of indirect selection for sole crop based on selection in intercrop, were variable and sometimes larger than effects of direct selection, but selection based on the mean of both systems gave almost the same results and sometimes better results than direct selection for sole crop. These data showed that even if selection for intercrop only is not justified, selection based on the mean of both systems may improve the selection efficiency. Similarly, Hamblin and Zimmermann (1986) also found that selection on mean yield of sole crop and intercrop was always more efficient for both planting systems than selection in single environment for the alternate system (Table 10), and the mean was a better selection criterion to improve yield for both systems than "tolerance to stress", defined as the difference between yield in sole crop and in intercrop. These authors concluded that bad lines can be eliminated based on performance in a single system (for example sole crop) but the final identification of the best lines has to be made including all environments to which they should be adapted. Bean and maize, or any other species intercropped with beans, are grown in many geographical regions in more than one cropping system, and recommended lines should perform well across all or most of the different conditions in which they are grown. There are also doubts, whether or not a specially developed cultivar, for intercropping conditions would be the best approach for a seed production program that has to follow the breeding of a new cultivar.

A conclusion from the foregoing discussion is that special breeding programs for intercrop would not be justifiable unless intercropping is virtually the only planting system in which the crops are grown.

IV. How Could Bean Breeding Programs Approach The Intercropping Question?

The previous discussion considered beans as the system component of interest. From another point of view, in the bean-maize intercrop, maize yields are usually not affected or suffer very little from competiton from the bean plant, whereas bean may suffer a severe yield decrease of 80% or more. Furthermore, there are interactions of maize and bean cultivars in terms of bean yields, when different maize cultivars are used (Davis and Garcia, 1983; Ramalho et al., 1983). Harper (1967) and Fyfe and Rogers (1965) had previously suggested that if two species are to be grown together, the greatest level of ecological combining ability will be achieved by breeding both crops simultaneously. Hamblin et al. (1976), had suggested a method that allows it to be done, based on a diallel design. Hamblin and Zimmermann (1986) concluded that to obtain maximum crop yields in intercrop, plant breeders must breed for the cropping system rather than breed individual components.

Geraldi (1983) used a diallel approach with maize and bean lines in combination, each one of them with all others. The resulting yields of each crop were converted in "equivalent production" based on market price ratios of maize to bean, and analysed the data as an adaptation of Gardner and Eberhart (1966) model for diallel crosses. The best maize/bean combinations were those where there were large general effects of intercropping. In the case of bean cultivars, the best were those that interfered less with maize (high "combining ability"). Some exceptions of high specific "combining" ability also occurred. The only problem with this and other diallel methodologies is the size of experiments needed to test all combinations of the lines of the two species. For 10 bean and 10 maize lines, with 10 being a very small number of lines to be considered in any breeding program, a trial of 100 treatments is needed. For slightly larger, but still small numbers, the experimental size becomes too large to be handled efficiently.

A more reasonable approach would be, for all species involved, to work on early generation selection (screening phase) of a large number of lines, in the most simplified system (sole crop), with later testing of a much smaller number of entries of the different species in all systems that they should be grown in the region, in all possible combinations with the best lines of the other species. It increases the work only in the final phases of the program. The final decision on which line to name and release for each species should be made based on the average yield of lines across all testing environments. To make rapid yield gains on intercrop, selection in the early stages (sole crop) could be practiced under high planting density, as used by Guazzelli (1976).

From programs like the one suggested above, it would be possible to create and identify genotypes that would perform better in the average of a range of different cropping systems, but in some cases, they could perform not as well in each one of them alone as if they were specially developed for that from the begining, though the difference may not be as large as to be taken into account.

Conclusions

As final remarks, it is important to point out the following:

- Bean germplasm developed for sole crop may also be good for intercrop or for relay crop, but that is not always true. Interactions exist and have to be considered.
- There is no clear answer on how different or how similar bean lines developed especially for intercrop or for relay crop should be. There is no defined ideotype for those systems. Competitive ability seem to give an immediate yield advantage to genotypes grown in intercrop but selection to increase competitive ability may cause unwanted side effects that can decrease plant efficiency for seed production. Disease resistance, on the other hand, is important for all cropping systems.
- Special breeding programs, totally devoted to intercrop are not a good option unless intercropping is the only planting system in which crops are grown in a region.
- For all species that are grown in an intercrop situation with beans, early generation selection should be made in the cropping system which is most easily managed (sole crop) with final testing of the best

selected lines of each species being made in all systems and in all combinations among them. Final decisions on the releases to be made should be based upon averages across all testing systems.

Last, but not least, intercropping will probably decrease in importance throughout the world with time, but in the near future (until the end of century at least), it is from this system that a large proportion of bean production will come. As long as no good harvesting machines for beans are developed, as long as poor farmers exist, with small areas and no expensive and sophisticated production systems, without irrigation facilities, intercrop will continue to be responsible for a significant proportion of bean production.

References

Andrews, D.J. 1974. Responses of sorghum varieties to intercropping. Exp. Agr. 10:57-63.

Andrews, D.J. and Kassam, A.H. 1976. The importance of multiple cropping in increasing world food supplies. In: Papendick, R.I.; Sanchez, P.A. and Triplett, G.B. (eds.). Multiple cropping, pp.1-11. A.S.A. Special Publ. 27, Amer. Soc. Agron., Madison, WI.

Antunes, I.F. and Teixeira, M.G. 1982. Produtividade de genotipos de feijao em monocultivo e no cultivo associado com milho nas épocas das águas e da seca em Goiania, GO. In: EMBRAPA- Proc. la. RENAFE, 83-88.

Black, J.N. 1958. Competition between plants of different initial seed sizes in swards of subterranean clover (Trifolium subterraneum L.) with particular reference to leaf area and the light microclimate. Aust. J. Agr. Res., 9:299-318.

Chagas, J.M. and Aquino, A.R.L. 1981. Yield of climbing bean cultivars under two cropping systems. Ann. Rep. Bean Improv. Coop., 24:56-57.

Davis, J.H.C.; Garcia, S. and Tejada, G. 1980. Seleccion en generaciones tempranas de frijoles volubles en associacion com maiz. XXVI Reunion Anual del Programa Cooperativo Centroamericano para el Mejoramiento de Cultivos Alimenticios (PCCMA)-Guatemala. 16pp.

Davis, J.H.C. and Garcia, S. 1983. Competitive ability and growth habit of indeterminate beans and maize for intercropping. Field Crops Res., 6:59-75.

Donald, C.M. 1963. Competition among crop and pasture plants. Adv. Agron., 15:1-118.

Donald, C.M. and Hamblin, J. 1976. The biological yield and harvest index as agronomic and plant breeding criteria. Adv. Agron., 28:361-405.

Donald, C.M. and Hamblin, J. 1983. The convergent evolution of annual seed crops in agriculture. Adv. Agron., 36:97-143.

Francis, C.A.; Flor, C.A. and Temple, S.R. 1976. Adapting varieties for intercropped systems in the tropics. In: Papendick, R.I.; Sanchez, P.A. and Triplett, G.B. (eds.). Multiple cropping, pp.235-254. A.S.A. Spec. Publ. 27. Amer. Soc. Agron., Madison-WI.

Francis, C.A.; Prager, M.; Laing, D.R. and Flor, C.A. 1978a. Genotype x environment interactions in bush bean cultivars in monoculture and associated with maize. Crop Sci., 18:237- 242.

Francis, C.A.; Prager, M. and Laing, D.R. 1978b. Genotype x environment interactions in climbing bean cultivars in monoculture and associated with maize. Crop Sci., 18:242- 246.

Fyfe, J.L. and Rogers, H.H. 1965. Effects of varying variety and spacing on yields and composition of mixtures of lucerne and tall fescue. J. Agr. Sci. (Cambridge), 64:351-359.

Gardner, C.O. and Eberhart, S.A. 1966. Analysis and interpretation of the variety cross diallel and related populations. Biometrics, Raleigh, 22:439-452.

Geraldi, I.O. 1983. Método de anàlise estatística para combinacao de cultivares em consòrcio. Doctor Degree Thesis, ESALQ, USP, Piracicaba, SP, Brasil, 120pp.

Guazzelli, R.J. 1975. Competicao intergenotípica em feijao (Phaseolus vulgaris L.): estimacao da capacidade competitiva. Master Degree Diss., ESALQ, USP, Piracicaba, SP, Brasil, 62pp.

Guazzelli, R.J. 1976. Competicao intergenotípica em feijao (Phaseolus vulgaris L.): estimacao de parámetros genéticos. Doctor Degree Thesis, ESALQ, USP, Piracicaba, SP, Brasil, 88pp.

Guazzelli, R.J. and Kluthcouski, J. 1988. Avaliacao de germoplasma de feijao (Phaseolus vulgaris L.) para o consórcio simultáneo com milho. EMBRAPA-CNPAF. Comunicado Tècnico no. 21.F(no prelo).

Hamblin, J. 1975. Effect of environment, seed size and competitive ability on yield and survival of Phaseolus vulgaris genotypes in mixtures. Euphytica, 24:435-445.

Hamblin, J. and Evans, A.M. 1976. The estimation of cross yield using early generation and parental yields in dry beans (Phaseolus vulgaris L). Euphytica, 25:510-520.

Hamblin, J.; Rowell, J.G. and Redden, R. 1976. Selection for mixed cropping. Euphytica, 25:97-106.

Hamblin, J. and Zimmermann, M.J.O. 1986b. Breeding common bean for yield in mixtures. In: Janick, J. (ed.). Plant breeding reviews, 4:245-272. AVI Publ. Co. Westport, Conn.

Harper, J.L. 1967. A. Darwinian approach to plant ecology. J. Ecol., 55:247-270.

Paniagua, C.V. 1977. Identification and stability analysis of traits important to yield of beans in associated culture. Ph.D. Thesis, Michigan State University, East Lansing, MI. 76pp.

Pinchinat, A.M.; Soria, J. and Bazan, R. 1976. Multiple cropping in tropical America. In: Papendick, R.I.; Sanchez, P.A. and Triplett, G.B. (eds.). Multiple cropping. pp.51-62. A.S.A. Special Publ. 27. Amer. Soc. Agron., Madison, WI.

Ramalho, M.A.P.; Oliveira, A.C. de and Garcia, J.C. 1983. Recomendacoes para o planejamento e análise de experimentos com as culturas de milho e feijao consorciadas. EMBRAPA- CNPMS. Documentos, 2. 74pp.

Santa-Cecìlia, F.C.S. and Ramalho, M.A.P. 1982. Comportamento de cultivares de feijao em monocultivo e em associacao com milho. Ciencia e Prática, 6:45-54.

Serpa, J.E.S. and Barreto, A.C. 1982. Competicao de cultivares de feijao em consorciacao com o milho, nas micro regioes homogeneas 123 e 130 do Estado de Sergipe. EMBRAPA-UEPAE Aracaju. Pesquisa em Andamento No. 6. 6pp.

Teixeira Monteiro, A.A.; Vieira, C. and Silva, C.C. 1981. Yields of twenty bean cultivars under two cropping systems. Ann. Rept. Bean Imp. Coop., 23:49-50.

Vieira, R.F. and Aidar, H. 1984. Avaliacao de cultivares e linhagens de feijao em consórcio com o milho e em monocultivo. (EMBRAPA-CNPAF. Pesquisa em Andamento, 51). 7pp.

Wiley, R.W. and Osiru, D.S.O. 1972. Studies on mixtures of maize and beans (Phaseolus vulgaris L.) with particular reference to plant population. J. Agr. Sci. (Cambridge), 79:517-529.

Zimmermann, M.J.O. 1983. Genetic studies on common bean in sole crop and intercropped with maize. Ph.D. Dissertation. Univ. of California, Riverside, CA, 86pp.

Zimmermann, M.J.O.; Rosielle, A.A. and Waines, J.G. 1984a. Heritabilities of grain yield of common bean in sole crop and in intercrop with maize. Crop Sci., 24:641-644.

Zimmermann, M.J.O.; Rosielle, A.A.; Waines, J.G. and Foster, K.W. 1984b. A heritability and correlation study of grain yield, yield components and harvest index of common bean in sole crop and intercrop. Field Crops Res., 9:109-118.

Zimmermann, M.J.O.; Rosielle, A.A.; Foster, K.W. and Waines, J.G. 1985. Gene action for grain yield and harvest index of common bean grown in sole crop and in intercrop with maize. Field Crops Res., 12:319-329.

Table 1. Correlation between yields of bean cultivars in sole crop and in intercrop with maize (Adapted from Hamblin and Zimmermann, 1986).

No. of cultivars	r	Reference	Comments	
19	0.88**	Francis et al., 1978a	Trial 2	
20	0.51*	Francis et al., 1978a	Trial 3	
17	0.72***	Francis et al., 1978a	Trial 2	common cultivars
17	0.55*	Francis et al., 1978a	Trial 3	
20	0.81***	Francis et al., 1978b	Trial 2	
20	0.41 n.s.	Francis et al., 1978b	Trial 3	
18	0.83***	Francis et al., 1978b	Trial 2	common cultivars
18	0.54*	Francis et al., 1978b	Trial 3	
59	0.66***	Antunes and Teixeira, 1982	Trial 1	
64	0.54***	Antunes and Teixeira, 1982	Trial 2	
34	0.69***	Antunes and Teixeira, 1982	Trial 1	common cultivars
34	0.50***	Antunes and Teixeira, 1982	Trial 2	
49	0.84***	Vieira and Aidar, 1984		
40	0.65***	Santa-Cecilia and Ramalho, 1982	Year1	common cultivars
40	0.89***	Santa-Cecilia and Ramalho, 1982	Year2	
8	0.28 n.s.	Chagas and Aquino, 1981		
10	0.61 n.s.	Davis and Garcia, 1983	Short maize	
10	0.24 n.s.	Davis and Garcia, 1983	Medium maize	
10	0.41 n.s.	Davis and Garcia, 1983	Tall maize	
9	0.43 n.s.	Serpa and Barreto, 1982	Site 1	common cultivars
9	0.91***	Serpa and Barreto, 1982	Site 2	
40	0.64***	Ramalho et al., 1983		
8	0.89***	Araujo, R.S. (personal commun.) Applied N		
8	0.43 n.s.	Araujo, R.S. (personal commun.) Rhizobial N		

*, **, *** = significant at the probability levels of 5%, 1% and 0.1%, respectively.
n.s. = non significant.

Table 2. Effect of selection of the highest yielding 33% of cultivars in one environment on the number selected in the alternate environment, and selection efficiency (Adapted from Hamblin and Zimmermann, 1986).

No. cult.	No. sel.	No. alt. env.	No. exp. chance	Sel eff. %	Corr.	Reference
19	6	4	2	50	0.88***	Francis et al., 1978a
20	6	2	2	0	0.51*	Francis et al., 1978a
20	6	3	2	25	0.81***	Francis et al., 1978b
20	6	1	2	25	0.41 n.s.	Francis et al., 1978b
59	20	13	7	46	0.66***	Antunes and Teixeira, 1982
64	21	13	7	43	0.54***	Antunes and Teixeira, 1982
49	16	14	5	82	0.84***	Vieira and Aidar, 1984
40	13	7	4	33	0.65***	Santa-Cecilia and Ramalho, 1982
40	13	11	4	78	0.98***	Santa-Cecilia and Ramalho, 1982
40	13	5	4	11	0.64***	Ramalho et al., 1983

*, *** = Significant at the probability levels of 5% and 1%, respectively.

n.s. = non significant.

Table 3. Correlations between sole crop and intercrop or relay crop (Adapted from Hamblin and Zimmermann, 1986).

Data source	Corr. coef.	Comments
Francis et al., 1978a	0.72***	Sole crop x simultaneous intercrop, trial 2
Francis et al., 1978a	0.55*	Sole crop x simultaneous intercrop, trial 3
Francis et al., 1978b	0.83***	Sole crop x simultaneous intercrop, trial 2
Francis et al., 1978b	0.54*	Sole crop x simultaneous intercrop, trial 3
Antunes and Teixeira, 1982	0.69***	Sole crop x simultaneous intercrop, trial 1
Antunes and Teixeira, 1982	0.50**	Sole crop x simultaneous intercrop, trial 2
Santa-Cecilia and Ramalho, 1982	0.65***	Sole crop x simultaneous intercrop, year 1
Santa-Cecilia and Ramalho, 1982	0.89***	Sole crop x simultaneous intercrop, year 2
Teixeira Monteiro et al., 1981	0.71**	Sole crop x relay crop, location 1
Teixeira Monteiro et al., 1981	0.29	Sole crop x relay crop, location 2
Antunes and Teixeira, 1982	0.33**	Sole crop x relay crop, year 1
Antunes and Teixeira, 1982	0.46***	Sole crop x relay crop, year 2

*, **, *** = Significant at the probability levels of 5%, 1% and 0.1%, respectively.
n.s. = non significant.

Table 4. Phenotypic and genotypic correlations among four traits of common bean and grain yield in intercrop and in sole crop (Adapted from Zimmermann et al., 1984b).

Trait correlated to grain yield	Genotypic correlation		Phenotypic correlation	
	Intercrop	Sole crop	Intercrop	Sole crop
Number of pods	3.58	1.30	-0.34**	0.42 n.s.
Seeds per pod	-0.95	-0.14	-0.21 n.s.	0.05 n.s.
100 seed weight	1.39	0.20	0.68**	0.06 n.s.
Harvest index	1.80	-0.20	0.77**	-0.11 n.s.

*, ** = Significant at the probability levels of 5% and 1%, respectively.
n.s. = non significant.

Table 5. Path coefficient analysis of the effects on grain yield of yield components of beans grown in intercrop with maize and in sole crop (Adapted from Zimmermann et al., 1984b).

Type of effect	Intercrop	Sole crop
Effect of total number of pods		
Direct effect	0.451	1.115
Indirect effect via seeds/pod	0.399	0.307
Indirect effect via 100 seed weight	-1.190	1.002
Total correlation	-0.34**	0.42
Effect of number of seeds per pod		
Direct effect	0.782	0.472
Indirect effect via number of pods	0.230	0.724
Indirect effect via 100 seed weight	-1.222	-1.146
Total correlation	-0.21 n.s.	0.05 n.s.
Effect of 100 seed weight		
Direct effect	1.608	1.318
Indirect effect via number of pods	-0.334	-0.847
Indirect effect via seeds per pod	-0.594	-0.411
Total correlation	0.68**	0.06 n.s.

*, ** = Significant at the probability level of 1%.
n.s. = non significant.

Table 6. Genotypic correlations between the two cropping systems for F2 derived F4 and F5 progenies from three crosses (Adapted from Zimmermann et al., 1984a).

Crosses	Correlations
Dark Red Kidney 2602 x Turtle Soup 39	1,08
California Small White 7775 x Turtle Soup 39	0,41
Gloria x Turtle Soup 39	0,25
All lines	0,99

Table 7. Models that fit the observed data for grain yields and harvest index of three common bean crosses. The genetic parameters that were included in the models showed estimated values larger than two times the estimates of their standard errors (Adapted from Zimmermann et al., 1985).

Crosses	Models			
	Grain yield		Harvest index	
	Intercrop	Sole crop	Intercrop	Sole crop
Dark Red Kidney 2602 x Turtle Soup 39	m+a-d+dd	m+ad	m-d+dd	m+a+aa
California Small White 7775 x Turtle Soup 39	m-a+d	m+d+ad	m-a+d+ad-dd	m+d
Gloria x Turtle Soup 39	m+d	m-a+d+aa	m+a+d+aa	m+a

m = mid parental value; a = additive effect; d = dominance effect; aa = additive by additive epistasis; ad = additive by dominant epistasis; dd = dominant by dominant epistasis.

Table 8. Standard unit heritabilities % determined by correlations between grain yield of F_4 and F_5 bean lines for two cropping systems (Adapted from Zimmermann et al., 1984a).

Crosses	Heritabilities %	
	Intercrop	Sole crop
Dark Red Kidney 2602 x Turtle Soup 39	53	51
California Small White 7775 x Turtle Soup 39	36	40
Gloria x Turtle Soup 39	50	28
All lines	60	54

Table 9. Realized selection responses (kg/ha) to a 40% selection intensity for grain yield, expressed as deviations from the population mean (Adapted from Zimmermann et al., 1984a).

	Selection for intercrop			Selection for sole crop		
		Indirect selection			Indirect	
Crosses	Direct	In sole crop	On mean	Direct	In intercrop	On mean
Dark Red Kidney 2602 x Turtle Soup 39	78	29	45	53	67	49
California Small White 7775 x Turtle Soup 39	42	33	39	83	53	82
Gloria x Turtle Soup 39	53	12	52	43	-9	84
All lines	91	45	63	140	30	139

Table 10. Selection efficiency % of three selection criteria: mean yield (SC +M)/2, tolerance (SC-M) and single environment selection (S) for the alternate system (Adapted from Hamblin and Zimmermann, 1986).

Source	Selection criteria	Test environments		
		Sole crop	Intercrop	Alternate
Antunes and Teixeira (1982)				
Year 1. Simultaneous intercrop	(SC+M)/2	86	57	-
	(SC-M)	-57	-29	-
	S	-	-	43
Year 1. Relay crop	(SC+M)/2	57	29	-
	(SC-M)	-57	14	-
	S	-	-	14
Year 2. Simultaneous intercrop	(SC+M)/2	86	57	-
	(SC-M)	-29	0	-
	S	-	-	43
Year 2. Relay crop	(SC+M)/2	43	86	-
	(SC-M)	-43	14	-
	S	-	-	29
Santa-Cecilia and Ramalho (1982)				
Site 1. Simultaneous intercrop	(SC+M)/2	78	66	-
	(SC-M)	-22	33	-
	S	-	-	33
Site 2. Simultaneous intercrop	(SC+M)/2	89	89	-
	(SC-M)	-22	-22	-
	S	-	-	78

BREEDING FOR YIELD IN SOYBEANS: EARLY GENERATION TESTING AND SPECIFIC ADAPTATION TO HIGH VERSUS LOW YIELD ENVIRONMENTS

Richard L. Cooper*

Abstract

Selection of an appropriate breeding procedure can have a significant impact on the success of a breeding program. Prior to 1960, nearly all soybean breeders used the pedigree procedure to develop high yielding pure lines. However, a major disadvantage of the pedigree procedure is that selection for yield potential in the early generations is based on visual estimates of yield, which can be quite inaccurate. In the early 1970's, soybean breeders began to adopt a modified pedigree procedure which has become known as the single-seed-descent (SSD) procedure. In this method, a single seed is advanced from each F_2 plant and the procedure repeated each succeeding generation until homozygosity is reached in the F_5 or F_6 generation, resulting in a single pure line from each F_2 plant. This procedure has the advantage over the pedigree procedure in that more F_2 plants can be sampled per cross, homozygosity can be reached much quicker (at least 2 generations can be grown per year) and all yield testing is done with pure lines, increasing selection efficiency. However, a major disadvantage of the SSD procedure is the lack of opportunity for selection within selected F_2 families. There are two major bottlenecks in the breeding of self-pollinated crops. The first is the selection of the parents to be used in a cross. If the genes necessary for obtaining a high yielding recombinate are not present in the parents, no breeding procedure will be effective. The second is the individual F_2 plant. Since there is

---

* USDA, ARS Research Agronomist and Adjunct Professor, Dept. of Agronomy, Ohio Agricultural Research and Development Center, The Ohio State University, Wooster, Ohio 44691, U.S.A.

no intermating during the generation advance to homozygosity, all the genes necessary for a high yielding recombinate must be present within a single F_2 plant. Thus if F_2 plants which contain a superior complement of yield genes can be identified, selection for high yielding recombinates within these F_2 families should be effective. An early generation testing (EGT) procedure has been developed in soybeans for the identification of the best crosses in the F_3, the best F_2-derived lines in the F_4 and the best pure lines, from the best F_2 family from the best crosses, in the F_5 and subsequent generations.

As soybean yields have increased, it has become increasingly more difficult to select a single cultivar that is highest in yield over the entire yield range. Broadly adapted, "universal" cultivars tend to be too short in low yield environments and too tall and lodge in high yield environments. In 1969, I initiated a breeding program to develop semidwarf cultivars with specific adaptation to high yield environments. The approach taken was to make crosses between two diverse germplasm pools, northern U.S. adapted indeterminate (Dt_1) cultivars and southern U.S. adapted determinate (dt_1) cultivars, and to select from these crosses, determinate types adapted to the Midwest. When the determinate trait (dt_1) is introduced into indeterminate cultivars by backcrossing, to produce dt_1 isolines, short, semidwarf plant types are obtained but yields are significantly reduced compared to the Dt_1 recurrent parent. However, by selecting simultaneously for the desired semidwarf determinate plant type and high yield, through the use of the early generation testing procedure, those determinate semidwarf F_2 plants, from the north by south crosses, which received the genetic background genes necessary for producing a high yielding determinate semidwarf plant type could be identified. Using this procedure, 8 high yielding determinate semidwarf cultivars have been identified and released. In high yielding environments where early lodging of the taller indeterminate cultivars is frequently a barrier to higher yields, these determinate semidwarf cultivars have exceeded the yields of the indeterminate cultivars 1000 to 1500 kg/ha. These results suggest the

EGT procedure may be effective in other self-pollinated crops where the goal is to introduce yield genes from diverse germplasm sources to develop high yielding cultivars of a specific plant type.

Philosophy of and Initial Experience with Early Generation Testing

In 1962, when I first began my career in soybean (Glycine max (L.) Merr.) breeding, the pedigree method was the standard procedure used by nearly all soybean breeders. A major weakness of the pedigree procedure, however, is that selection for yield potential in the F_3 thru F_5 is based on visual estimates. Research has shown that in soybeans, the ability of the plant breeder to visually identify the highest yielding lines is quite limited (Hanson, et al., 1962). My own experience in Minnesota confirmed this. A surprising number of low yielding lines were advanced to the F_6 when I used the pedigree procedure. The difficulty with visual estimates of yield is magnified when differences in plant type, row spacing and seeding rate are involved.

With the publication of an article on the single-seed-descent (SSD) procedure by Brim in 1966, many soybean breeders began to shift from pedigree to the SSD procedure. The major appeal of the SSD procedure was the rapid generation turnover, at least 2 generations per year, which decreased the time from crossing to release of a new cultivar from a cross.

Part of the philosophy of the SSD procedure is the assumption that plant breeders cannot effectively select for yield in early generations, so why not advance the genetic materials to homozygosity as quickly as possible and do all yield testing with homozygous lines. Another advantage of the SSD procedure over the pedigree procedure is that more F_2 plants can be sampled, with one pure line descendant from each of many F_2 plants.

It is the trade off for this advantage, however, which concerned me the most about the SSD procedure. There is very little if any within F_2

family sampling by this procedure. Thus an F_2 plant which received a superior complement of yield genes would have, in the purest sense of the SSD procedure, only one pure line descendant to represent it. The basic question then becomes, is it better to test one pure line from each of 1000 F_2 plants or 100 pure lines from each of 10 selected F_2 plants. The key to this answer is whether in fact soybean breeders can identify those F_2 plants which received a superior complement of yield genes. It was on this basis I began my research in 1966 to develop and test an early generation testing (EGT) procedure for soybeans. With both the pedigree system and the SSD procedure, yield is the last trait selected for, yet it is the most important. The objective of the EGT procedure was to reverse this priority and select for yield first.

In a self-pollinated crop like soybeans there are two major bottlenecks to success in developing superior yielding pure line recombinates. The first is the selection of the parents, usually two in soybeans. If the genes to produce a superior yielding recombinate are not present in the two parents, no breeding method will be effective in developing a superior yielding cultivar from that cross. This is why most soybean breeders make many crosses per year (100 or more) in search of that best cross. Secondly, and perhaps less obvious, is that all the genes necessary for a superior yielding recombinant must be present within a single F_2 plant. This is true because in most breeding programs of self-pollinated crops there is no intermating in the early generations as the lines are advanced by selfing to homozygosity. A basic assumption of the EGT procedure was that if all the genes necessary for a superior yielding recombinate are present within a single F_2 plant, these genes should express themselves in the yield of their F_3-progeny (F_2-derived F_3 line). Research by Brim and others have reported gene action for yield in soybeans is primarily additive, thus supporting this hypothesis (Brim and Cockerham, 1961).

In an exhaustive thesis research study by Roger Boerma (presently Dr. Boerma, soybean breeder at the University of Georgia), the EGT procedure was compared with the pedigree and SSD procedures, using four different crosses. The results of this research were published in Crop Science in three articles (Boerma and Cooper, 1975a, 1975b, 1975c). Like many such long-term studies, it became obvious enroute to completion of the study that some modification in the EGT procedure would be needed to make it a practical method. Some way had to be found to reduce the large amount of yield testing required in the early generations. However, much was learned about the EGT procedure in this 10-year study.

First, it was established that F_2 plants which received a superior complement of yield genes did express it in the yield of their F_2-derived F_3 progeny. Secondly, it was also established that yield of a heterogeneous F_2-derived line was indicative of the yield potential of the pure lines that could be derived from it. One surprise, however, was how uniform some F_2-derived lines appeared, almost as uniform in appearance as a pure line. Of course some F_2-derived lines were quite variable as to maturity which would limit the value of yield data obtained. However, in this study a maturity range of up to 10 days was considered acceptable. Segregation for such yield unrelated traits as flower color, pubesence color and hilum color were not considered a problem.

In this long-term study, effort was made to remove some of the genotype x environmental variance by the use of multiple reps and locations in the F_2-derived F_4 and F_5 lines. One-row plots were used in the F_3 and F_4, and 3-row plots in the F_5, harvesting the middle row to minimize border effects. Results from this study indicated that yield testing in three unbordered tests (1 location in the F_3 and 2 locations in the F_4) resulted in the loss of high yielding early lines due to the border effects which favored the later maturing lines. Early, high yielding lines were obtained from the same crosses where the SSD procedure was used. Also testing of all lines in multiple reps, locations and years to enable selection of

F_2-derived lines based on the F_3, F_4, F_5 mean resulted in a large and expensive yield testing program. Since the yield of the best pure lines obtained by the EGT procedure in this study were equal to those of the SSD procedure, but no better, the conclusion reached was that the SSD procedure would be the more efficient because of the less yield testing required (Boerma and Cooper, 1975a).

However, I was encouraged by the results of this study which confirmed that the basic assumptions of the EGT procedure were valid, namely F_2 plants which receive a superior complement of yield genes reflect this in the yield of their F_2-derived progenies and secondly, the yield of a heterogenous F_2-derived line is indicative of the yield potential of the pure lines that can be derived from it. Thus, even before completion of this study, I began to adopt the EGT procedure as the standard method in my main breeding program, modifying the procedure to overcome the major disadvantage of this procedure, namely the large amount of yield testing required in the early generations.

The Modified Early Generation Testing Procedure

I reasoned that in a standard pure line yield testing program, the plant breeder does not test all his lines in multiple locations and years before he makes his selections. In actual fact, breeders make selections each year, advancing only the highest yielding lines for testing the next year. So why not handle heterogenous F_2-derived lines like pure lines, namely advancing only the top yielding lines, for example the top 33%, to the next year. Using this approach, the modified EGT procedure greatly reduced the amount of yield testing required in the early generations, converting it into a practical and viable alternative to other breeding procedures (Cooper, 1982).

For the remainder of my presentation on breeding methods, I will discuss the modified EGT procedure that I have been using for the past 15 years in the development and release of 8 high-yielding soybean cultivars. The procedure is outlined in Table 1.

The numbers reflect the available resources of my project which determined the size of the program. These numbers, for example, number of crosses per year, can be modified up or down depending on available resources. By reducing the number of F_2-derived lines from 300 per cross used in the original Boerma-Cooper procedure, to 30 F_2-derived lines per cross and using single rep, single location data as the basis for selection in the F_3 through F_6, it was possible to increase the number of crosses that could be evaluated per year from 10 to 100, using the same number of yield plots. To partially offset the disadvantages of single rep data, family selection is practiced, with lines within a family (or cross) used as a form of replication. For example, if 90% of the pure lines derived from a single F_2-derived line were high yielding, all the lines would be advanced for a second year of yield testing. Another important difference from the Boerma-Cooper procedure is the alternating of 1-row and 4-row yield plots to minimize biased selection against earlier and shorter lines due to border effects of adjacent plots. In the F_3 and F_5, single-row plots were used because of the seed limitations from a single plant. In the F_4 (F_2-derived F_4 lines) and F_6 (F_4-derived F_6 lines) sufficient seed is available from the previous year's 1-row plots to permit planting of bordered row plots. Also, this permits pulling single plants from the border rows of F_2-derived lines to obtain F_4-derived lines without influencing the yield data obtained from the middle 2-rows (note, 3-row plots could be used as well, but 4-row plots accommodated direct harvest with a plot combine).

Basically the procedure consists of making crosses and growing F_1s in the first year, F_2 plants in the second year, 30 F_2-derived F_3 lines per cross for yield testing in 1-row 3 m plots the third year, growing the highest yielding F_2-derived F_3 lines as F_2-derived F_4 lines in 4-row, 6 m plots the fourth year and pulling 10 to 50 plants from the border rows to be single plant threshed as a source of F_4-derived lines. These single plants are held until the yield data of the F_2-derived lines are analyzed and only those plants from the highest yielding lines are threshed and advanced for yield testing as F_4-derived F_5 lines in 1-row, 1 meter plots the fifth year. In the sixth year after the cross was made, the highest yielding F_4-derived F_6 lines are yield tested in 4-row, 6 m plots. Thus lines which reach the F_6 yield test were selected based on 3 years of previous yield testing, allowing the plant breeder to concentrate his advanced stages of yield testing on genetic materials of known high yield potential. In cases where an F_2-derived F_3 line segregates too widely for meaningful yield data, single plants can be pulled and yield testing begun in F_3-derived F_4 lines.

The 30 F_2-derived F_3 lines per cross provide a form of replication in determining the yield potential of each cross and often permits the elimination of many crosses in the F_3 generation. In the bordered row, F_2-derived F_4 lines, those F_2 plants that received a superior complement of yield genes, within the selected crosses, can be identified and single plants pulled from the border rows to advance for yield testing as F_4-derived pure lines. Thus the objective of this modified EGT procedure is to first identify the best crosses, then the best F_2 plants within the best crosses and ultimately the best pure lines from the best F_2 plants from the best crosses. This sequential method of selection enables the plant breeder to control the size of his breeding program based on actual yield data and concentrate his more costly advanced stages of testing (multiple reps and locations) on breeding material of known high yield potential. The EGT procedure enables the plant breeder to base his early selection decisions on the trait of greatest importance in soybean breeding, seed yield.

A major weakness of the pedigree procedure is that even though yield is the most important trait, it is the last trait selected for. As previously stated, visual estimates of yield have serious limitations, especially if comparing differences in plant type. In soybeans, many lines can often be carried along, based in visual estimates of yield, only to discover in the first yield test, usually in the F_6 generation, they are not competitive in yield with existing cultivars. The SSD procedures is based partially on the assumption that early generation testing would not be effective in identifying crosses or F_2 families within these crosses that they have higher yield potential. If this were true, using the SSD procedure to advance progeny from a cross to homozygosity and concentrating yield testing on pure lines only would be the most efficient.

Compared to the pedigree procedure (used by nearly all soybean breeders prior to the mid-1960's) the SSD procedure, as described by Brim, 1966, offered the following advantages:

1. Permits sampling of a larger number of F_2 lines.
2. Advancing F_2 plants by single seed descent to the F_4 or F_5 generation increases the variance among progeny means and thus increases the expected progress from yield selection.
3. More rapid generation turnover shortens the time period from making of a cross until release of a new cultivar.
4. Less record keeping required.

Because of these advantages over the pedigree procedure, the SSD procedure has now been adopted by many soybean breeders.

The major disadvantage of the SSD procedure is the loss of opportunity for selection within selected F_2 families. It was this concern that led me to explore the possibility of an early generation testing procedure that would permit identification of F_2 plants which received a superior complement of yield genes and enable the plant breeder to take advantage of the genetic variance within these selected F_2 families. Compared to the SSD procedure, the modified early generation testing procedure has the following advantages and disadvantages.

Advantages:

1) Crosses with superior yield potential can be identified in the $F_{2.3}$ generation.
2) F_2 plants which receive a superior complement of yield genes can be identified and their progeny more extensively sampled.
3) The sequential method of yield selection enables the breeder, on the basis of yield data, to control the size of his program in the early generations.
4) The more costly advanced stages of yield testing (multiple replications, locations, and years) are limited to genetic materials of known high yield potential.

Disadvantages:

1) Fewer F_2 plants per cross are sampled. However, this is partially compensated for by utilizing recombination within selected (for high yield) F_2 subpopulations, and concentrating of effort on the best crosses.
2) Higher cost of early generation yield testing. This is partially offset by the winter nursery costs associated with SSD.
3) Slower generation advance. Although comparative data with other breeding methods are not yet available, this modified EGT procedure has proven to be an effective and practical breeding procedure in soybeans and other self-pollinated crops and a viable alternative to the more commonly used pedigree and SSD procedures. This procedure is now being adopted by other soybean breeders in the U.S.

Developing Cultivars With Specific Adaptation to High and Low Yield Environments

Historically it has been the goal of most soybean breeders to select cultivars with broad adaptation over a wide range of environments, the "universal variety" approach. When soybean yields were in the 1,000 kg/ha to 3,000 kg/ha range, this was not too difficult a task. Within the last 10 years, however, top grower yields have increased to the 4,000 kg/ha range and occasionally reach the 5,000 kg/ha level. Maximum yield research has shown that yields as high as 6,700 kg/ha are now possible (PPI, 1983a, 1983b, 1984; Cooper, 1984; Lawn et al., 1984; CSIRO, 1983). Thus it has become increasingly more difficult to develop a single cultivar which will be the highest yielding across the entire yield range (1,000 to 6,700 kg/ha). Those cultivars which produce the highest yields at the lower yield range (1,000 to 3,000 kg/ha) tend to get too tall and lodge in the more productive environments (3,500 to 5,500 kg/ha). Conversely, those lodging resistant cultivars that produce the highest yields in high yield environments tend to be too short for best yields in low yield environments.

A. Semidwarf cultivars

When I first began soybean research in Illinois in 1967, on a highly productive soil in central Illinois (13,000 kg/ha maize yields) the best cultivars then available reached a height of nearly 5 feet before they severely lodged in the early pod fill stage following a severe rain storm. Subsequent research in this environment, using artificial supports to prevent lodging, demonstrated that early lodging could reduce potential yield by as much as 21% in soybeans (3,700 kg/ha vs 4,700 kg/ha) (Cooper, 1971a, 1971b).

Based on these observation, I initiated in 1969 a semidwarf breeding program in soybeans, analogous to the successful semidwarf programs in wheat and rice, to overcome the lodging barrier to higher soybean yields (Cooper, 1981; 1985). Several approaches to developing semidwarf types were considered [e.g. shorter indeterminate (Dt_1), semideterminate (Dt_2) or determinate (dt_1) growth types] (Bernard, 1972). Preliminary research indicated the determinate trait, present in nearly all southern U.S. cultivars, when introduced by backcrossing into the northern indeterminate cultivars produced a highly resistant, short statured, semidwarf plant type. The semideterminate trait, Dt_2, failed to reduce lodging enough in high yield environments while changes in indeterminate height were more of a continuous nature with no dramatic change in plant height or lodging resistance. Thus, the determinate trait (characterized by abrupt stem termination after formation of a terminal flower bud) was selected for use in developing a high yielding semidwarf plant type.

The determinate germplasm pool in soybeans and the indeterminate germplasm pool had largely been separated for many years because of the selection for indeterminate types in northern China and determinate types in southern China (Probst and Judd, 1973). This separation of germplasm pools was continued in the United States, with the photoperiodically sensitive soybean cultivars separated into determinate types adapted to the shorter days in the southern U.S. (Maturity Groups V thru VIII) and the indeterminate types adapted to the longer days in the northern U.S. (Maturity Groups 00 thru IV). Crosses between these two germplasm pools resulted in many unadapted types, segregating widely for maturity and for stem termination type. These results discouraged earlier efforts by soybean breeders to develop cultivars from crosses between southern determinate and northern indeterminate cultivars.

Development of dt_1 isolines in an indeterminate background reduced plant height nearly 50% in some cultivars, but unfortunately it also significantly reduced yields (Hicks et al., 1969). Thus it became obvious that the backcrossing approach to introduce the dt_1 trait into northern indeterminate cultivars would not be effective in developing high yielding, determinate, semidwarf cultivars. It was postulated that with the isolation of these two germplasm pools that plant breeders, by selecting for yield in determinate types in the more southern latitudes had empirically selected for a genetic background which complemented the determinate trait (dt_1). Similarly, breeders in more northern latitudes had selected for a genetic background that complemented the indeterminate trait (Dt_1). This would help explain why isolines in either direction (i.e., dt_1 in an indeterminate background or Dt_1 in a determinate background) tended to result in lower yielding genotypes.

Thus the objective of the semidwarf breeding program was not only to introduce the determinate trait into an earlier maturing genotype adapted to the northern U.S., but also to obtain from the southern determinate cultivars, unknown genes complementary to the determinate trait. This was accomplished by crossing high yielding southern determinate cultivars with high yielding northern indeterminate cultivars and growing out a large F_2 population. Determinate (dt_1) F_2 plant types with early enough maturity for adaptation to the northern U.S. were selected and progeny tested for yield as F_2-derived F_3 lines by the EGT breeding procedure. By selecting for early dt_1 plants plus high yield, those F_2 plants which received the complementary genes needed from the southern determinate germplasm for obtaining high yielding determinate semidwarf plant types, were obtained empirically (i.e. without knowing what gene or genes were involved).

The early generation testing procedure played a key role in my success in developing high yielding determinate semidwarf cultivars. Because of the contrasting plant types, it would have been impossible to visually identify the highest yielding lines. Furthermore, I did not know what a high yielding determinate semidwarf variety would look like. Fortunately, with the use of the EGT procedure, I did not need to know. I let the yield data from F_2-derived F_3 and F_4 lines identify those plant types for me.

Some researchers have suggested that the EGT procedure would be effective only in narrow, good by good crosses. I disagree and submit the success in developing high yielding semidwarf soybean cultivars from the crosses between two diverse germplasm pools as evidence that the EGT procedure works well in wide crosses if properly applied. The key to the success of the EGT procedure in wide crosses is the simultaneous selection for the plant type desired (architecture, seed size, maturity, etc.) and yield. In this manner the breeder can identify those crosses with the best combining ability for high yield, within the desired plant type, and obtain the complement of background genes from the parental sources necessary for combining the plant type desired with high yield. By delaying yield testing until homozygosity, as in the pedigree procedure, much of the opportunity for yield selection within superior yielding F_2 families is lost. In the SSD procedure there is no opportunity for selection within selected high yielding F_2 families.

I cite as an example of the effectiveness of the EGT procedure in wide crosses the results of an F_2-derived F_4 yield test in 1973. After three disappointing years in trying to identify high yielding semidwarf plant types, I noted 3 plots of an exceptional plant type in the test of 102 F_2-derived F_4 lines tracing to 34 different crosses. The three plots were extremely lodging resistant, short statured and expressed delayed leaf senescence relative to their maturity. When yields were taken, these lines ranked first, second and seventh, in yield and all traced to the same cross of Williams, an indeterminate Maturity Group III cultivar, by Ransom, a determinate Group VII cultivar. The highest yielding two lines equalled the yield of the high yield indeterminate check cultivar, Williams. Because of their exceptional yield, approximately 50 plants were pulled from the border rows of each line to be single plant threshed and yield tested as F_4-derived F_5 lines the next year. It was apparent in the F_5 that the yield of the F_2-derived lines were indicative of the yield potential of the pure lines that could be derived from them. Nearly all the F_4-derived lines from the lowest yielding (seventh ranked) F_2-derived

F_4 lines were lower in yield than the lowest yielding lines obtained from the other two F_2-derived lines. From the two highest yielding F_2-derived lines, 54 pure lines (F_4-derived) were obtained, the poorest of which outyielded the standard check cultivar Williams, with an average yield advantage of 1,080 kg/ha. The highest yielding line (later released as the determinate semidwarf cultivar, Sprite) exceeded the yield of Williams 2,150 kg/ha. Three cultivars, varying in maturity by 14 days,were released from one F_2 family (Pixie, Elf and Gnome) and two cultivars from the other F_2 family (Sprite and Hobbit). Many other high yielding lines were dropped to avoid undue duplication. By the SSD procedure, only one pure line would have been obtained from each of these F_2 plants.

In high yield environments, where lodging is frequently a barrier to higher soybean yields, the semidwarf cultivars, Sprite and Hobbit, have exceeded the yield of Williams 1,000 to 1,500 kg/ha (Cooper, 1981, 1985). In dry years, however, this advantage may be lost because water becomes the overriding yield limiting factor. To compensate for the specific adaptation of semidwarf cultivars to high yield environments, a soybean production system has been developed specifically for semidwarf cultivars (Cooper, 1981, 1985). First, they should be planted only in environments with a history of high yield (> 3,000 kg/ha) and should be solid-seeded in 17-cm row width at a seeding rate of 750,000 seeds/ha. This is in contrast to 76-cm row widths at 375,000 seeds/ha commonly used for indeterminate cultivars. Averaged over 10 years in two diverse environments in Ohio, solid-seeded Sprite averaged 800 kg/ha higher yield than 75-cm row Williams at one location and 1,000 kg/ha more at the other. The yield advantage ranged from 0 to 2,000 kg/ha depending on rainfall during the growing season. Since the solid-seeded Sprite equalled the yield of 75-cm Williams in dry years and was much higher in favorable moisture years, this resulted in the higher average yields over the 10-year period. Based on these results, a production system called HYSIP (high-yield-system-in-place) has been developed for soybean production (Cooper, 1987). Since it is not possible to predict in advance the good moisture years, the grower is encouraged to have the high-yield-system-in-place (in this case the solid-seeded semidwarf system) every year in order to take advantage of the favorable moisture years and long term higher average yields.

B. Drought tolerant cultivars

When I first arrived in Ohio in 1977, I noted there were many marginal soils (too wet early in the season and too dry late in the season) where the normal indeterminate cultivars being grown were quite short and low in yield. As a carryover from my indeterminate breeding program (conducted before the determinate semidwarf program was initiated), a very tall, vigorous vegetative growth, breeding line was identified as having superior yield potential on drought prone soils where yields were in the 2,000 to 3,000 kg/ha range. However in high yield environments, this line lodged severely and was considered undesirable in environments where the yield potential was above 3,300 kg/ha. This line was released as the cultivar, Amcor, and recommended specifically for marginal soils and for double cropping, where its greater vegetative growth gave it a yield advantage over shorter indeterminate cultivars (Walker and Cooper, 1982). In 1978, I initiated a new breeding program with the objective of developing cultivars with specific adaptation to marginal (primarily drought prone) soils. The approach taken was to select for taller, more vigorous growing cultivars, which will produce adequate vegetative growth under the temporary drought conditions often experienced on some soils in the Midwest. The requirement for lodging resistance was relaxed, since the cultivars developed from this program will not be recommended for the more productive environments where lodging can become a problem. The first lines from this program are just now entering the advanced stages of testing. Like with the semidwarf program, I have found it relatively easy to obtain a new plant type (e.g. short, determinate semidwarfs or very tall, vigorous indeterminates). The difficult part is combining these new plant types with high yield. This is where I have found the EGT procedure a superior breeding method in the developing of high yielding new plant types from wide crosses. Since all selection for yield, beginning in the F_3, is based on actual yield data, I do not have to know what the high yielding new plant type will look like. I can use the yield data obtained to identify which determinate semidwarf or in this case, tall indeterminate lines, carry the yield genes necessary for a superior yielding cultivar.

Summary

As mentioned previously, it is the belief of some researchers that the EGT procedure is limited to only narrow crosses of good x good lines. I disagree with this conclusion based on my experience in the successful use of the EGT procedure in wide crosses to develop high yielding new plant types. It is for you to decide whether the EGT procedure will be of value in your Phaseolus breeding programs. If you have as a major goal combining high yield with specific plant types from wide crosses, it is my belief that the EGT procedure, as described here, would prove to be an effective breeding method.

References

Bernard, R. L. 1972. Two genes affecting stem termination in soybeans, Crop Sci. 12:235-239.

PPI (Potash and Phosphate Institute). 1983a. New world record corn and soybean research yields in 1982. Better Crops 67, 4-5, PPI, Atlanta, Georgia.

_________. 1983b. Soybeans topped 100 bu/A in maximum yield research in Ohio. Better Crops 67, 8-9, PPI, Atlanta, Georgia.

_________. 1984. 1983 soybean research yields top 118 bu/A. Better Crops 68, 6, PPI, Atlanta, Georgia.

Boerma, H. R. and Cooper, R. L. 1975a. Comparison of three selection procedures for yield in soybeans. Crop Sci. 15:225-229.

_________ and _________. 1975b. Performance of pure lines obtained from superior yielding heterogeneous lines in soybeans. Crop Sci. 15:300-302.

_________ and _________. 1975c. Effectiveness of early generation yield selection of heterogeneous lines in soybeans. Crop Sci. 15:313-315.

Brim, C. A., and Cokerham, C. C. 1961. Inheritance of quantitative characters in soybeans. Crop Sci. 1:187-190.

_________. 1966. A modified pedigree method of selection in soybeans. Crop Sci. 6:220.

Cooper, R. L. 1971a. Influence of early lodging on yield of soybean [Glycine max (L.) Merr.]. Agron. J. 63:449-450.

_________. 1971b. Influence of soybean production practices on lodging and seed yield in highly productive environments. Agron. J. 63:490-493.

_________. 1981. Development of short-statured soybean cultivars. Crop Sci. 21:127-131.

_________. 1982. Early generation testing as an alternative to the single seed descent breeding method in soybeans. Agron. Abstr. p. 62.

_________. 1984. Maximum yield research in soybeans (> 5500 kg/ha. Agron. Abstr. p. 124.

_________. and Jeffers, D. L. 1984. Use of nitrogen stress to demonstrate the effect of yield limiting factors on the yield response of soybeans to narrow row systems. Agron. J. 76:257-259.

_________. 1985. Breeding semidwarf soybeans. Chpt. pp. 289-309. In: J. Janick (ed.) Plant Breeding Reviews. Vol. 3. AVI Publishing Company, Inc., Westport, Conn.

_________. 1987. The High-Yield-System-In-Place (HYSIP) concept for soybean production. Agron. Abstr. p. 108.

Hanson, W. D.; Leffel, R. C.; and Johnson, H. W. 1962. Visual discrimination for yield among soybean phenotypes. Crop Sci. 2:93-96.

Hicks, D. R.; Pendleton, J. W.; Bernard, R. L.; and Johnston, T. J. 1969. Responses of soybean plant types to planting patterns. Agron. J. 61:290-293.

Lawn, R. J.; Troedson, R. J.; Garside, A. L.; and Byth, D. E. 1984. Soybeans in saturated soil - a new way to higher yields. Program and Abstracts. World Soybean Research Conference III. pp. 67-68. August 12-17, 1984, Iowa State University, Ames, Iowa.

CSIRO (Commonwealth Scientific and Industrial Research Organization). 1983. Soybean response to controlled waterlogging. Rural Research, 120, 4-8, CSIRO, East Melbourne, Victoria, Australia.

Probst, A. H. and Judd, R. W. 1973. Origin, U.S. history and development, and world distribution. p. 1-15. In: B. E. Caldwell (ed.), Soybeans: Improvement, production and uses. Amer. Soc. Agron., Madison, WI.

Walker, A. K. and Cooper, R. L. 1982. Adaptation of soybean cultivars to low yield environments. Crop Sci. 22:678-680.

Table 1. Modified early generation testing (EGT) breeding procedure for soybeans.

Year	Generation*	Number	Plot Size
1	Cross	100/year	field crossing block
1	F_1	5 plants/cross	space plants, winter nursery or greenhouse
2	F_2	300 plants/cross	18 m row, 17 seeds/m, 75 cm row width
3	$F_{2.3}$	30 lines/cross	1-row, 3 m plots, 100 cm row width, harvest 2.5 m, 1 rep
4	$F_{2.4}$	1 to 30 lines/selected cross	4-row, 6 m plots, 75 cm row width, harvest 5 m 2 center rows, 1 rep
5	$F_{4.5}$	10 to 50 lines/selected F_2 family	1-row, 3 m plots, 100 cm row width, harvest 2.5 m, 1 rep
6	$F_{4.6}$	1 to 50 lines/selected F_2 family	4-row, 6 m plots, 75 cm row width, harvest 5 m, 2 center rows, 1 rep, 1 location

* Selection in the $F_{2.3}$, $F_{2.4}$, $F_{4.5}$ and $F_{4.6}$ based on actual yield data ($F_{2.3}$ equals F_2-derived F_3 line; $F_{4.5}$ equals F_4-derived F_5 line, etc.).

BREEDING FOR YIELD IN OTHER LEGUMES

F.J. Muehlbauer*

Introduction

Yields of cool season food legumes (Pea, Lentil, Chickpea and Faba bean) are generally considered poor when compared to important world crops such as wheat and maize. Explanations for the chronic poor yields of the food legumes range from the often quoted "yield barrier", "narrow genetic base", "lack of research on food legumes in general" to "biological limitations". Of these cryptic explanations for poor yields, the latter may be an important factor of why food legume yields have not kept pace with the more prominent cereal grains. Also, it is possible, as some say, that these legumes simply do not respond to selection for yield or are indifferent to selection (Bunting, 1988). Nevertheless, research programs have begun to identify important factors that limit productivity and breeders have begun to make progress in yields.

Breeding programs on most of these crops have been initiated recently and it is possible that systems of breeding and philosophy of breeding developed and proved to be effective for the cereal grains do not transfer readily to the legume crops. Then too, many early breeding programs for the food legumes have tended to concentrate on breeding for improved nutritional quality (usually higher protein concentration) and not on improved yields. In retrospect, this direction of breeding may have curtailed or reduced advances in yields that might otherwise have been made. More recently, breeding programs have begun to focus on overcoming

---

* Research Geneticist, U.S. Department of Agriculture, Agricultural Research Service. Pullman, WA 99164, U.S.A.

biotic and abiotic stresses on the expectation, often realized, that yield would be improved. Concurrent with the development of breeding programs for the other food legumes, there has been a concerted effort by many centers and research institutions to collect and preserve the indigenous landraces and wild forms of these legumes, and to make those collections available to breeders.

Approaches to yield improvement have included appropriate phenology, altered architectural types, more favorable partitioning of biomass into seeds and broader adaptation and stability of yields over locations and seasons. Recent developments in biotechnology may make it possible to better understand the genetic mechanisms underlying yield and other quantitative traits that affect yield. These and other issues that affect breeding for yield are reviewed and discussed herein.

Germplasm Available

The landraces of the food legumes have been collected and are maintained in numerous collections worldwide (Table 1). There are regions of the world that are underrepresented including areas where these crops have either evolved or where they are now important. Prime examples include China for faba beans, Afghanistan for lentils, and China and Ethiopia for peas. The seemingly large number of accessions (Table 1) maintained for these crops may be misleading. Exchanges between breeders and germplasm curators have undoubtedly resulted in much duplication between collections. Rather than an unwanted burden, this is probably a good safeguard against loss of accessions. In any case, there appears to be sufficient genetic variation in the food legume crops on which to base breeding programs.

Germplasm collections contain mostly indigenous landraces and improved cultivars collected in areas easily accessible to collectors. Unfortunately, many early expeditions to collect germplasm have ignored the wild ancestoral species which might have easily been collected. The habitats of the wild species of these crops can be readily defined and characterized in addition to appropriate times for collection of seeds. Fortunately, the wild species are not likely to be easily lost because of their indigenous nature and their ability to survive in their native habitats. Successful explorations (Ladizinsky et al., 1984; Muehlbauer et al., 1988) and others have provided numerous accessions of wild species that are now maintained in the U.S. Department of Agriculture, Plant Introduction collection at Pullman, Washington and in the ICARDA collection at Aleppo, Syria.

Breeding efforts in chickpea, lentil and faba bean were limited until the international centers, ICARDA and ICRISAT, began extensive work on this group of crops. Germplasm is available and there appears to be a developing network of breeders in national programs devoted to the improvement of these crops. Short term efforts have been concerned with broad adaptation and certain disease problems. Long term goals focus on improved yield potential.

Constraints to Yield

There are numerous constraints to yield in the cool season food legumes. Faba bean has exceptionally high yield potential that has been estimated to be 5-6 tons/ha; however, the problem is mostly of instability of yield. Infestations of Orobanche in the Mediterranean region and northern Africa, Egypt in particular, is a major problem. Chocolate spot, is also considered a major field limiting factor. Yield instability is thought to be the result of a high percentage of flower and pod abortion due to heat, drought and other stresses. In this latter case, independent vascular supply (Bond, et al. 1985) to the developing pods may ultimately improve yields.

Adaptation of the lentil crop to mechanical means of harvest is currently the major goal of breeding in the dry areas of the middle east. The high cost of hand labor needed for harvest of the lentil crop is becoming prohibitive and has actually reduced the area sown to the crop in many countries that have traditionally produced lentils. Good progress is being made in the development of tall, non-lodging genotypes which are expected to be more adaptable to machine harvesting.

Other constraints to lentil yields include shattering (Erskine, 1984), lentil rust (*Uromyces fabae*), Ascochyta blight, *Sitona* weevil, susceptibility to numerous viruses, and parasitism by several species of *Orobanche*.

Ascochyta blight (*A. rabiei*)is the major constraint to yield of chickpea in nearly all regions where the crop is grown. Resistance has been identified at ICARDA and is being incorporated into improved cultivars. However, variation among biotypes of the fungus may overcome present sources of resistance and cause difficulties in breeding. Chickpea crops can also be seriously affected by Fusarium wilt (*Fusarium oxysporum* f. sp. *ciceri*) and various root rots although resistance is available and is being incorporated into improved cultivars.

Pea root rot caused by *Fusarium solani* f. sp. *pisi* and *Pythium ultimum* is considered the most devastating disease of peas. In addition, *Aphanomyces eutechies* is a particularly devastating root disease of peas in cool wet regions. Fusarium wilt (incited by *Fusarium oxysporum* f. sp. *pisi*, downy and powdery mildew (incited by *Peronospora viciae* and *Erysiphe polygoni*, respectively) can also be constraints to yields of peas. Insect pests such as the pea weevil (*Bruchus pisorum*) and the leaf weevil (*Sitona lineatus*) seriously limit yields. Numerous aphid borne viruses can also affect the pea crop.

Methods of Breeding for Yield

Yield improvement of the food legumes by means other than reducing the yield depressing effects of diseases and pests has involved some combination of appropriate phenology to avoid stress periods, altered plant architecture, adaptation to environment, increased total biomass, and more favorable partitioning to the seeds. Methods of breeding have ranged from pureline selection in landraces to cyclical recurrent selection to obtain favorable combinations of genes.

Conventional methods of breeding cool season food legumes

Methods of breeding food legumes are the same as those used for other self-pollinated crops. These methods include: mass and pureline selection, bulk population breeding, pedigree selection, single seed descent, and cyclical schemes. These methods of breeding the food legumes have been well documented (Bond, et al. 1985; Davies, et al. 1985; Hawtin, et al. 1980; Muehlbauer and Slinkard, 1985; Muehlbauer, et al. 1980; Robertson, 1985; and Singh, et al. 1985).

Mass and pureline selection. Selection within introduced germplasm and indigenous landraces has led to improved crop uniformity and user acceptance; however overall yield potential and adaptation to the environment has not changed appreciably. This approach has been followed by recently established programs in order to quickly provide improved cultivars. Most programs quickly turn to hybridization and selection to recombine traits considered important.

Hybridization and selection. Breeding programs for the food legumes normally produce large numbers of crosses designed to recombine desired traits. Procedures for hybridization have been described in detail (Bond, et al. 1980; Gritton, 1980; Muehlbauer, et al. 1980; Auckland, et al. 1980). Following hybridization the populations are usually handled using conventional techniques. The bulk population method appears to be the most popular. A description of these methods and how they are employed in the food legumes is as follows:

Bulk population. The bulk breeding method has become the preferred method for lentil and chickpea breeding because of the ease of application and the difficulties often encountered with other methods. Simplicity and the relatively low cost makes it an attractive method for programs attempting to produce cultivars with broad adaptation. With the bulk method, large populations are available for multi-location evaluation and selection. However, there is a possibility that genetic variation can be lost due to genetic shifts within successive generations of bulking. This is particularly true in wide crosses in which the parents differ greatly for such traits as plant height, flowering time and seed size. Tall, late flowering segregants that produce large numbers of small seeds can rapidly become predominant during generation advance. Desired genotypes might easily be at such low frequency in the population in later generations that their selection can be very difficult.

The food legume breeding program at Pullman, Washington, USA has adapted a modification of the bulk method that combines certain aspects of mass selection. Hybrid populations are mass selected in each generation of advance for highly heritable traits. Selection is then practiced in the F_5 and later generations.

A modification of the bulk method, single seed descent, is known to maintain genetic variation in breeding populations during successive generations of inbreeding (Haddad and Muehlbauer, 1981). However, the method is not widely used in grain legume breeding because it tends to be tedious and occasionally a large percentage of plants have been lost thus reducing variation available for selection.

ICARDA uses a combination of the bulk and pedigree method.

Populations are usually advanced to the F_4 by the bulk method after which the pedigree method is used. With this modification, promising bulk populations can be identified for subsequent selection of individual plants. After individual plant selection, usually in F_4, the progenies are handled using pedigree selection procedures. A possible disadvantage of this procedure is the reliance on F_4 plant selection and assuming there will be some correlation with later generation performance. Slinkard at Saskatoon, Canada uses F_2 derived bulk populations and selects primarily for yielding ability (Muehlbauer and Slinkard, 1985).

The pedigree method of breeding is not generally used in grain legumes possibly because of the plasticity exhibited by individual plants and their tendency to expand and occupy available space. Performance of individual plants, upon which selection is usually practiced, can therefore be very different from that in more densely sown stands as used in the final evaluation of a potential new cultivar. Also, there can be a high degree of non-additive genetic effects in early generations of hybrid populations, particularly those from wide crosses, that can lead to bias on the part of the selector.

The backcross method. Backcrossing has been especially useful in the grain legumes for transferring single genes to otherwise acceptable genetic backgrounds. The method has been used successfully in the transfer of single genes for resistance to diseases and for the incorporation of genes that affect plant habit, leaf structure, flowering time and other simply inherited traits. The backcross method imposes a limitation on improvements that can be made by breeding since additional changes are usually not made in the recurrent parent.

Population improvement. Population improvement or cyclical selection involves the overall improvement of the germplasm pool used in the breeding of improved cultivars. The methods of population improvement and how such methods are applied to the grain legumes were recently reviewed (Muehlbauer et al. 1988). The general lack of an efficient mechanism of male sterility and the difficulty in obtaining large amounts of crossed seed in the grain legumes has prevented the adoption of population improvement methods in most of the grain legumes except faba bean. In that crop, the high percentage of natural outcrossing makes recurrent selection feasible. Controlled intercrossing of the other food legumes by hand pollinations should be considered. The Diallel Selective Mating System of Jensen (1978) is a systematic means of obtaining recurrent selection populations with a minimum of hand cross pollinations.

Breeding for Improved Yield Potential

Comparisons of food legume yields with those of the cereals are often made and usually found to be unfavorable for the legumes. Minimal research on the legumes compared to cereals may be the reason; however, energy requirements for seed yield in legumes may be greater than that of the cereals and therefore such comparisons may be misleading. Also, there has been a general trend toward displacing food legumes to marginal land and to limit production inputs for the legumes.

Several approaches have been used to breed for improved yield potential in the food legumes. These include alterations of plant architecture, more favorable partitioning, improved adaptation to environment, and adaptation to abiotic stresses.

Alterations of plant architecture

Genetic and growth habit variations for plant form are available in the food legumes. There are genes for altered leaf structure, flowering time, podding habit, and numerous other genes that affect plant structure and form. Alterations of plant form currently being attempted for the purpose of improving yield are described as follows:

Peas. Forms of pea plants not previously available were made possible with the discovery of the 'afila' gene by Goldenburg (1965). The afila gene (af) converts leaflets to tendrils which has proved to be a valuable trait for improved standing ability. The additional tendrils of afila plants intertwine and produce a canopy which resists lodging. Canopy leaf area is reduced by an estimated 25-30 percent; however, yields have been comparable to normal leafed types. The reason may be that the afila leaf allows solar irradiation to reach leaves in the lower part of the canopy for photosynthesis. In normal leafed types, there tends to be a great deal of mutual shading of leaves which in turn may reduce their photosynthetic activity. Besides the presumed benefit of greater light penetration, the reduced leaf area and better standing ability may reduce the incidence of foliar diseases such as: Sclerotinia white mold, Botrytis grey mold and possibly others (Davies et al., 1985). Reduced leaf area types appear to promote early and rapid maturity which is particularly important for quality dry peas. Breeders in the European Economic Community have begun to focus on the development of so-called semi-leafless (af) cultivars for combining peas. The peas are intended for use as protein supplements for animal feeding and therefore high yield is the most important breeding objective.

Pod dehiscence of peas intended for dry seed harvest can be a serious problem that can significantly reduce yields. Genes are available that can reduce the problem and include the p and v genes for reduced pod fiber. Cultivars such as 'Colt' and 'Umatilla' have one of these genes, and have been released.

As a result of the work of Murfet (1977) on major genes controlling flowering in peas it is now clear that the trait once considered quantitatively inherited can now be explained by the action of several major genes. As a result of this work flowering time and thus phenology of peas can be accurately predicted from the genotype. Appropriate phenology for pea cultivars is essential if the pea crop is to take the best advantage of the environment in which it is grown.

Lentil. Larger and more stable grain yields are the major objectives of lentil breeding programs worldwide. Adaptation to stress environments, especially in regions of low rainfall, is also a primary objective. As the higher yielding and more easily produced cereals assume the better land areas, lentils have been displaced to progressively poorer areas, usually with less rainfall, poorer soils and generally stony areas. This situation presents a difficult challenge for breeders of how to maintain or improve yields for generally poorer production areas. What makes the problem particularly difficult is the absence of efficient machine harvesting methods.

Currently, most lentil crops in the Middle East and north Africa are harvested by hand pulling because the short vine height and rough soil surface precludes machine harvest. A major goal in most breeding programs in that region is to increase the canopy height to accommodate mechanical harvest. Improved straw and residue yield is also important because of the value placed on lentil straw as animal feed. In some instances, the straw and residues from the threshing operation have commanded prices greater than that of the grain. Total biological yield of lentil crops is thus an important selection criterion. The correlation between seed and straw yields is strong and positive and so simultaneous selection for both traits is possible.

Several traits are considered to be important for the success of mechanical harvesting and include increased plant height, pods borne well above the soil surface, erect growth habit, improved standing ability, reduced pod dehiscence, and reduced pod drop.

A clearance of about 15 cm between the soil surface and the lowest pod is required for successful mechanical cutting or pulling of lentil plants (Khayrallah, 1981; Diekmann and Papazian, 1985). This leads to the view that mechanical harvesting of lentil would be facilitated by the introduction of tall cultivars with lowermost pods borne well above the soil surface. Genetic variation for plant height and lowest pod height in the ICARDA collection ranged from 10 to 45 cm and 6 to 30 cm, (Solh and Erskine, 1981). It was also found that the two traits are positively correlated which indicates that selection for both traits is possible. However, tall plants have a tendency to lodge and both traits are highly affected by the environment (Saxena and Hawtin, 1981).

Relative pod indehiscence has been identified in lentil, and selection was feasible for this trait simply by the delaying of harvest. However, significant variability for pod shattering, which accounts for as much as twice the loss caused by pod dehiscence, does not seem to be available (Erskine, 1985).

Non-lodging lentil cultivars could be a very important development toward the success of mechanical harvesting in stony areas and also to reduce losses in those areas where lentil is mechanically harvested already. Stem thickness, stem lignification, and greater tendril production and activity may be important contributions to lodging resistance in lentil. Good progress is being made toward types that retain canopy structure at maturity.

Tall, erect lentil types such as those considered important for successful mechanized harvest of lentil may have reduced yield potential. From experience, it seems that erect genotypes with acute branch angles tend to be relatively poor yielding and do not compete well with weeds. Their poor competitive ability is the result of a reduced ability to fill available space. By not covering the soil surface as rapidly as more spreading types, there can be losses of limited soil moisture. Also, the slower rates of canopy closure in upright types tend to provide an advantage to weeds, which then deplete water even more. Genotypes that rapidly cover the soil surface and develop a full canopy should allow for successful mechanical harvest of acceptable seed and straw yields. It seems that variability for traits that would contribute to successful mechanical harvesting is available in lentil germplasm.

In the absence of basic improvements in yield potential, reduced losses from pod and seed shattering could improve harvested yields significantly. Shattering has averaged 15% in the USA and Erskine (1984) has reported similar estimates of shattering. Shattering losses can result from either pod dehiscence or pod drop. Erskine (1984) reported that pod drop was the most serious of the two types of shatter. Some small-seeded lentils have pods that retain their integrity during threshing. The strongly indehiscent pod trait carried by some small seeded lentil genotypes should be transferred to large seeded cultivars to reduce losses from pod dehiscence.

Introgression of microsperma types (small seeded) with macrosperma types (large seeded) is viewed as a potentially productive strategy for hybridization because the two types evolved from and became important in different ecological regions and are therefore likely to possess different genes and adaptive complexes. ICARDA has utilized accessions of _Lens orientulis_, the presumed progenitor of the cultivated form in their hybridization program and have made selections that have recently appeared in international yield trials.

Chickpeas. The major objective of the chickpea breeding programs in the major production areas is to overcome the devastating effects of Ascochyta blight. Improvement of yield potential cannot be considered when faced with this disease. To avoid losses from the disease the crop is sown in the spring when the dry conditions inhibit the spread of the disease. Consequently, yield potential is greatly reduced.

Improved yield potential could be realized if it were possible to plant the crop in the fall or early winter and allow the crop to take advantage of the cool moist winter season for plant growth. Fall or winter sown chickpeas yield substantially more when compared to spring sown crops; however, an epidemic of Ascochyta blight can completely destroy the crop. Resistance to the disease will allow winter sowing and make it possible to obtain higher yields. This is a prime example of how resistance to a disease can make it possible to obtain better water use efficiency. Vegetative and early reproductive phases take place under cool, moist conditions while periods of high evaporative demand come later.

Tall upright plant habit for chickpea is also an important selection criterion for chickpea breeders who are attempting to adapt the crop to machine harvesting. Taller more upright cultivars might be grown at higher plant populations which, depending on available moisture, could improve yield potential.

Faba bean. Yields of faba bean are erratic between seasons and sites where the crop is grown. Excessive flower and pod abortion is generally considered the most likely cause.

Independent vascular supply to individual flowers and to developing fruits could be of major importance in the development of cultivars with stable pod setting and seed yields (Bond et al. 1985).

Cultivars with strong stems, few branches and concentrated pod setting are being sought by breeders. Reduced vegetative growth after final fruit setting also may be beneficial to high yields.

True determinant types of faba bean have been isolated and may hold promise for future breeding for improved stability of yield. Breeders have concentrated on determinant plant habit, but determinant cultivars with high yields are yet to be made available.

In areas of low insect activity, autofertile faba bean cultivars are sought. The autofertility trait is being used in breeding high yielding cultivars for such areas. Autofertile lines will require an alteration of approaches to breeding (Bond et al. 1985).

Partitioning

For all of the legumes it is generally agreed that grain yields can be improved through increased biomass and a more favorable partitioning into the seeds. Tall and erect types that are relatively compact and non-competitive with neighboring plants in a stand could allow increased plant density and greater total biological yield. With comparable partitioning into seeds, yields would increase accordingly while the additional crop residues would provide much needed forage for livestock.

Breeding for Adaptation and Yield

Multi-location testing

Results of testing for yield potential are generally less consistent than are the results of testing other traits. Large environmental effects can be estimated by multi-location testing targeted to the major production areas. Large genotype x environment effects are usually not wanted but often cause complications for selection. The choice often has to be made between development of cultivars for broad adaptation or for specific adaptation. International centers, with their mandate of improving crops for a wide area, have very successfully used multi-location testing to identify broadly adapted genotypes. As those programs have advanced, there has been an increasing emphasis on specific adaptation and selection of genotypes for more specialized uses.

Regression analyses

Regression of genotypic yields obtained at specific locations on the mean of all genotypes at particular locations has been suggested (Findlay and Wilkenson, 1963) as a means of identifying selections with broad adaptation. The method is not widely used possibly because of the need for a large number of genotypes and locations of testing in order to obtain reliable estimates. Also, it is likely that performance of genotypes, including their adaptation, can be estimated directly without having to use regression methods.

Molecular Approaches to Crop Improvement

Until rather recently, only morphological markers were available for genetic studies in plant species. Their use in plant breeding was limited by their relatively low number that were available in most crosses, their often deleterious effects and their usual epistatic effects on other characters. Because of these disadvantages in the use of morphological markers, their direct use in breeding as 'tags' for important genes has been quite limited. Molecular markers seems to have much greater utility for applied breeding. Large numbers of alleles can be found at molecular marker loci. Genotypes of individual plants can be easily determined because of the condominant expression of molecular markers. Molecular markers usually are neutral and have no deleterious effects.

Isozymes is a term coined for "isoenzyme" and refers to enzymes that catalyze the same reaction. Isozymes can be distinguished by their differential mobility in some type of strata; usually starch gels or polyacrylamide gels. Isozyme profiles of individual plants can be determined on relatively small samples of leaves, seeds, or roots. They can therefore be used extensively in genetic and breeding studies similar to the use of morphological markers. Weeden et al. (1988) recently reviewed the application of isozyme analysis in pulse crops.

Isozyme analysis of plant genomes is liminted by the number of enzyme assays available and the degree of polymorphism available in the species of interest. Fortunately, there is available another type of molecular marker termed "Restriction Fragment Length Polymorphisms" (RFLPs). RFLPs focus directly at the DNA level and were made possible through the use of a wide range of restriction endonucleases that are used to isolate unique DNA sequences of a plant genome. Such unique sequences can then be cloned and used to probe gels containing restricted nuclear DNA. Polymorphisms of restricted DNA can then be identified and mapped in the same manner as other molecular, or morphological markers. Presumably there is virtually no limit to the number of RFLPs that can be mapped in a plant genome and therefore "high density" gene maps can be developed for use in detailed genetic analyses and in plant breeding. Possible uses might include the identification of "tags" for important genes, the use of highly density gene maps to study quantitative genetic variation and the monitoring of introgression of genes from exotic sources.

Tags for important genes

Useful linkages between isozyme markers and disease resistance genes are known in pea. The linkage of a seed esterase (Est-s) with the gene for resistance to Fusarium wild race 1 (Fw) was demonstrated by Hunt and Barnes (1982). The extremely close linkage reported should make it possible to select plants with resistance to wild by choosing plants with the Est-s allele associated with the dominant gene for resistance. Similarly, an allozyme of Phospho-gluco-mutase (Pgm-p) can be used as a marker for the gene which controls resistance to bean yellow mosaic virus in pea (Weeden et al., 1984). Other close linkages, it found, may permit the breeding and selection for resistance to certain diseases without actually having the disease present.

Study of quantitative variation

High density gene maps have been proposed and used in the study of quantitative genetic variation in crop plants (Stuber et al., 1982; Stuber et al., 1987) with success. Recently, Havey and Muehlbauer (submitted), developed a genetic linkage map for lentil that contains 37 morphological, isozyme and DNA markers. It was estimated that 50% of the lentil genome would be linked to within 10 cM of one or more of the mapped loci. Studies of quantitative variation can therefore be attempted.

Introgression of genes from exotic sources

Molecular makers might be very useful in demonstrating the introgression of genes from wide sources into the working genepool used by breeders. Many of the food legumes are considered to lack sufficient genetic variation for significant improvement. The transfer of molecular marker alleles found in wild or exotic germplasm sources to a cultivated background would facilitate the introgression of closely linked loci that may be difficult to identify in breeding populations.

Summary

Nearly all breeding programs for the food legumes have had as their ultimate goal the increase in grain yield and improved stability of yield over seasons and locations. Progress in resistance to common diseases of these crops including Ascochyta blight, Botrytis grey mold, root rots and wilts, among others, have made these crops generally more stable in terms of yield and in some cases have made it possible to grow these crops in seasons more favorable for growth and yields. Ascochyta blight resistance in chickpea is a classic example of how the crop may eventually be able to take full advantage of the cool moist winter season in the Mediterranean region and the Middle East.

Appropriate phenology, to take best advantage of time available for crop growth, is an important concept for breeders to consider in their hybridization and selection programs. Similarly, improved plant morphology toward resistance to lodging of tall upright types that are adaptable to machine harvesting is also an important selection consideration as is reduced pod and seed shattering.

Multi-location testing of breeding material is still relied on by breeders to identify selections with broad adaptation and stable yields.

Population improvement involving forms of recurrent selection have not been widely used in food legume breeding other than in faba bean. The lack of an efficient male sterility system to facilitate intercrossing is the primary reason the method has not been widely used. The use of wild relatives of the grain legumes is feasible in _Cicer_ and _Lens_.

The use of high density gene maps to study quantitatively inherited traits may provide a clearer understanding of such traits and provide a basis for parental selection.

References

Auckland, A.K. and L.J.G. van der Maesen. 1980. Chickpea. In: W.R. Fehr and H.H. Hadley (eds.), Hybridization of Crop Plants. American Society of Agronomy, Madison, Wisconsin, U.S.A. p. 249-259.

Bond, D.A., D.A. Lawes and M.H. Poulsen. 1980. Broadbean. In: W.R. Fehr and H.H. Hadley (eds.). Hybridization of Crop Plants. American Society of Agronomy. Madison, Wisconsin, U.S.A. p. 203-213.

Bond, D.A., D.A. Lawes, G.C. Hawtin, M.C. Saxena and J.H. Stephens. 1985. Faba bean (_Vicia faba_ L.). In: R.J. Summerfield and E.H. Roberts (eds.), Grain Legume Crops. Collins. London. p. 199-265.

Bunting, A.H. 1988. A personal review of the International Food Legume Research Conference. In: R.J. Summerfield (ed.), World Crops: Cool Season Food Legumes. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 1155-1167.

Davies, D.R., G.J. Berry, M.C. Heath and T.C.K. Dawkins. 1985. Pea (Pisum sativum L.). In: R.J. Summerfield and E.H. Roberts (eds.), Grain Legume Crops. Collins. London. p. 147-198.

Diekmann, J. and J. Papazian. 1985. Mechanization of production of faba beans, chickpeas and lentils. In: M.C. Saxena and S. Varma (eds.). Proceedings, Faba Beans, Kabuli Chickpeas and Lentils for the 1980's. An International Workshop 16-20 May, 1983. ICARDA. Aleppo, Syria. p. 281-290.

Erskine, W. 1984. Selection for pod retention and pod indehiscence in lentils. Euphytica 34:105-112.

Findlay, K.W. and G.N. Wilkinson. 1963. The analysis of adaptation in a plant breeding programme. Aust. J. Agric. Res. 14:742-754.

Goldenburg, Jose B. 1965. "Afila" a new mutation in pea (Pisum sativum L.) Boletin Genetico, Instituto de Fitotecnia, Castelar, Argentina, p. 27-28.

Gritton, E.T. 1980. Field Pea. In: W.R. Fehr and H.H. Hadley (eds.), Hybridization of Crop Plants. American Society of Agronomy. Madison, Wisconsin, U.S.A. p. 347-356.

Haddad, N.I. and F.J. Muehlbauer. 1981. Comparison of random bulk population and single-seed-descent methods for lentil breeding. Euphytica 30: 643-651.

Hawtin, G.C., K.B. Singh and M.C. Saxena. 1980. Some recent developments in the understanding and improvement of Cicer and Lens. In: R.J. Summerfield and A.H. Bunting (eds.), Advances in Legume Science. HMSO. London. p. 613-624.

Hunt, J.S. and M.F. Barnes. 1982. Molecular diversity and plant disease resistance: An electrophoretic comparison of near-isogenic lines of wilt resistant or susceptible Pisum sativum L. cv. William Massey. Euphytica 31:341-348.

Jensen, N.F. 1978. Composite breeding methods and the DSM system in cereals. Crop Science 18:622-626.

Khayrallah, W.A. 1981. The mechanization of lentil harvesting. In: C. Webb and G.C. Hawtin (eds.). Lentils. Commonwealth Agricultural Bureaux. Farnhan Royal. England. p. 131-141.

Ladizinsky, G., D. Braun, D. Goshen and F.J. Muehlbauer. 1984. The biological species of the genus Lens L. Bot. Gaz. 145:253-261.

Muehlbauer, F.J. and A.E. Slinkard. 1985. Lentil Improvement in the Americas. In: M.C. Saxena and S. Varma (eds.), Proceedings, Faba Beans, Kabuli Chickpeas and Lentils in the 1980's, An International Workshop 16-20 May, 1983. Aleppo, Syria. pp. 351-366.

Muehlbauer, F.J., W.J. Kaiser and Z. Kutlu. 1988. Collection of food legume germplasm in Turkey. Plant Genetic Resources Newsletter (in press).

Muehlbauer, F.J., A.E. Slinkard and V.E. Wilson. 1980. Lentil. In: W.R. Fehr and H.H. Hadley (eds.), Hybridization of Crop Plants. American Society of Agronomy, Madison, Wisconsin U.S.A. p. 417-426.

Muehlbauer, F.J., R.J. Redden, A.M. Nassib, L.D. Robertson and J.B. Smithson. 1988. Population improvement in pulse crops: an assessment of methods and techniques. In: R.J. Summerfield (ed.), World Crops: Cool Season Food Legumes. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 943-966.

Murfet, I.C. 1977. The physiological genetics of flowering. In Sutcliffe, J.F. and Pate, J.S. (eds.), The Physiology of the Garden Pea, London: Academic Press, p. 385-430.

Robertson, L.D. 1985. Genetic improvement of faba beans for increased yield and yield stability. In: M.C. Saxena and S. Varma (eds.). In: Proceedings, Faba Beans, Kabuli Chickpeas and Lentils in the 1980's. An International Workshop 16-20 May, 1983. ICARDA. Aleppo, Syria. p. 35-53.

Saxena, M.C. and G.C. Hawtin. 1981. Morphology and growth patterns. In: C. Webb and G.C. Hawtin (eds.) Lentils. Commonwealth Agricultural Bureaux, Farnhan Royal. England. p. 39-52.

Singh, K.B., M.V. Reddy and R.S. Malhotra. 1985. Breeding kabuli chickpea for high yield, stability and adaptation. In: M.C. Saxena and S. Varma (eds.). Proceedings, Faba Beans, Kabuli Chickpeas and Lentils in the 1980's. An International Workshop 16-20 May, 1983. ICARDA. Aleppo, Syria. p. 71-90.

Solh, M. and W. Erskine. 1981. Genetic Resources. In: C. Webb and G.C. Hawtin (eds.) Lentils. Commonwealth Agricultural Bureaux. Farnhan Royal. England. p. 53-67.

Stuber, C., M. Goodman and R. Moll. 1982. Improvement of yield and ear number resulting from selection at allozyme loci in a maize population. Crop Science 22:737-740.

Stuber, C., M. Edwards and J. Wendel. 1987. Molecular marker-facilitated investigations of quantitative trait loci in maize. II. Factors influencing yield and its component traits. Crop Science 27:639-648.

van der Maesen, L.J.G., W.J. Kaiser, G.A. Marx and W. Worede. 1988. Genetic basis for pulse crop improvement: collection preservation and genetic variation in relation to needed traits. In: R.J. Summerfield (ed.), World Crops: Cool Season Food Legumes. Kluwer Academic Publishers, Dordrecht, The Netherlands. p. 55-66.

Weeden, N.F., R. Provvidenti and G.A. Marx. 1984. An isozyme marker for resistance to bean yellow mosaic virus in Pisum sativum. Journal of Heredity 75:411.412.

Weeden, H.F., D. Zamir and Y. Tadmar. 1988. Application of isozyme analysis in pulse crops. In: R.J. Summerfield (ed.), World Crops: Cool Season Food Legumes. Klower Academic Publishers, Dordrecht, The Netherlands.

Table 1. Accessions of cool season food legumes in major germplasm collections. (From van der Maesen, et al. 1988).

Institute and location	Species conserved			
	Cicer	Lens	Pisum	Vicia sect. faba
1. Ege Agric.Res.Introd.Centre Menemen, Turkey			2000	
2. Ethiopian Genebank Addis Ababa, Ethiopia	717	413	1860	1298
3. Geneva Pisum Collection Geneva, NY, USA			>5000	
4. Germplasm Laboratory Bari, Italy			5000	2000[a]
5. ICARDA Aleppo, Syria	4500	6000		5000
6. ICRISAT Patancheru, India	14400			
7. INIA Mexico City, Mexico	1600			
8. John Innes Institute Norwich, England			2000	
9. NBPGR New Delhi, India			1400	
10. Netherlands Genebank Wageningen, The Netherlands			800	700
11. Nordic Genebank Lund, Sweden			5000	
12. NSSL Fort Collins, CO, USA	2698	702	2213	18
13. Pakistan Agr.Res.Council Islamabad, Pakistan	626	144	10	13
14. USDA NE Reg. Station Geneva, NY, USA			2800	
15. USDA NW Reg. Station Pullman, WA, USA	3431	1973		295
16. Vavilov Inst.Pl.Industry Leningrad, USSR	1685	2470	5550	2525[a]
17. ZG Kulturpfl. Gatersleben, DDR	40	160	2000	1300

[a] Other sections also included.

35674

DRY BEAN PRODUCTION AND CONSUMPTION IN THE YEAR 2000: PROJECTIONS, THOUGHTS AND GUESSES WITH EMPHASIS ON LATIN AMERICA AND AFRICA

Willem Janssen*

Summary

Bean production trends in Latin America and Africa from 1966 to 1976 and from 1976 to 1986 are analyzed. In the first period production growth in Africa was satisfactory, but mainly based on area expansion. In the second period production growth in Africa slowed down considerably, with the exception of the Southern African region.

In Latin America the performance of the bean production sector was very different. From 1966 to 1976 production growth was very slow, afterwards it sped up, especially in Mexico and Central America. The improvement of bean production was due more to area expansion than to yield increases.

In the year 2000 bean production in Africa has to be 72% above present levels to satisfy demand. In Latin America production has to increase 42%. The production increases in Africa have to be based to a larger extent than in history on yield increases. A drastic improvement in the performance of the bean sector is needed. In Latin America, the required production increases are less and performance of the bean production sector is better. Consequently the chance to satisfy future demand appears bigger.

---

* Economist, Bean Program, CIAT, A.A. 6713, Cali, Colombia.

In Latin America bean production will increasingly be determined by market forces. Farmers will become more market oriented; will start relying to a large extent on purchased inputs; and will grow those beans that provide most income. The decision to grow beans will be made on the basis of profitability. The case of soybeans versus bean yields shows that marginalization of beans is to a large extent a function of profitability. Beans will need to be more productive in order to maintain their role in the agricultural sector.

Within Latin America, beans will remain an important food crop for poor consumers. Nevertheless, for beans to maintain its role in the urban diet, digestibility, convenience, storage and marketing need to be addressed in more detail. Beans will most probably be grown by small farmers, but for different reasons than in history. Instead of home consumption, sales will be the principal objective. This suggests that increased emphasis is needed on yield potential and commercial quality.

In Africa food security is the principal objective of bean production improvement. Urban versus rural income data suggest that food security will be more at risk in the rural areas. African farmers are less market integrated and traditional production improvement strategies, which emphasizes resistance more than commercial quality, will be appropriate.

The evidence suggests that bean production increases will be more easily obtained in Latin America than in Africa. The challenges ahead are very big, especially in Africa, but should still be faced with confidence and enthusiasm.

Acknowledgements

To Douglas Pachico, for the access to his data on beans in Africa and Latin America and to Jairo Castaño for support in data processing.

Introduction

Research for the problems of today is often an activity of doubtful value. By the time that appropriate solutions have been found, drastic changes might have appeared, that reduce the relevance of the proposed solutions. Research should be based on a solid assessment of future production and consumption. The research agenda of today is a function of the expected circumstances of the future.

Of course a profound understanding of present circumstances is vital for accurate production and consumption predictions. In fact, the only way to make reasonable predictions is by understanding historic developments, projecting and modifying these for the future. It should be clear, however, that the value of understanding the present and the past lies in the future.

This paper will try to contribute some information and some speculation to our understanding of bean production and consumption in the year 2000. Most of the information comes from trend analysis and cross-section analysis of bean production and consumption. The speculation involves a judgment on the relevance of past trends for future projections. Both information and speculation are needed to obtain a vision of beans in the year 2000 that is more than a mechanical analysis or a mere opinion.

The look ahead to the year 2000 is more urgent than many of us might have thought. For example the development of an improved variety, takes some six and half years, not as an average but as a minimum (J. Kornegay, 1988). The successful extension and dissemination of an improved variety takes another three or four years. This means that the crosses of the varieties that we hope to see successfully grown in the year 2000, should be made before 1991.

The present paper will first analyze historic production and consumption trends in Africa and Latin America and derive projections for the year 2000. Afterwards some major challenges for the bean sector in Africa and Latin America will be described. Newly arising issues in bean production and consumption will be discussed, mainly by analyzing developments in Latin America. Finally some conclusions on the future of beans will be drawn.

Historic Bean Production Trends

The area planted with beans grew very rapidly in most of Africa during the late sixties and early seventies. Afterwards the rate of area expansion decreased considerably to levels of some 1.8% per year. In both periods area expansion was the main component of bean production increases. The reduction of the rate of area expansion in the second period is indicative for the land scarcity faced in the bean production regions of Africa (Table 1).

In Latin America the trends are more complex. Brazil maintained more than 2% annual area expansion for most of the last 25 years. In the Andean countries the area planted with beans decreased from 76 to 86. Mexico and Central America are cases were area growth was accelerated in the second part of the period. From 1976 to 1986, land constraints were not as binding in Latin America as in Africa (Table 1).

Bean yields in Africa increased in the first period, at a considerable rate in the Great Lakes and a more modest rate in Southern Africa. In Eastern Africa yield growth was negative. In the late seventies and early eighties only Southern Africa was capable of maintaining a reasonable growth rate in yields. In the Great Lakes yield increases were more modest than before, in Eastern Africa yields continued to fall (Table 2).

In Brazil yields fell through both periods, rapidly in the beginning and more slowly in the late seventies and early eighties. In the Andean region and Mexico, yield increases leveled off during the twenty years of study. Only in Central America were falling yield levels converted in rising yield levels (Table 2).

Production growth is roughly the sum of area and yield growth. Production growth leveled off in Eastern Africa and the African Great Lakes. In Southern Africa bean production grew at a steady 2.6% per year (Table 3).

In Brazil a decreasing production trend was converted in an increasing trend. In Mexico a similar but even more marked conversion took place. Also Central America was able to increase the dynamics of its bean production. Only in the Andean region did production growth slow down.

Bean production was more dynamic in Africa than in Latin America in the late sixties and early seventies. Area expansion was the major reason. In the years from 1976 to 1986 the area expansion in Africa slowed down, while yields did not increase more rapidly than before. Opposite to Africa, in Latin America area expansion was very sluggish in the sixties and seventies but obtained more momentum towards the eighties. This was the major reason for the dynamic production growth in the second ten year period. Yields, in Latin America did not show a consistent increase.

Will the growth in bean production, as occurred in the last decade be sufficient to maintain consumption levels? To assess this, expected population growth from 1985 to 2000 is reported in Table 3. These data show that only in Mexico and Central America bean production grew rapidly enough to satisfy population growth. In all the other regions bean consumption will have to fall, or beans will have to be imported, if present trends continue.

This conclusion is consistent with what has been observed in the last 20 years. Apparent consumption levels of pulses (this includes other species, which for the regions in question are of secondary importance) fell from 13.1 kg per head per year to 12.2 in Africa and from 16.2 to 13.2 kg in Latin America. Production has lagged behind population growth, consequently consumption per head has been falling.

Projections of bean consumption trends

On the basis of available income elasticities and income and population growth, bean demand has been estimated for the year 2000. The results of these projections for Africa are reported in Table 4. Due to high population growth, bean demand is projected to increase very rapidly. For every region, bean production has to increase with some 70% in the next fifteen years, in order to satisfy demand. This will be a major challenge, especially for the Great Lakes region where production growth was very low in the period between 76 and 86.

The same figures for Latin America are given in Table 5. In Latin America the growth of consumption will be considerably slower than in Africa, mainly because of lower population growth. Consequently the growth of production to satisfy demand is more modest. Production has to increase with 42% if bean exporting countries (Argentina and Chile) are excluded from the analysis. If these are included, production only has to increase with 32%. The biggest deficits are shown for Mexico and Central America. Nevertheless, these were the only two regions which maintained production growth rates higher than population growth in the last decade, partly to eliminate bean imports. Their projected deficits are highest, but they still are the regions that have most potential of actually satisfying future bean demand.

The production challenge that lays ahead for Africa is enormous and will need major attention by scientists, development specialists and national governments. Within the presented scenario and excluding totalitarian measures that divert beans from domestic consumption to export the possibility to export beans appears extremely remote. For Latin America, the scenario is slightly better.

Strategic considerations for bean production developments in Latin America and Africa

Bean production has to be consistent with the agricultural sector and the national economy in which it takes place. As can be seen in Table 6, Latin America and Africa are at very different stages of development.

First of all, the average income in Latin America is about three times the average income of Africa. In Latin America, most people do now live in an urban environment and find employment outside agriculture. In Africa most people still live in the countryside and depend on agriculture for their living. Income differences between agriculture and the rest of the economy are large on both continents. Nevertheless, the fact that non-agricultural incomes in Africa are almost six times the agricultural incomes, indicate that in Africa most poverty is still concentrated in the countryside. At the same time average protein and calorie availability are more worrying in Africa than in Latin America.

In Latin America the market will become the focus of bean production development. The large majority of beans consumed will be purchased. In a similar way farmers will be increasingly income oriented and will try to maximize their income per day of work. If they are not able to earn a reasonable income in the countryside, they will probably migrate. Future bean production in Latin America will have to pay increasing attention to market requests (quality!) and to farmers desires to increase labor productivity by technifying their production. In short, a major effort should be made to make beans a more attractive crop both to producers and to consumers.

In Africa food security is the main issue (Mellor, Delgado and

Blackie, 1987). Food security should be focused on the rural areas, where presently most poverty is found. The possibility to expand the area of production is limited and attention should be focused on land productivity. The reduced potential for area expansion also suggests that sustainability problems will become very important in the region.

Two other suggestions should be made with respect to Africa. To a large extent Africa depends on agriculture for obtaining foreign exchange. Hence bean production has to be integrated with cash crops or export crops. Finally it appears that beans have consumption potential in certain regions, where they are not traditionally consumed (e.g. the Central Province of Zambia). If feasible production areas can be, found bean consumption could be stimulated in such non-traditional areas.

Future Bean Consumption Issues

As was written before, the importance of markets is a principal issue with respect to bean consumption. Table 7 shows what urbanization implies with respect to markets. Although urban consumers depend less on beans than rural consumers, the importance of bean purchases is considerably higher in the urban areas. This is not only true in a relative sense (% of beans purchased) but also in an absolute sense (grams of beans purchased). The implications are that bean quality characteristics as appreciated in the market will increase their importance relative to agronomic characteristics. Similarly appropriate storage and marketing will become as critical to consumption levels as costs of production.

In the future beans will remain a very important food product for many poor consumers. These are around in very large numbers, also in Latin America. In Brazil the poorest sixty percent of the population has an income per year of some US$448. In Mexico the poorest 40% has to live with US$515/years. In Peru the poorest 60% of the population survives with US$286 per capita per year. For comparison, the average income per capita in the developing world is US$610 per year.

The effects of income on bean consumption are not strong. Normally bean consumption increases with rising incomes in the lower income strata, levels of in the middle income strata and decreases in the wealthiest strata. (internal data, Bean Economics, CIAT). Of course income elasticities vary according to bean type. In Colombia, preferred large grain types have positive income elasticities and less preferred small grain types have negative income elasticities (Pachico, Londoño and Duque, 1983). On average, income elasticities in Latin America are very close to zero. Since average incomes in Africa are lower, income elasticities are positive on that continent (around 0.2).

Nevertheless, in countries such as Brazil bean consumption has fallen significantly over the last fifteen years. (Table 8). The evidence suggests that is due partially to price increases and urbanization. For the period from 1971 to 1981 44% of consumption decrease could be explained by the price and 16% by urbanization. The other 40% is due to other reasons, among which the following can be suggested: 1) Although beans in Brazil as well as in the rest of Latin America do not have clear substitutes (such as lentils, chickpeas), the prices of some partial substitutes decreased very rapidly. This was for example the case of poultry (technological change) and wheat (policies). 2) Urban consumers tend to prefer food products that are easy to digest such as vegetables, animal proteins or rice. Bean digestibility is rather low, a factor against its consumption potential in urban areas. 3) People tend to spend more time away from home, especially if housewives work, and prefer food which can be rapidly prepared. Beans have long cooking times and do not fit these requirements. 4) Food marketing has changed drastically. Products are available that before could not be obtained, because of better road infrastructure and transport capacity. Food preservation has improved rapidly, especially in case of meat and dairy products. Before beans were among the products that could be marketed most easily in the urban environment, now that advantage has eroded by food marketing developments of other products. Considering that beans are appreciated by many nutritionists for its healthy nature, it must be clear that studies to improve the feasibility of beans in the urban diet could have a very high pay-off.

Future bean production issues

Beans are an outstanding small farm crop, as can be appreciated in Table 9. It is one of the most important crops for small farmers, and what is more, small farmers are its most important producers. Will beans be grown by small farmers in the future? The available evidence suggests this will be the case but also suggests that production methods might change rapidly.

Whether beans will be grown by small or by large farmers depends to a large extent on the costs of production. Table 10 shows production costs for three systems in Costa Rica. The "tapado" system is a traditional low input system, practiced by small farmes with no principal land constraints or with hilly land. The "espeque" system is a production system with more intensive land preparation and more care of the crop. The "semi-mechanized" system is only practiced by large farmers and depends on mechanized land preparation.

At a full cost basis the semi-mechanized system is most efficient. However machinery and input costs (cash costs) are high for this production system. If land costs are left out of the calculation (farmers often do not value the cost of land since it is their own), the "semi-mechanized" systems is already less attractive. If labor costs are reduced (again, farmers often do not cost their own labor) the semi mechanized system is the least attractive. It appears that in a situation of competition (for example because of low prices) the "espeque" and "tapado" systems are less vulnerable. The conclusion should be that the flexibility of the small farmer will be an important instrument to compete with large farmers.

Evidence from Brazil supports the thesis that the small farmer will continue to produce most beans (IBGE, various years). Bean production in the states of Parana and Rio Grande do Sul diminished from 1976 to 1986. In areas with many small producers such as the Northeast and the state of Santa Catarina production increased rapidly.

The small producer of the future will not be similar to the small producer of the past. Small farmers, when integrated in the market, tend to discover quickly the potential of inputs as a land-enhancing mechanism. (Pachico, 1984). For example, in the coastal fringe of Peru, all bean farmers use chemical control methods, 72% made use of credit and 46% purchased seed. If input use can be held within reasonable limits, this might reduce the demand for disease and insect resistance in bean varieties. At the same moment, the demand for integrated control strategies will increase.

The market oriented small farmer will judge beans on their income potential. In most cases beans are not the only crop that a farmer grows. The role of beans in the farm system will depend strongly on their relative profitability with respect to other crops. If by improving productivity, the profitability of beans improves, this will be rapidly reflected in growth in the area planted, as shown in Guatemala and Costa Rica.

If beans do not compete, they will be pushed out of production systems. Clear evidence in this respect comes from Brazil, where during the seventies beans were pushed towards marginal production areas by soybeans. Figure 1 shows the soybean/dry bean yield ratio for the U.S.A. and Brazil. Since 1971, when soybean production took off, bean yields have been less than fifty percent of soybean yields. Even if it is taken into account that bean yields in the South of Brazil are 40% above average yields, the ratio remains above two in 11 out of 16 years and above the ratio for the U.S.A. in all years.

The brief comparison of soybean and bean yields would suggest that beans were marginalized because the yields were low. Such a conclusion has rather strong implications for the research process. More emphasis on yield appears to be needed to improve the attractiveness of the crop.

Conclusions

Bean production trends over the last twenty years have been very erratic. Until 1976 production grew more quickly in Africa than in Latin America, afterwards Latin American production recovered, especially in Mexico and Central America. Neither in Latin America nor in Africa has bean production risen quickly enough to maintain consumption per capita at historic levels. Especially in Africa, this in worrying.

If present consumption levels are projected towards the year 2000, larger deficits between existing production and future demand slow up. In some regions where bean production has become more dynamic, like Mexico and Central America, demand might be met. In other regions and especially in Africa the challenge of providing sufficient beans for internal consumption is enormous. Thinking about exports is very unrealistic.

Although Latin America is the major bean producing continent, production growth will mainly have to occur in Africa. Given the low income levels and the very precarious protein and calorie availability, it is of extreme importance that this production growth will be realized.

Bean production development has to be built on different premises in Africa and Latin America. In Latin America the market will dominate the development of bean production and put additional requests on the research agenda. Beans will increasingly be sold by farmers and bought by consumers. To some extent the commodity needs to be repositioned in urban markets.

In Latin America beans will remain a small farm crop, but the small farmer, however, will be increasingly sales oriented. If beans do not provide sufficient income they will be replaced by other crops. Labor productivity in beans should become a principal area of research. Yield, potential and earliness will be important characteristics.

Although bean consumption is not very income dependent, it might suffer from a tendency towards more digestible and more convenient foods. At the same time marketing technology in other products is improving rapidly, for example cold storage for meats. If the prices of other products decrease and the price of beans stays constant, beans might still loose importance in the diet. In an urban environment, the consumer price is not only dependent on production but also on marketing costs. Research to diminish the cost of storage and urban marketing to improve consumer quality will be very useful.

In Africa, food security is the main issue. The challenge is to increase food availability per capita for a quickly growing population on a reduced land basis. Not labor but land productivity will be the focus This might, among others, imply shifts from bush beans to climbing beans. At the present stage of development marketing considerations are less important in Africa. Since African farmers are less integrated in the market and have reduced access to inputs, genetic resistance and nitrogen fixation capacity are highly valued. Additional requests on the African research agenda will be made by concerns on sustainability of the fragile African highland production systems.

Where will most progress be made? The conventional wisdom states that farmers that are well integrated in the market are better targets for production improvements than their subsistence colleagues. In Latin America considerable research efforts have been dedicated to beans in the last 15 years. In several countries the results of these research efforts are now being expressed in production statistics. Production trends have improved in the last decade and population growth has slowed down. The outlook for bean production in Latin America should be rather optimistic.

In Africa, production growth has slowed down, population growth remains very high and farmers are less integrated in the market society. The challenge for Africa is definitely bigger and the chance of satisfying future bean demand is less. Nevertheless, optimism is in the nature of the scientist. With the emerging results from Latin America in the back of our mind, we should aim for appropriate progress in Africa.

References

CIAT Bean Economics. Internal data, Cali, Colombia.

CIAT Bean Program 1987. Annual Report, Cali, Colombia.

CFP, 1987. Internal data on price series. Brasilia, Brazil.

FAO, various years. Production Yearbook, Rome Italy.

IBGE, 1978. Estudio Nacional da Despesa Familiar. Rio de Janeiro, Brazil.

IBGE, various years. Anuario estadistico do Brazil, Rio de Janeiro, Brazil.

Kornegay, J. 1988. Personal communication, CIAT, Cali, Colombia.

Lopez Cordovez, L. 1982. Trends and recent changes in the Latin American food and agricultural situation. Cepal review, No. 16.

Mellor, J.W., C.L. Delgado and M.J. Blackie 1987: Accelerating food production in Sub Saharan Africa. John Hopkins University Press, Baltimore, U.S.A.

Pachico, D.H. 1984, Bean technology for small farmers, Biological, Economic and Policy issues. Agricultural Administration, vol 15, pp 71-86.

Pachico, D.H., N. de Londoño and M. Duque, 1983. Economic factors, food consumption patterns and nutrition in Cali. Seminar 4, 1983, CIAT, Cali, Colombia.

World Bank 1987. World development report 1987, Oxford University Press, New York, U.S.A.

Table 1. Growth rates in bean area (% year)[1].

	1966/75	1976/86
Eastern Africa	7.0	3.0
African Great Lakes	3.3	-0.3
Southern Africa	2.2	1.8
Brazil	2.0	2.5
Mexico	-3.0	3.3
Central America	1.6	3.7
Andean Region	0.6	-0.6

Source: Revised FAO-Data.

[1] Bean producing regions mentioned include the following countries:
  a) Eastern Africa: Ethiopia, Kenya, Somalia, Sudan, Uganda.
  b) African Great Lakes: Rwanda, Burundi, Zaire.
  c) Southern Africa: Tanzania, Zambia, Malawi, Botswana, Lesotho, Swaziland, Angola, Mozambique, Zimbabwe, Madagascar.
  d) Central America: Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama.
  e) Andean Region: Venezuela, Colombia, Ecuador, Peru, Bolivia.

Table 2. Growth rates in bean yields (% year)[1].

	1966/75	1976/86
Eastern Africa	-7.0	-0.5
African Great Lakes	2.6	0.7
Southern Africa	0.4	0.9
Brazil	-3.1	-1.0
Mexico	2.3	0.5
Central America	-1.0	0.6
Andean Region	1.8	1.0

Source: Revised FAO-Data.

[1] See footnote 1, Table 1.

Table 3. Growth rates in bean production (% year). Expected growth rates of population 1985-2000[1].

	1966/76	1976/86	Expected population growth rate 1985-2000
Eastern Africa	6.3	2.5	3.2
African Great Lakes	5.9	0.4	3.2
Southern Africa	2.5	2.7	3.3
Brazil	-1.1	1.5	1.8
Mexico	-0.6	3.8	2.2
Central America	0.6	4.3	2.5
Andean Region	2.4	0.4	2.1

Source: Revised FAO-Data.
World Development Report, 1987.

[1] See footnote 1, Table 1.

Table 4. Bean demand in the year 2000 versus average supply in 1984/1986[1].

	Expected demand in the year 2000 (000 tons)	Average supply 1984/1986 (000 tons)	Deficit (000 tons)	Deficit (% or production) supply
Great Lakes Region	968	593	375	63
Southern Africa[2]	840	487	353	72
Eastern Africa[3]	1926	1090	1836	77
Others	312	192	130	71
Total	4046	2352	1694	72

Source: FAO-Production Statistics.
Internal data, Bean Economics.

[1] See footnote 1, Table 1.
[2] Data for some countries are not available.
[3] Kenya-data not available in FAO-Statistics, developments in Kenya are assumed to be on same trend line as in rest of the region.

Table 5. Bean demand in the year 2000 versus average supply in 1984/1986[1].

	Expected demand in the year 2000 (000 tons)	Average supply 1984/1986 (000 tons)	Deficit (000 tons)	Deficit (% or production) supply
Brazil	3296	2465	831	34
Mexico	1535	989	546	55
Andean Region	340	260	80	31
Central America	442	290	152	52
Others	338	454	-126	-27
Total	5940	4459	1481	33
L.A. without Chile and Argentina	5840	4125	1715	42

Source: FAO-Production Yearbook.
Internal data, Bean Economics.

[1] See footnote 1, Table 1.

Table 6. Socio economic parameters for Latin America and Africa

	Latin America	Africa
Average income, 1985 (US$/head years)	1660	550
% Rural population 1985	31	75
$\frac{\text{Non agricultural income, 1980}}{\text{Agricultural income}}$	3.2	5.9
Protein availability 1985 (grams/cap/day)	68	49
Calorie availability 1985 (calories/cap/day)	2712	2158

Source: World Development Report 1987.
FAO Production Yearbook 1986.

Table 7. The importance of beans and beans purchases in the diet in Brazil 1974-1975.

	Grams of bean protein per day	% of protein intake	% purchased	Grams of bean protein purchased
Urban:				
Recife	8.7	14.1	93	8.1
Belo Horizonte	9.5	16.6	95	9.0
Rio de Janeiro	11.6	16.6	97	11.3
Sao Paulo	11.1	16.4	95	10.5
Rural:				
North East	21.0	33.7	32	6.7
Minas Gerais	19.7	32.3	33	6.5
Sao Paulo	16.9	25.9	68	11.5
South	16.7	22.5	31	5.2

Source: IBGE, ENDEF, 1977.

Table 8. The reduction of bean consumption in Brazil from 1971-1981.

	Urban	Rural	Total
Consumption 1971 (kg/cap/head)	19.4	35.7	26.4
% of population	56	44	
Consumption 1981 (kg/cap/head)	14.1	26.0	17.9
% of population	68	32	
<u>Effect of</u>:			
Urbanization (kg)			1.36
(%)			16
Price increases (kg)	2.33	4.26	3.74
(%)	44	44	44
Other factors (kg)	2.13	3.88	3.40
(%)	40	40	40

Source: CFP, Brasilia.
IBGE, Rio de Janeiro.
Pachico, et al., 1986.

Table 9. The dimensions of entrepreneurial and small-farm agriculture in Latin America, Early 1980's.

	Entrepreneurial agriculture (%)	Small-farm agriculture (%)
Number of economic units	22	78
Area covered	82	18
Supply of permanent crops	59	41
Supply of annual crops of which:	47	53
Maize	49	51
Potatoes	39	61
Rice	69	32
Sugar cane	79	21
Beans	23	77

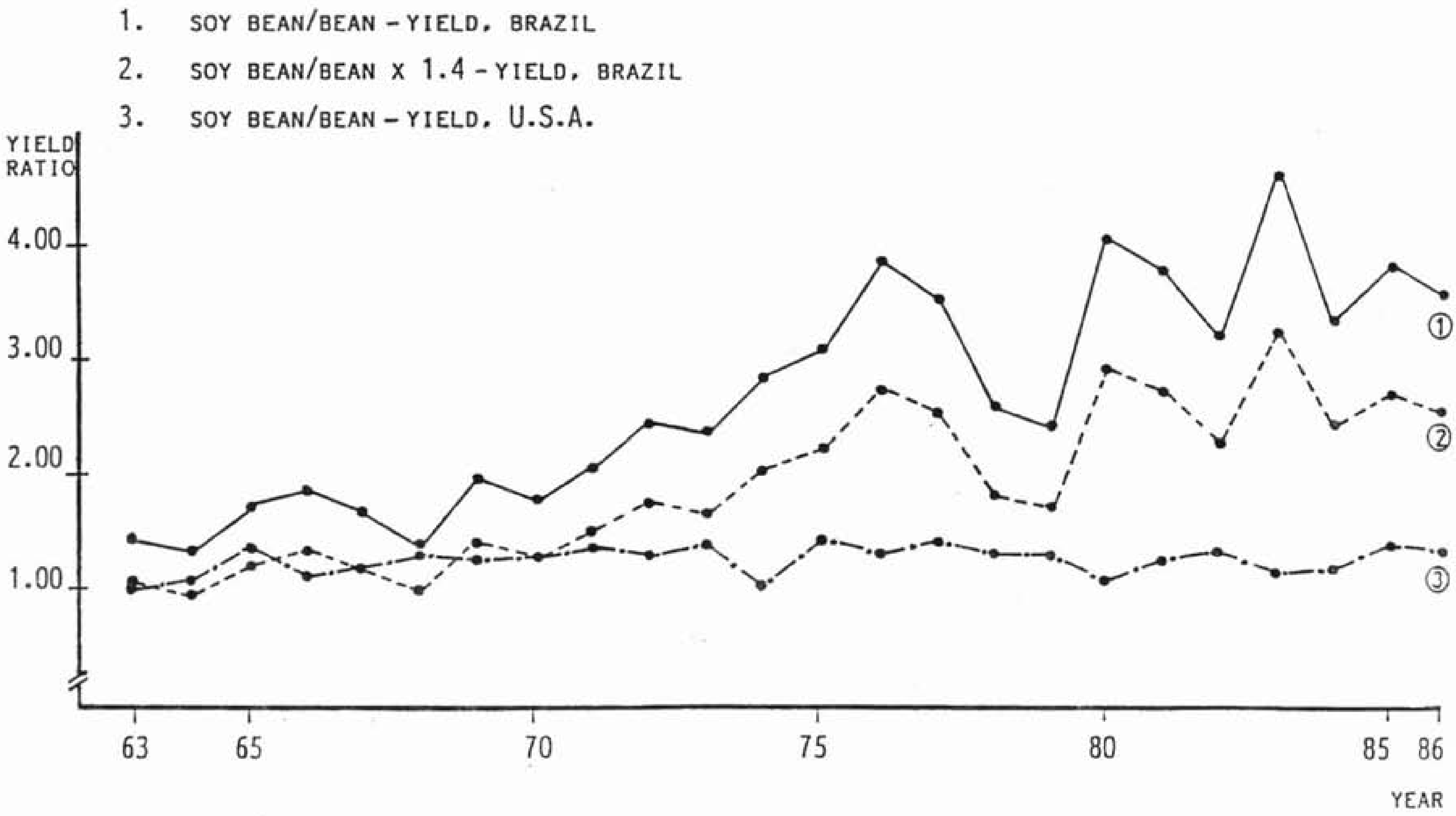
Source: Lopez Cordovez, 1982.

Table 10. Costa Rica production cost in different production systems, 1986/1987.

	"Tapado"	"Espeque"	"Semi-mechanized"
Yield (kg/ha)	513	1039	1380
Production costs (US$/ha)	224.4	446.3	555.2
Prod. costs/kg (US$)	0.44	0.43	0.40
% machinery costs	---	---	34
% input costs	10	33	28
% land costs	34	17	15
% interest costs	4	7	7
Prod. costs/kg (land costs=0)	0.29	0.36	0.34
Prod. costs/kg (land+labor costs=0)	0.06	0.17	0.28

Source: CIAT, Bean Program, Annual Report 1987.

FIGURE 1: SOY BEAN VERSUS BEAN YIELD-RATIO, 1963-1986 U.S.A. AND BRAZIL



SOURCE: FAO, PRODUCTION YEARBOOKS, VARIOUS YEARS.

35675

THE FUTURE OF SMALL BEAN PRODUCERS IN MEXICO AND THEIR RELATIONSHIP WITH COMMERCIAL FARMING

Rogelio Lépiz*

Summary

In the last 20 years, Mexico has registered a small reduction in surface area harvested, from 2.1 to 1.8 million hectares, and a moderate increase in grain production, from 0.91 to 0.99 million tons annually. This has been possible because of an increase in yields from 427 to 555 kg/ha.

For the same period, there is evidence of a change in bean producing areas. Production has shifted from states in the central part of the country, such as Jalisco and Veracruz, toward the northern region located in the central high plain, especially the states of Zacatecas, Durango, and Chihuahua. In 1985, these states harvested 60% of the national surface area dedicated to beans.

The information presented previously reflects the types of producers found in Mexico. In the central part of the country, bean producers are typically small farmers. More than 80% grow less than five hectares of beans, they produce principally for their own consumption, the chief labor force is the family, they use traditional production systems, their productivity are generally low and so is their income, and they carry out economic activities outside the production unit. On the other hand, more than 70% of the producers in the northern part of the country, including

---

* Researcher for the Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias (INIFAP) of Mexico, currently at CIAT, A.A. 6713, Cali, Colombia.

Nayarit and Sinaloa, present characteristics of teh so-called commercial farmers.

Regarding the situation of small bean producers in Mexico over the last 15 years, one can appreciate a reduction in their number and in the volume of their production. This has been caused by the displacement of the area devoted to beans from the central to the northern part of the country. It is estimated that in some of the central states there has been a reduction of 203,000 small producers, who have stopped producing 20% of the national total. This situation has been brought about by the push toward planting maize in this region, by the use of herbicides and a mechanical harvest which does not permit the planting of associated beans, by the scarcity and high cost of manpower, and by the displacement of bean by other crops with less risk and greater return.

Notwithstanding this, the situation has not changed in other central and southern states of the country, and in the near future, an increase in the number and participation of small producers can be anticipated. This is due to the growing demand of farmers without land and the agricultural policy which is pushing the small farm beyond what is technically and economically recommendable.

On the other hand, from the socioeconomic point of view, the future of the small producers is not very promising. In spite of the fact that in the last few years, interest in this sector has increased, research and development programs focused on improving income through greater productivity are not sufficiently broad. There are problems in financing not only for new programs, but also to serve those that are already in progress. Technology generated on experimental fields is being utilized very little by small producers. Extension services are limited and they have become part of a bureaucracy. Small producers do not have capital and have few possibilities of obtaining it, especially when they are common landholders (ejiditarios[1]).

Because of the previous explanation and knowing that this sector is not going to disappear, but on the contrary, that its participation will increase in important over time, an intensification of research and development programs tending to achieve an improvement in income and social well-being is required. Achieving this will not be easy and will require a great coordinated effort among the different parties that intervene in production. In research, work focused on this sector should be intensified, to consider the production units as a system, and on a regional level, to identify real production problems, their causes, and possible solutions, and to evaluate promising technologies in fields and with the participation of producers. Upon releasing the recommendation of a technological component, all the necessary support for it to be successful should be contemplated.

Introduction

As happens in the majority of bean producing countries of Latin America, a great percentage of farmers who dedicate themselves to growing this legume in Mexico are small producers. These producers are principally located in the central and southern area of the country where, in the last 15 years, the surface area for beans has been reduced considerably. Reduction has been greater in the states of Jalisco and Veracruz--395,000 hectares having been removed from 1970 to 1985. On the other hand, in the northern part of Mexico, where commercial farming predominates, plantings of beans have increased notably, from 444,000 hectares in 1970 to 1,100,000 hectares in 1985. This signifies an increase of 148% and represents 62% of the national surface area harvested in 1985.

---

[1] Producers who cultivate federal lands called ejidos.

This shift in production regions, which implies a reduction in the participation of small producers in the national production of beans, plants doubts about the causes of the change, and regarding the future of the small bean producer, especially regarding priorities in the near future for research and development programs.

As is well known, in the last few years there has been much interest on the part of public institutions, and on a smaller scale of private ones, and programs oriented toward improving production of small producers (who traditionally have been forgotten) have been established. One cannot say that in all cases there has been success, but something has been achieved.

The question now is for the attention that small bean producers should receive in relation to commercial farmers. If the tendency is for small producers to disappear, is it worthwhile to invest in resources for this sector? On the contrary, if their number is maintained or eventually increases, what should be done and how far should we go?

This document attempts to go over the previous topics under the weak light of the lack of abundant statistical data, and takes into account experiences and results of work with small producers in Mexico and other countries of the world.

Evolution of Bean Production in Latin America

According to statistical information (FAO, 1986), Brazil and Mexico continue to be the two countries in Latin America that produce the most beans. In the three-year period 1984-1986, Brazil harvested more than five million hectares annually (63.6% of the total) and produced 2.5 million tons (55.4%). Mexico, on its behalf and for the same period, harvested an average of 1.8 million hectares (21.1%) and produced 0.99 million tons of grain annually (22.2% of the total). Both countries harvested 84.7% and produced 77.6% of the total for Latin America (Tables 1 and 2).

Another group of countries that distinguished themselves in bean production were Argentina, Guatemala, Colombia, and Chile, whose surface area harvested totaled 7.2%, with production reaching 12.2% of the total for Latin America. These countries, notwithstanding their reduced surface area dedicated to the growing of beans, make a good contribution to production in the region because of their high yields, which averaged 888 kg/ha for the three-year period of 1984-1986 (Table 3).

With regard to evolution of production in the region during the last 20 years, one can appreciate the following. Of the six principal bean producing countries, Brazil, Argentina, Guatemala, and Colombia increased significantly surface area harvested and, as a result, their production. Unitary yields in Brazil were reduced noticeably, from 657 to 511 kg/ha. In Argentina, they remained without changes, around 1020 kg/ha, while they increased in an important manner in Guatemala and Colombia upon going from 512 and 542 kg/ha to 670 and 769 kg/ha, respectively (Tables 1, 2, and 3).

With regard to Mexico, there was a slight reduction in harvested area, from 2.1 to 1.8 million hectares, and a moderate increase in production, from 0.91 to 0.99 million tons. This was possible due to the increase in unitary yields, which in the three-year period 1964-1966 were 427 kg/ha, and in 1984-1986, 555 kg/ha on the average.

Chile has maintained figures without many changes. Area has varied between 62,000 and 86,000 hectares harvested and production between 87,000 and 95,000 tons annually. One can appreciate a small decrease in unitary yields, from 1401 to 1104 in the period under reference. Another country that has registered increases in production is El Salvador, especially for increased productivity, which has gone from 556 to 769 kg/ha in the period mentioned.

Evolution of Bean Production in Mexico

Upon making an historical analysis of bean production in Mexico after 1925, some important changes can be appreciated (Figure 1 and Table 4). Up to the five-year period 1935-1939, there was a decrease in area harvested as well as in production obtained, and as a result, in consumption per person, which reached the lowest level of 6 kg per year. This depression was very possibly caused by irregularity and insecurity in the holding of land due to the armed movement begun in 1910.

From the priod 1935-1939 up to 1965-1969, there was dynamic and constant growth, a stage in which area increased at an annual rate of 4% and production increased 7% per year. The greatest increase in production was due to the combined effect of increase in area and in yields, which went from 204 kg/ha to 467 kg/ha. Such dynamic and sustained growth in this historic stage can be explained by the social stability which the country achieved, the creation of support institutions such as credit banks, and research and extension institutions, and the demand for the product brought about by generally higher per capita incomes. At the end of this period, per capita consumption reached the highest recorded level, 18.5 kg of beans per person per year.

In the decade of 1970, there was a notable decrease in area harvested and total production, in spite of the fact that yields continued to rise. The depression in production is explained on one the hand by the lack of stimulus for planting beans due to the freezing of product prices and includes the reduction of these in the years 1976 and 1977, from 21% and 17%, respectively, in relation to the price of 1975. On the other hand, production was affected by climatic hardships, especially in 1979, when drought and frost at the end of the cycle depressed production by 307,000 tons in relation to the year before (Lépiz, 1986).

In the five-year period 1980-1984, production recovered its growth, since the harvested area was near two million hectares, with yields over 600 kg/ha, and grain production was 1.2 million tons. In spite of this, and because of growing internal demand for this base product of national food intake, around 50,000 tons of beans have been imported annually (Table 4).

Dynamics of Bean Producing Zones

In addition to the variations in bean production between years, which chiefly reflect effects of climate and sale price, there have also been production changes in some of the important regions of the country which dedicate themselves to bean production.

Table 5 includes harvested area of this legume by states, for the years 1970, 1977, and 1985. By means of this information, one can appreciate the following. Among the principal bean producing states in Mexico, Chihuahua, Durango, Zacatecas, and Tamaulipas significantly increased area harvested, from 444,000 hectares in 1970 to 1,100,000 in 1985. This signifies an increase of 148% and represents 62% of the national area harvested in 1985 (Fig. 2).

The group of producing states which remained more or less constant in bean production were Sinaloa, Nayarit, Querétaro, Guanajuato, Puebla, Oaxaca, Chiapas, and Yucatán. According to data in Table 5, Sinaloa and Nayarit really reduced their area harvested in the years which were included. Nevertheless, upon observing their production in the complete historical cycle, in reality they have maintained a more or less constant area.

The group of producing states which significantly reduced the area dedicated to this crop were Aguascalientes, Jalisco, Michoacán, the state of Mexico, and Veracruz. In 1970, they harvested 642,000 hectares, and in

1985, this figure barely reached 133,000 hectares. There was a very important reduction in Jalisco (300,000) and also in Veracruz (95,000). The five states mentioned harvested 37% of the national area in 1970, but only 7% in 1985 (Fig. 3).

All of this indicates an internal movement in bean producing areas in the last 15 years. There is a clear displacement in bean production from the central area of the country toward the northern region located in the central high plain, that is, toward the states of Zacatecas, Durango, and Chihuahua, which most increased area dedicated to beans in this period.

Types of Bean Producers

As occurs in the majority of the Latin American countries, if not in all of them, small bean producers are much more numerous than large ones in Mexico. Even though statistical information isn't available now to support the previous affirmation, there isn't the slightest doubt for the author that in that country, the number of so-called small producers, small farmers, or subsistence farmers is greater in relation to the number of commercial farmers, impresarios, or capitalists.

What is not possible to affirm is which of the two kinds of farmers contributes the largest volume of grain to national production. Again this is because of the lack of statistics, and because there is no clear definition of what is a subsistence farmer vs which producer is a commercial farmer.

As has been commented by other authors, there is no single criterion which defines the small producer. Aspects related to landholding, extension and quality of land, social and economic factors, and climatic effects all should be considered. The interaction of all of these and the variation in the domination of one of them from one region to another makes it impossible to separate things into black and white.

Based on this, one generally leaves to the judgment of the reader the definition and identification of the small producers, pointing out only some of the characteristics which they have in common. In this document, we will not give a definition. On the other hand, we will note some of the characteristics of small producers in Mexico:

1. They own and/or cultivate an area generally no larger than five hectares.
2. They dedicate the largest extension to basic food crops.
3. Their central objective is to produce food for the family and afterward sell products.
4. The principal labor force is the family.
5. They usually work on the basis of their own resources (scarce), with the least investment of capital and at low risk.
6. They use complex production systems of more than one species, in single crop, associated crop, intercrop, or relay crop.
7. The agronomic management of crops is traditional, with few modern technological inputs.
8. Productivity and production are very low, and so is income.
9. They carry out economic activities outside the production unit and suffer from migration of the family labor force to the big cities.
10. They have a low level of schooling and deficient health and educational services.
11. They are generally located in isolated regions, on low quality terrains, and face climatic problems during production.

On the other hand, commercial farmers grow larger extensions than five hectares; they can dedicate themselves to basic grains and to industrial crops or crops for export; the principal objective is to produce for the market (business); they use machinery and a hired labor force; they work with credit and a high investment of capital, with single cropping systems, and high technological inputs; their productivity, production, and income are high; they are located near roadways and generally on fertile terrains, with favorable climate or with irrigation available; and at the same time, they have access to different social services, such as education, medicine, and recreation.

According to the statistical information in Table 5, in the last 15 years in Mexico, important changes in bean production areas have occurred. One can appreciate the displacement in production of this legume from the central states (Jalisco, the state of Mexico, and Veracruz) toward the northern states of the semi-arid high plain. In 1985, Zacatecas, Durango, and Chihuahua harvested more than one million hectares, which in total represented 60% of the national area.

This information reflects type of bean producer involved. In the central and southern areas of the country, producers of this legume are typically small farmers. Without any doubt, more than 80% grow less than five hectares, they produce first for their own consumption, the principal labor force is the family, they use traditional production systems, their production and productivity are generally low, and they carry out economic activities outside the production unit (Table 6).

With regard to bean producers in the northern part of the country, also including the coastal states such as Nayarit, Sinaloa, and Tamaulipas, more than 70% are on the side of the commercial farmers, although they might not meeting all the requirements of the case. Tables 7 and 8 and Figs. 4 and 5 show variation in area which the producers of the plains of Durango and Sombrerete, Zacatecas, dedicate to the planting of beans. In Durango, for example, 72% grow more than five hectares, and in the region of Sombrerete, Zacatecas, 92% do. The principal target of these crops is the national market. Producers use machinery chiefly for the work of soil preparation, planting, and harvesting; they contract labor outside the family for work such as weeding; and they make investments with their own capital or that which comes from bank credit for the purchase of agrochemicals, soil preparation, and harvesting. In spite of the previous statements, and especially regarding producers from the semi-arid high plains, some of their characteristics are more typical of small producers. They don't always use high technological inputs (e.g. they plant native varieties); climatic conditions are adverse (scarce [450 mm annually] and irregular [periods of 10 to 20 days without rain] rainfall); and as a result productivity and production are low (470 kg/ha in 1985).

The Future of Small Bean Producers

In this paper, the concepts of small farmers, small producers, subsistence farmers, and producers for self-consumption have been used as equivalents. Nevertheless, the term small producers or small farmers has been preferred. When speaking about subsistence farmers, the combination of words implies a strong inclination with reference toward small producers who live under very critical conditions at the survival level. The same applies to the concept of farmer or producer for self-consumption, where we would be referring strictly to those who produce solely for family consumption.

On the other hand, and although statistical information is not available, it is the author's opinion that in the case of Mexico and Latin America in general, the percentage of bean producers in real subsistence conditions or who produce exclusively to satisfy their own consumption needs is very low. For that reason, the concept of small producers or farmers has been preferred, where all those at the subsistence and self-consumption level are included.

Upon speaking about the future of small bean producers in Mexico in relation to their number and their participation in the national production of this legume, and according to statistical data in Table 5 already commented upon, one can affirm that there is a clear tendency toward reduction. This is primarily due to the displacement of the bean area from the central to northern regions of the country, as has already been pointed out. Upon making an estimate for the reduction in the number of small producers in the states where, in the last 15 years, a decrease in the harvested area of 509,000 hectares has been registered, and assuming an area of 2.5 hectares for each producer, the reduction represents a loss of 203,600 small producers. On the other hand, upon making an estimate of the reduction in production and considering an average yield of 500 kg/ha in the area indicated, 254,800 tons of grain have not been produced. This volume represents around 20% of the current national production. From the preceding estimates we would have to discount bean area which, upon being transferred to northern states, is also being grown by small producers. There are no data for attempting an estimate of this area.

Some of the possible causes which have brought about the reduction in area harvested and number of bean producers in the central axis of the country from Jalisco to Veracruz could be the following, not necessarily listed in the order of their importance.

1. The government's policy of supporting maize production in the states of Jalisco, Mexico, and Veracruz, with favorable conditions for this crop.

2. The use of technologies in the growing of maize, such as the use of herbicides and mechanical harvesting, which have restricted the planting of beans in association.

3. The scarcity and high cost of manpower in the region because of increased employment in industrial centers such as Aguascalientes, Jalisco, Mexico, and Veracruz.

4. The increase in time dedicated to outside-the-farm activities brought about by nearness to big cities and factory centers, which have elevated producers' purchasing power and permitted them to obtain beans in the market.

5. The displacement of beans by crops with less production risk, such as sorghum and maize, or with a greater return, such as vegetables.

6. In some cases, severe damage caused by diseases such as golden mosaic in the northern part of Veracruz, and fungal infections in Jalisco, or severe attack of pests (Epilachna and Apion) in Michoacán have made bean crops unprofitable.

In spite of the tendency toward reduction in the number of producers and production itself in some states of the central area of the country, upon making a historical and social analysis, it can be affirmed that this form of production is not going to disappear. The same statistics show that in some states such as Yucatán, Chiapas, Oaxaca, and Puebla, typically of small producers, changes in the sense with which they have been discussed here have not occurred.

On the contrary, and in spite of the fact that the population growth rate has been reduced, there is a constant migration from the country to the cities and as a percentage, the agricultural population has diminished, but the number of people requiring land in the country continues to grow. Due to this increasing demand, the limited amount of new land, and the fact that through agrarian reform laws, the small farm is continuing to be pushed beyond the limits recommended for economic productivity, the number of small farmers is increasing.

On the other hand, and from the social, economic, and technological point of view, the future of small agricultural producers is not very promising. As has occurred in other developing countries, it has only been in the last few years when in Mexico the governments, through public institutions of education, research, extension, and credit are making serious efforts to incorporate this sector into development. Nevertheless, because of economic problems which occurred in this country during the last years of this decade, there are financing problems not only for increasing research to benefit small farmers, but for maintaining ongoing research and development programs. Until now, agricultural technology developed on experimental farms and in research laboratories has been used very little by small producers. Extension services are insufficient, with personnel with little experience and motivation and a bureaucratic structure that reduces efficiency. Small producers do not have capital to invest in inputs, and have very few possibilities for obtaining such capital. This is even worse for the ejidatarios, who, in order to be able to get credit, have to organize themselves in credit associations. Many of these producers are located in isolated areas, where inputs cannot be obtained, and there are marketing problems for their products. Others are farming marginal land, with severe problems with soil and climate. In general, their productivity is low, and as a result, their income is much below that which is obtained in the cities (2/3 below in 1970). Finally, communication, educational, and health services are not improved at the rate desired to achieve their incorporation into national development.

Research and Development Programs

In spite of a future with little promise for small farmers and other producers who dedicate themselves to bean production on a small scale, there currently exists the belief in the need to reduce the separation between small producers and commercial farmers, and associated differences in income and services between rural areas and urban and industrial centers.

For the moment, it is unknown how far one can go or what improvements can be achieved. What is certain and urgent is that much can be done. It is necessary to accept the hypothesis (or, just in case, reject it) that the small producer is rational, that his lack of education does not signify the absence of intelligence, that just like any human being he aspires to material and social improvement, and that, as a result, he is capable of assimilating and incorporating technological innovations into his production system.

Definitely, as many researchers have noted, the path is not simple: to achieve an improvement in income and in the small farmers' social well-being will require a great coordinated effort among the different components which intervene in production.

With regard to research, there currently exists a serious preoccupation of researchers and leaders of the Instituto Nacional de Investigaciones Forestales Agrícolas y Pecuarias (INIFAP) in Mexico, that there will be a greater use by producers of technology which has been developed for other crops. With this purpose, INIFAP is helping the Productora Nacional de Semillas (PRONASE) produce basic seed, and it is performing trials for validation and diffusion of promising technological components to the terrain of producers. At the same time, on a regional level, INIFAP searches for greater integration between research and extension service, and seed production and credit.

Regarding research, INIFAP looking for results which will respond to the real necessities of farmers, especially those of small producers. With this purpose, and on a regional level, it is being insisted upon that work be done on real production problems.

In spite of the previous statements and also as has been explained, in order to achieve an improvement in production, in income, and in the well-being of small producers, it is an indispensable condition to intensify efforts which are currently being undertaken and to support regional research programs closely linked to those of production of inputs (seeds, fertilizers, etc.) and services (credit, insurance, commercialization). In research projects, although one may work on the basis of products (beans, for example), one must not lose the holistic perspective of the production unit as a system. Equally, one must use current diagnostic techniques to identify problems, causes, and possible solutions, to evaluate promising technologies in farmers' fields, and to involve them in carrying out these trials and in the final selection of a technological component to recommend.

Upon releasing the recommendation and starting diffusion of a technological component, the support necessary to assure its success should be contemplated. First, the technology should have a solid experimental back-up, and it should signify an advantage for the producer. It should be widely diffused. When promotion is done, if it is a question of an input (seed, inoculant, agrochemical), it should be available and within reach of producers. The necessary support institutions should be involved in an organized and responsible manner. Finally, the evolution of the technological component should be followed up to know about its success or failure, and to serve as feedback for the whole process.

Bibliography

Biggs, H. H. and Tinnermeier, R. L. 1974. Small farm agricultural development problems. CSU, Fort Collins, Colorado.

Byerlee, D. y Collinson, M. 1983. Planeación de Tecnologías apropiadas para los agricultores: conceptos y procedimientos. CIMMYT, México.

CATIE. 1978. Small farmer cropping systems for Central America. Second annual report. 1976-1977. Turrialba, C. R.

CIAT. 1974. Small farm systems. Program Progress Report.

CIAT. 1984. International Bean Trials Workshop. Cali, Colombia.

CIAT. 1987. La investigación de fríjol en campos de agricultores de América Latina. Memorias de un Taller. Cali, Colombia.

FAO. 1986. Anuario FAO de producción. Volumen 40. Roma, Italia.

Fernández y Fernández, R. 1978. La empresa ejidal. Centro de Economía Agrícola, C. P., Chapingo, México.

Harwood, R. R. 1979. Small farm development. Understanding and improving form systems in the humid tropics. Westview Press Boulder, Colorado.

INIFAP. 1982. Diagnóstico agropecuario del distrito de Guadalupe Victoria, Dgo. (Mimeógrafo).

Johnson, D. 1979. A reconnaissance survey and mapping of bean production in Guatemala (Mimeógrafo).

Lépiz, R. 1980. Programa nacional de fríjol. Plan de investigación. INIA, SARH, México.

Lépiz, R. 1986. Investigación en fríjol en México. INIFAP,México (Mimeógrafo).

Luna, C. 1985. The Mexican dry bean industry: a supply and demand analysis. MSU, East Lansing, Mich. (Mimeógrafo).

Martin, F. and Ruberté, R. 1980. Techniques and plans for the tropcial subsistance farm. USDA, SEA, ARM. New Orleans,

Navarro, L. 1982. Developing technology for small farms; a case study in Central America. CATIE, Turrialba, C. R.

Plascencia, J., Borges, E. M. y Reyna, E. 1986. Fríjol: oferta, demanda e inversión en la investigación agrícola. Foll. Inv. No. 66. INIFAP, México.

Ruthenberg, H. 1985. Innovation policy for small farmers in the tropics. Clarendon Press. Oxford.

Sanders, J. H. y Alvarez P. C. 1978. Evolución de la producción de fríjol en América Latina durante la última década. CIAT, Cali, Col.

SARH. 1983. Econotecnia Agrícola. SAR-DGEA, México.

SEARCA. 1985. Applied agricultural research for small farmers in Asia. SEARCA. Los Baños, Philippines.

Streeter, C. P. 198 . Reaching the developing world's small farmers. A special report from the Rockefeller Foundation. New York, N. Y.

Table 1. Evolution of harvested area (1000 ha) of beans in Latin America in the last 20 years.

	1964-1966		1974-1976		1984-1986	
Country	Average	% of total	Average	% of total	Average	% of total
Brazil	3243	51.9	4140	60.1	5374	63.6
Mexico	2149	34.4	1680	24.4	1781	21.1
Argentina	32	0.5	129	1.9	230	2.7
Chile	62	1.0	74	1.1	86	1.0
Guatemala	86	1.4	103	1.5	167	2.0
Colombia	72	1.2	104	1.5	126	1.5
Honduras	74	1.2	78	1.1	67	0.8
Nicaragua	59	0.9	71	1.0	91	1.1
Haiti	40	0.6	41	0.6	85	1.0
El Salvador	27	0.4	53	0.8	59	0.7
Peru	58	0.9	57	0.8	62	0.7
Venezuela	89	1.4	83	1.2	68	0.8
Ecuador	65	1.1	66	1.0	47	0.5
Paraguay	32	0.5	59	0.9	51	0.6
Dominican Republic	38	0.6	44	0.6	55	0.6
Cuba	37	0.6	35	0.5	35	0.4
Bolivia	9	0.1	9	0.1	9	0.1
Costa Rica	49	0.8	36	0.5	48	0.6
Panama	19	0.3	14	0.2	10	0.1
Uruguay	5	0.1	4	0.15	5	0.1
Latin America	6249	100.0	6884	100.0	8456	100.0

Source: Sanders and Alvarez, 1978; FAO, 1986.

Table 2. Evolution of bean production in Latin America in the last 20 years (in thousands of tons).

	1964-1966		1974-1976		1984-1986	
Country	Average	% of total	Average	% of total	Average	% of total
Brazil	2130	58.6	2117	53.5	2465	55.4
Mexico	917	25.2	1047	26.4	989	22.2
Argentina	32	0.9	132	3.3	237	5.3
Guatemala	44	1.2	78	2.0	112	5.5
Colombia	39	1.1	75	1.9	97	2.2
Chile	87	2.4	73	1.9	95	2.1
Honduras	50	1.4	54	1.4	40	0.9
Nicaragua	39	1.1	53	1.3	52	1.2
Haiti	41	1.1	44	1.1	48	1.1
Paraguay	30	0.8	42	1.1	41	0.9
El Salvador	15	0.4	37	0.9	45	1.0
Peru	46	1.2	36	0.9	48	1.1
Venezuela	43	1.2	37	0.9	36	0.8
Dominican Republic	25	0.7	35	0.9	45	1.0
Ecuador	28	0.8	28	0.8	29	0.6
Cuba	25	0.7	24	0.6	27	0.6
Bolivia	14	0.4	21	0.5	12	0.3
Costa Rica	19	0.5	16	0.4	28	0.6
Panama	6	0.2	4	0.1	3	0.1
Uruguay	3	0.1	2	0.1	3	0.1
Latin America	3635	100.0	3957	100.0	4452	100.0

Source: Sanders and Alvarez, 1978; FAO, 1986.

Table 3. **Evaluation of bean production (kg/ha) in Latin America in the last 20 years.**

Country	1964-1966	1974-1976	1984-1986
Brazil	657	511	459
Mexico	427	623	555
Argentina	1019	1021	1030
Chile	1401	987	1104
Guatemala	512	754	670
Colombia	542	719	769
Honduras	676	688	597
Nicaragua	661	739	571
Haiti	1025	1073	564
El Salvador	556	708	769
Peru	794	630	774
Venezuela	485	449	529
Ecuador	433	431	617
Paraguay	937	712	804
Dominican Republic	653	801	818
Cuba	675	686	771
Bolivia	1555	2333	1333
Costa Rica	388	444	583
Panama	316	286	300
Uruguay	600	500	600
Latin America	582	575	526

Source: Sanders and Alvarez, 1978. FAO, 1986.

Table 4. Five-year evolution of bean production in Mexico since 1925.

Five year period	Area harvested (ha)	Yield (kg/ha)	Production (tons)	Foreign Trade (tons)		Consumption kg per capita/year
				Imports	Exports	
1925/29	893.939	189	169.621	1.608	7.249	10.5
1930/34	666.367	198	132.000	2.533	3.755	7.6
1935/39	574.220	204	116.992	842	1.590	6.2
1940/44	698.460	223	156.026	86	6.224	7.2
1945/49	775.172	243	187.993	482	1.464	8.0
1950/54	997.969	287	286.591	29.094	218	11.4
1955/59	1'281.114	372	476.465	19.981	5.038	15.0
1960/64	1'683.671	413	695.186	10.951	10.865	18.0
1965/69	1'946.607	467	908.892	427	61.671	18.5
1970/74	1'764.076	536	945.759	13.873	15.912	17.4
1975/79	1'446.168	571	825.293	29.172	43.588	12.8
1980/84	1'913.499	632	1'209.855	-	-	-

Source: SARH, DGEA (1983); FAO (1985).

Table 5. Area harvested and bean yields in Mexico, by federal entities.

Entity	1970[1]		1977[2]		1985[3]	
	Area(ha)	Yield(kg/ha)	Area(ha)	Yield(kg/ha)	Area(ha)	Yield(kg/ha)
Baja California N	348	849	278	705	120	1.066
Baja California S	1.078	1.036	802	1.081	2.401	908
Sonora	2.198	1.608	2.160	1.181	8.147	1.023
Sinaloa	38.670	1.282	84.885	1.112	35.680	1.064
Nayarit	91.200	938	64.569	1.125	37.905	1.015
Colina	1.630	680	1.100	678	289	740
Chihuahua	49.970	750	146.713	320	149.308	445
Durango	169.742	410	162.518	338	285.680	492
Coahuila	3.169	800	8.613	896	6.164	751
Nuevo León	4.349	620	11.862	501	2.566	412
Tamaulipas	8.795	548	8.785	576	23.656	427
Zacatecas	215.231	397	411.215	289	641.412	471
Aguascalientes	30.900	415	28.148	442	18.388	341
San Luis Potosí	56.486	505	40.892	376	58.726	290
Jalisco	350.635	426	122.650	828	51.188	530
Michoacaán	85.264	255	91.745	195	19.803	722
Edo. de México	59.900	405	26.345	622	18.053	891
Querétaro	35.860	300	25.388	300	34.223	572
Guanajuato	130.725	508	45.034	655	112.577	307
Hidalgo	30.700	500	21.534	333	35.186	804
Puebla	43.100	316	72.255	254	57.543	468
Texcala	6.126	170	9.600	721	2.342	761
Morelos	5.668	1.005	7.787	1.034	1.671	1.039
Veracruz	120.065	1.130	47.115	519	25.262	559
Distrito Federal	150	720	3.693	926	354	675
Guerrero	25.500	642	35.050	616	13.066	525
Oaxaca	70.980	466	76.890	407	36.244	428
Chiapas	80.075	400	57.500	512	74.484	689
Yucatán	17.645	424	8.155	397	19.334	309
Campeche	10.440	410	4.221	881	531	166
Quintana	398	518	5.000	600	5.878	271
Tabasco	4.950	909	5.200	1.140	4.076	607
National	1'746.947	529	1'636.703	475	1'782.257	507

[1] Plascencia et al., 1986.

[2] Lépiz, R. 1980.

[3] SARH, 1987 (unconfirmed data).

Table 6. Characteristics of producers of beans associated with maize in highlands of Jalisco in Mexico.

87% plant from one to five hectares.
78% use seed stored from the previous year.
90% use native varieties.
65% use organic fertilizers.
73% use chemical fertilizers.
95% don't use credit.
74% prepare soil with their own or a rented tractor.
67% carry out weeding with animal traction.
85% don't receive technical assistance.
100% keep at least 100 kg for self-consumption.
They harvest an average of 350 kg/ha of beans.

Source: INIFAP, Jalisco. 1988.

Table 7. Extension of agricultural production units principally for beans in the region of the Durango plains in Mexico.

	Ranges of variation (ha)					
Municipality	0.5-5.5	5.6-10.5	10.6-15.5	15.5-20.5	20.6-25.5	> 25.6
Suchil	114	231	7	19	-	-
V. Guerrero	247	861	50	19	17	31
Poanas	1084	1162	2	39	10	45
N. de Dios	725	541	87	14	3	11
Pánuco	174	1004	32	17	2	11
G. Victoria	713	2787	235	126	16	99
Cuencamé	152	181	56	37	38	98
P. Blanco	114	408	124	38	9	100
Total	3323	7175	593	309	95	395
% of Total	28.0	60.3	5.0	2.6	0.8	3.3

Source: INIFAP-Durango, 1982.

Table 8. Extension of production units principally for beans in the municipality of Sombrerete, Zacatecas, Mexico.

Size (ha)	Subtotal (number)	Average
1.0- 5.0	421	7.8
5.1-10.0	2066	38.1
10.1-20.0	2290	42.3
20.1-30	263	4.8
> 10.1	379	7.0
Total	5419	100.0

Source: INIFAP-Zacatecas, 1982.

Figures

Fig. 1. Five years averages of bean production in Mexico. SARH. 1983. FAO. 1985.

Fig. 2. Area of beans harvested in selected states in northern Mexico. SARH. 1987.

Fig. 3. Area of beans harvested in selected states in central Mexico. SARH. 1987.

Fig. 4. Land area of agricultural production units in 14 municipalities in the area of the Llanos de Durango. Mexico. INIFAP. Dgo. 1982.

Fig. 5. Land area of agricultural production units in 14 municipalies in the municipality of Sombrerete, Zacatecas, Mexico.

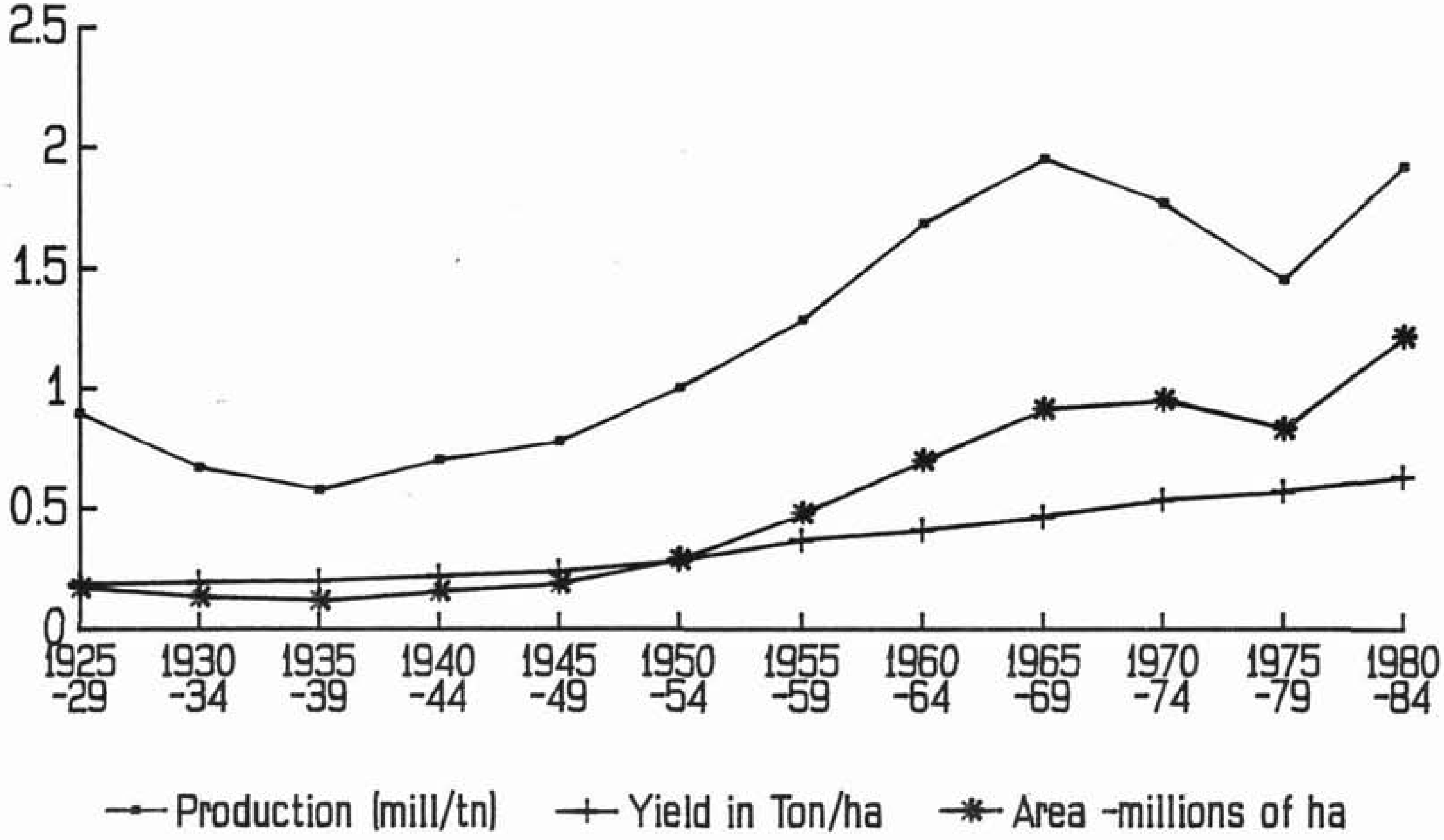


Figure 1. Five year averages of bean production in Mexico.

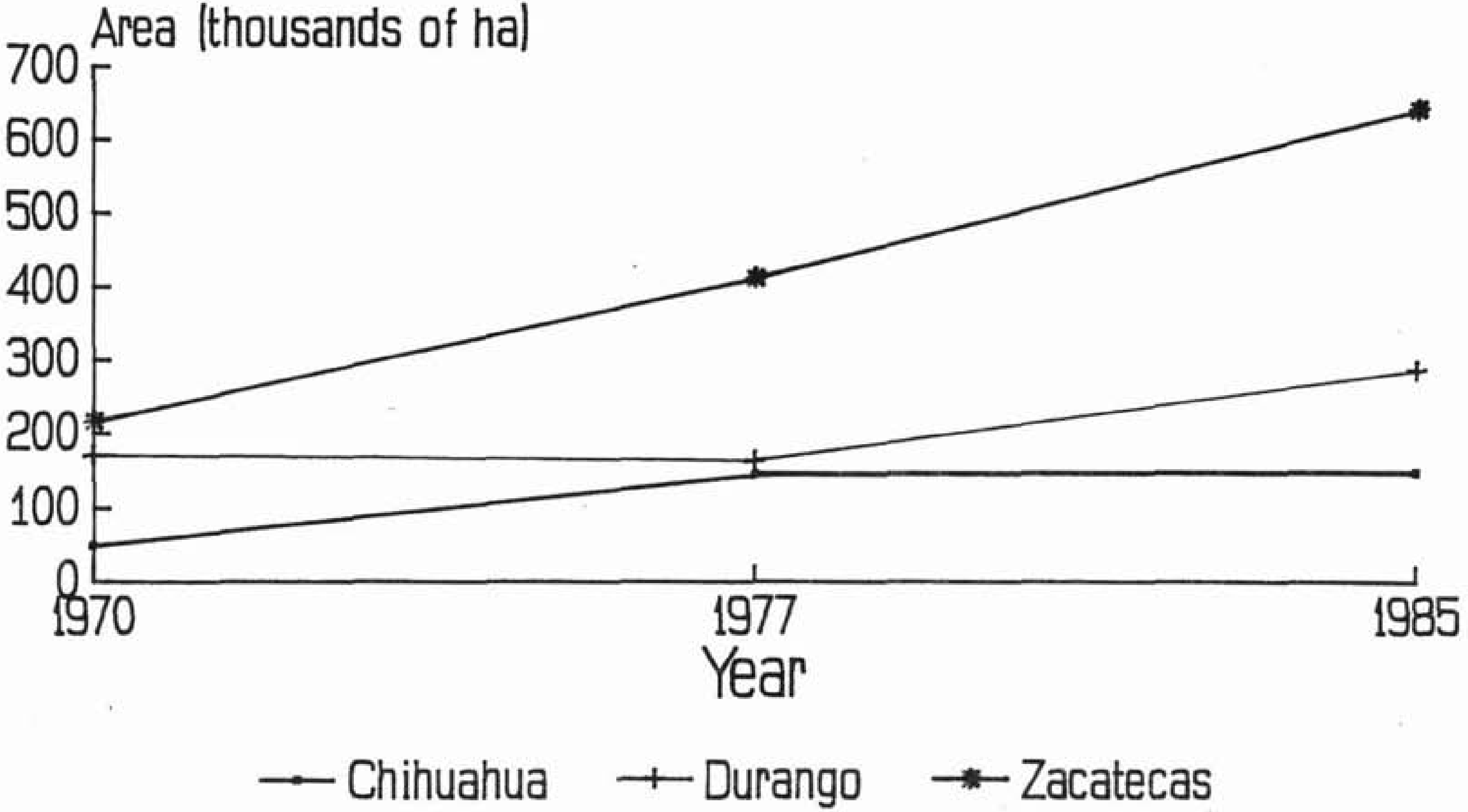


Figure 2. Area of beans harvested in selected states in northern Mexico. Sarh, 1987

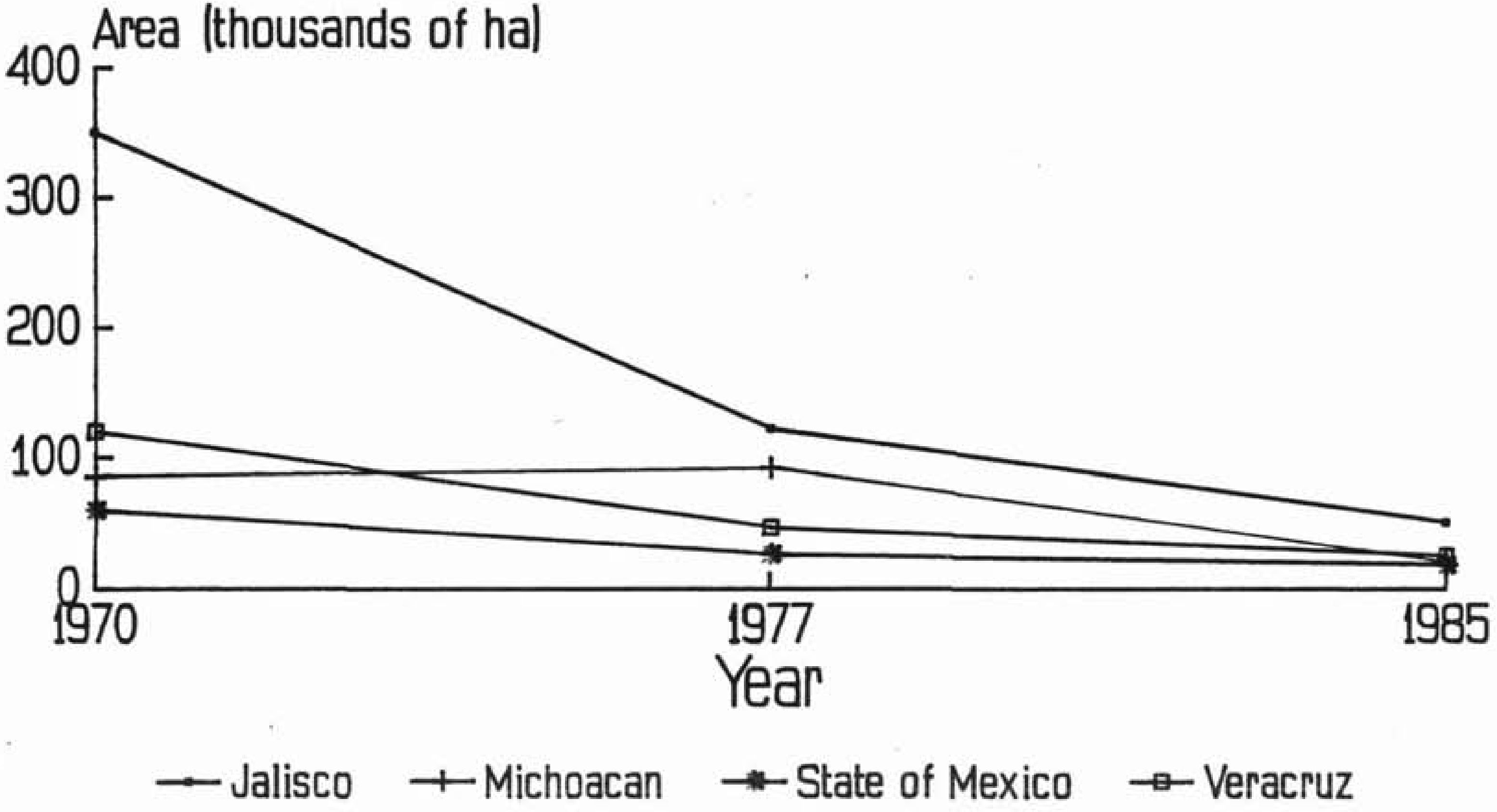


Figure 3. Area of beans harvested in selected states in central Mexico.
Sarh, 1987

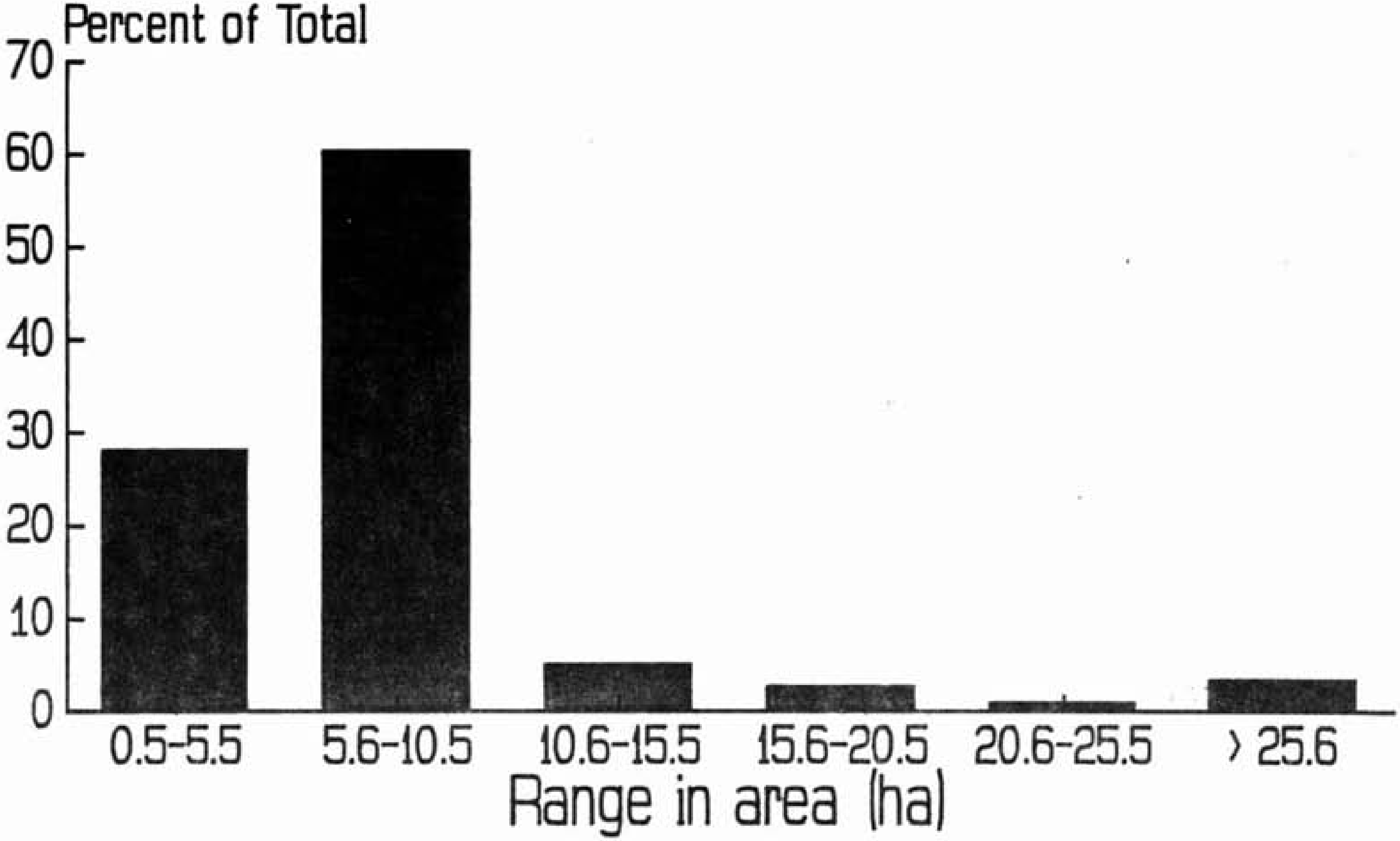


Figure 4. Land area of agricultural production units in 14 municipalities in the area of the Llanos de Durango-Mexico

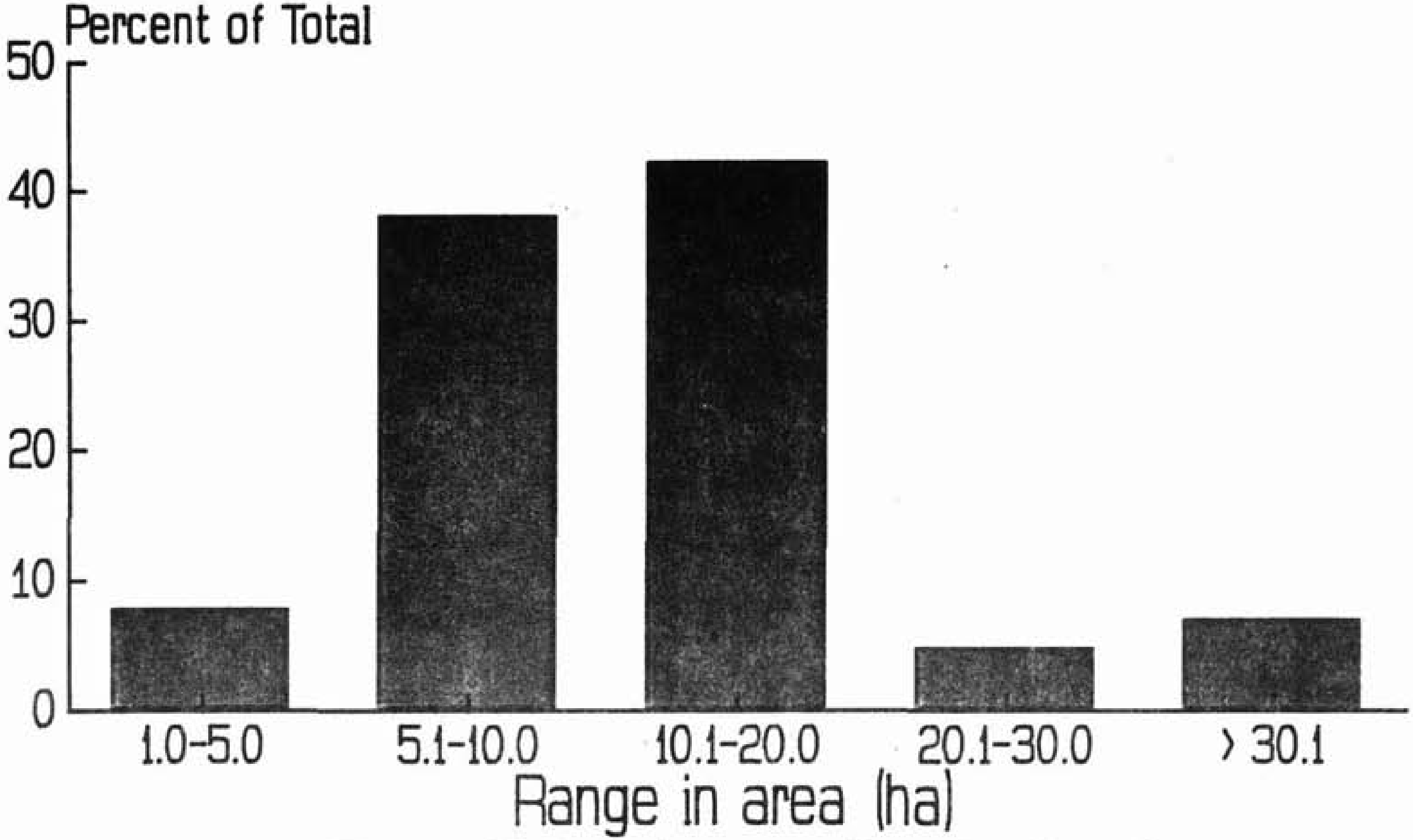


Figure 5. Land area of agricultural production units in 14 municipalities in the municipality of Sombrerete.Zacatecas

35676

BEAN PRODUCTION IN THE YEAR 2000: COMMERCIAL PRODUCTION

Joao Luiz Alberini*

Introduction

Brazil is the largest producer of common bean (Phaseolus vulgaris L.) in the world, having always been a great importer of the product as well. Bean is the Brazilian food par excellence, forming part of the habit of our people, mid-day and at dinner, constituting an important source of energy and protein, for urban and rural dwellers alike.

Retrospective

In the decades from the 40's through the 60's, bean production enjoyed the privilege of an assured yield in the principal established production systems, principally in the South, in new soils of good fertility, being an inseparable companion crop of coffee, and based in the abundant manual labor of migrants from Sao Paulo, Paraná or Minas Gerais.

Beans in that period were principally intercalated between rows of coffee, or associated with maize, maintaining a reasonable production garanteed by the good levels of organic matter and low costs of production.

In the decade of the 60's a new alternative presented itself to farmers in the south of Brazil: soybeans. Oil crop par excellence, and of high protein value, with potential for complete mechanization, this

---

* Melhorista Convenio: HATA-Genetica e Melhoramento/FT-Pesquisa e Sementes. Rua 14 de Julho, 1817, 8o. Andar, Sala 81. Campo Grande-MS, Brazil.

represented an escape for the large land owners from the "problem" of the new brazilian labor laws which had come to rural areas, and even had a great advantage of rotation with wheat, thus creating a production system, a type of "double-cropping", much promoted by the government of the "Brazilian miracle" and by the numerous multinational producers of inputs which had established themselves in the country. It was toward the end of the decade of the 60's that coffee production entered a serious international and internal crisis with the threat of coffee rust, that fatally damaged Brazilian coffee plantations at the beginning of the decade of the 70's, and drove out of those areas mixed cropping with beans, due to the need for mechanized chemical control of the disease. Finally, in 1975, a severe frost gave the final blow to Brazilian coffee production and expelled once and for all both the migrants and mixed cropping.

A new agricultural system was defined from that date onward in the Center-south of Brazil, the principal bean production region.

A thoroughly mechanized agricultural system based on annual crops, namely soybeans and wheat (in the same agricultural year) came to dominate the landscape of the south of the country, and the rural labor force migrated to the cities, in an intense and uncontrolled exodus.

Present Situation

Bean production in the whole of the country, with a few exceptions, was restricted to areas of quite pronounced slopes, where the mechanization of soybeans is impractical, in acid soils of low native fertility, in small and medium-sized land holdings with family labor to execute field operations of planting and harvesting. These small farmers, our "peasants", in the majority nearly illiterate, presented much resistance to technical changes, and although they were instructed for long periods, only after many years could customs be changed.

Great have been the efforts of research and extension in the past 10 years for this class of small farmers. Notwithstanding, other factors such as the difficulty of aquiring seed of improved varieties at reasonable prices; the non-availability of equipment that is both adequate and accessible to the small farmers, for cultivation, aplication of products, and threshing; lack of a storage structure at the small farm level; difficulties in commercialization (90% of this type of production is purchased by intermediaries at the farm gate at inferior prices); all these factors have had a negative effect and have led small land holders to sell their lots and to swell the ranks of the Brazilian slum dwellers.

A strong tendency toward the concentration of land into large land-holdings has been verified in recent years: 50,000 small holdings (of 5 to 20 ha) disappear yearly in the country, in spite of all the political speeches, and the creation of an "Agrarian Reform Ministry".

If we refer to Table 1, we will conclude that Brazilian production of rice, maize, soybean and wheat increased dramatically, while that of beans was maintained at the same level for the last 18 years. Quantities of bean imports also were maintained stable, at the cost of a severe reduction in per-capita consumption: from 26 kg in 1970 to 15 kg in 1987.

The average yields of soybean, maize, and wheat showed significant increases, around 50%, in the same period in which beans presented a decrease in productivity (Table 2). The increase in area planted, from 3,484,778 ha in 1970 to 5,524,427 ha in 1987, is due to new agricultural frontiers, principally in "cerrado" soils with or without irrigation.

In Brazil bean production is considered to be high risk and in fact, it is. In Paraná, Santa Catarina, Rio Grande do Sul and Sao Paulo, which are traditioned production zones, the principal harvest is called the "rainy harvest". It is planted in the driest months of the year (August, September and October) and harvested in the months of highest precipitation

(November, December and January). It is very common the occurrence of partial or total crop loss due to rains at harvest, which, being mannual, is slow and laborious.

The plantings in January/February/March in these regions are not practical due to the occurrence of Bean Golden Mosaic Virus (BGMV).

In the months of February and March, soybean harvest is initiated, and the white fly (Bemisia tabaci) migrates to the bean fields.

Large areas in the state of Paraná, nearly 100,000 ha, are planted with beans in the "early" season (July), as an experimental crop, so as to still permit the planting of soybean in November/December, as the principal crop.

It is the crop failures in different regions of the country, that lower the national average so dramatically from the potential of the crop, which with Brazilian varieties is around 3,000 kg/ha.

The same occurs in other regions of Brazil. The region of Irece, in Bahia, plants nearly 150.000 ha of beans in the months of February/March, the majority in irrigated systems. The probability of "normal" rainfall in the period do not equal even 50%, and crop failures are common in this region.

The most secure commercial production region presently on a large scale and where yield averages normally attain 2,200 kg/ha, is the winter crop in the north of Sao Paulo, in irrigated systems, and in irrigated zones of amended "cerrado" soils in Central Brazil.

Nevertheless, bean production in irrigated areas suffers strong competition from other species of high profitability, such as peas, industrial tomato, and lately, winter seed production of soybean, given the high international prices of the grain. These factors result in that the beans produced in these regions are of high cost, although of low risks.

Future

It is very difficult to make predictions about bean production in the next century, particularly if we consider the strong attachment to culinary traditions of the Latin population. Nevertheless, everything leads us to believe that the daily consumption of beans by Brazilian families should decrease in the next centry, principally in the more populous urban centers:

1) The modernization of family life, where the woman struggles to enter the labor market, will not permit the preparation of slow-cooking foods at mid-day, which will be gradually replaced by lunches or fast foods, American-style.

2) An intense labor of research and extention is being realized to increase the consumption of soybean in the diet, to feed the Brazilian people, particularly in the classes of low and medium buying power. The development of soybean varieties for human consumption is underway. Lines which exhibit absence of lipo-oxigenase enzymes, as well as absence of kunitz trypsin inhibitor and of good flavor are now in final stages of testing. Hundreds of home and industrial recipes for the production of milk, yogurt, cheese; for the use of flour in traditional pastries; for the use of textured protein, already on an industrial scale, in hamburgers, beef and other dishes; and for the consumption of black soybeans as such, are being distributed and demonstrated in schools, slums, churches, diverse associations and hospitals. Products of soy origin present great advantages from the nutritional point of view and are of low cost, and are accessible to families of low buying power. The food industry already offers to the consumer more than a hundred different soy-based products, and

publicity on the "miraculous" qualities of the same is intense.

In spite of all these considerations, it is important to remember that it falls to research a major role in the next years, of consciously changing some of its directions, to maintain, in the long run, bean production on a competitive scale with other products.

Among these measures, we consider the most important to be:

1) Development of new bean cultivars which lend themselves to mechanical harvest (such as with the same harvesters utilized for soybean and wheat) and the study and spread of these varieties to production systems of medium and large land-holdings, without fear of social conflicts. It is important in this respect that new alternatives that make better use of available manual labor on small land holdings be developed, such as: production of edible snails, earthworms, frogs, fish and crustacions, mushrooms, fruits and small animals, to improve family income and maintain in existence the small rural property holders.

2) Improvement of protein quality of bean, principally methionine content.

3) Control of golden mosaic, to make viable the planting in seasons of more adequate precipitation and temperature in the different regions of Brazil.

4) Improve the levels of symbiotic nitrogen fixation, to make it more competitive with soybean.

5) Develop studies of industrialization and conservaton of the product, for utilization in more rapid and practical forms, in the modern life of the next century.

Table 1. Evolution of Production.

	Production (Metric tons)					
Year	Rice	Beans	Maize	Soybean	Sorghum	Wheat
1970	7,553.143	2,212.834	14,216.000	1,508.540	170.000	1,844.263
1971	6,593.376	2,688.479	14,129.700	2,077.291	220.000	2,011.334
1972	7,824.483	2,675.962	14,891.400	3,222.631	249.993	982.901
1973	7,158.935	2,227.762	14,109.340	5,011.614	500.000	2,031.338
1974	6,483.818	2,235.437	17,284.200	7,876.209	483.000	2,858.530
1975	7,538.550	2,267.048	17,138.605	9,892.299	201.699	1,788.180
1976	9,559.188	1,841.161	17,763.200	11,075.193	490.000	3,225.830
1977	8,993.696	2,290.007	19,255.936	12,513.406	435.141	2,066.039
1978	7,296.142	2,193.977	13,569.401	9,540.577	227.502	2,690.888
1979	7,595.214	2,186.343	16,306.380	10,240.306	121.913	2,926.764
1980	9,775.720	1,968.165	20,372.072	15,155.804	180.292	2,701.613
1981	8,228.326	2,340.947	21,116.908	15,007.367	212.901	2,209.631
1982	9,734.553	2,902.657	21,842.477	12,836.047	226.473	1,826.945
1983	7,741.753	1,580.546	18,731.216	14,582.347	231.819	2,236.700
1984	9,027.363	2,625.676	21,164.138	15,540.792	312.716	1,983.157
1985	9,024.555	2,548.378	22,018.187	18,278.485	268.143	4,320.267
1986	10,404.676	2,219.478	20,541.227	13,334.691	370.122	5,638.470
1987*	11,092.083	2,417.206	27,621.981	16,707.039	505.877	4,534.376

Source: IBGE/GCEA/FECOTRIGO

* Estimate

Table 2. Evolution of average yields.

Year	Yield (kg/ha) Rice	Beans	Maize	Soybean	Sorghum	Wheat
1970	1.517	635	1.442	1.143	2.125	973
1971	1.384	683	1.339	1.210	1.833	886
1972	1.623	679	1.413	1.470	1.702	424
1973	1.493	584	1.424	1.386	2.000	1.104
1974	1.481	537	1.601	1.531	2.100	1.157
1975	1.450	570	1.550	1.698	2.326	610
1976	1.451	456	1.586	1.760	2.538	909
1977	1.501	503	1.632	1.770	2.450	655
1978	1.297	475	1.220	1.226	2.180	957
1979	1.393	519	1.441	1.240	1.700	764
1980	1.566	424	1.779	1.727	2.305	865
1981	1.349	466	1.833	1.765	2.309	1.151
1982	1.615	490	1.731	1.565	1.847	646
1983	1.515	389	1.750	1.792	1.701	1.190
1984	1.687	494	1.761	1.650	1.830	1.139
1985	1.895	479	1.866	1.800	1.576	1.614
1986	1.861	405	1.649	1.462	1.864	1.447
1987*	1.804	437	1.955	1.827	2.076	1.445
1988						

Source: IBGE/GCEA/FECOTRIGO
* Estimate

POSTER SESSION ABSTRACTS

35677

EVALUATION OF SEGREGATING POPULATIONS OF COMMON BEAN *Phaseolus vulgaris* FOR GRAIN YIELD

Rogelio Lépiz and Shree P. Singh

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

As part of a research project on yield improvement of common bean, segregating populations were evaluated in three localities of Colombia in the 1988-A season. The central objective was to determine if, in early generations, it is possible to evaluate and identify bean populations of high and low yield.

To this end 33 F_2 populations and three varieties were planted in Popayan, Santander de Quilichao, and Palmira, Colombia in a 6 x 6 lattice design with two repetitions and with an experimental plot of 4 rows wide by 3 m long. Twenty-five seed were planted per meter, and in Popayan plots were inoculated with anthracnose, and in Quilichao, with angular leaf spot. Data taken on diseases, adaptation, maturity, seed weight, and grain yield. Data were analyzed both by locality and in a combined analysis, and correlations among the various data were calculated.

In this phase of the project the data present differences for yield in each locality and in the combined analysis, and also a populations x locality interaction. There was no correlation in the behavior of the populations over localities: in Popayan and Palmira there was a negative correlation between diseases and adaptation, and a positive correlation between adaptation and yield. In spite of the differences between localities, the population-locality interaction, and low correlation in behavior of materials over localities, it was possible to identify F_2 populations of common bean of high and low yield in each locality and in the combined analysis.

35618

RESPONSE TO VISUAL SELECTION FOR YIELD IN F_2 AND F_3 GENERATIONS OF COMMON BEAN, *Phaseolus vulgaris* L.

Harold Patiño and Shree P. Singh

Centro Intternacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Lines of common bean, *Phaseolus vulgaris* L., were studied, these being derived from nine segregating populations of three types of crosses: simple, triple, and modified double. The objective was to evaluate the effect of visual selection for grain yield in F_2 and F_3 generatioons. From each cross were selected 15% of the superior lines, for a total of 149 lines. The 149 selected lines were evaluated together with 18 bulks of the discarded plants in F_2 and F_3, the 23 parents, ad 6 checks, in a partially balanced 14 x 14 lattice design with three repetitions. A density of 166.000 plants ha^{-1} was utilized, and 6.3 m^2 of each plot was harvested to estimate yield.

Differences were found between parents and the crosses. However, when means of selected and discarded lines in F_2 and F_3 and their parents were compared, or when the best parents and the best line in each cross were compared, it was concluded that visual selection for yield was not effective in any of the nine crosses studied.

35679

HERITABILITY OF YIELD OF COMMON BEAN IN SOIL WITH LOW PHOSPHOROUS CONTENT

Carlos Urrea and Shree P. Singh

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

The F_2 and F_3 generations of each of 22 crosses of common bean, <u>Phaseolus</u> <u>vulgaris</u> L., were evaluated in conditions of low and high fertility soil in CIAT-Quilichao. The objective was to estimate heritability of grain yield through the regression of the F_3's on their corresponding F_2's. The 44 entries were planted in a randomized block design with three repetitions in each of the treatments of low and high fertility. Each plot was 4 rows wide by 4 m long. An area of 4 m^2 was harvested from the two central rows to measure yield. The fields of low and high fertility received 26 and 78 kg/ha of P, respectively. Heritability values were .61 and .57 in conditions of low and high fertility, respectively.

35680

EFFECT OF SELECTION AT DIFFERENT DENSITIES ON THE YIELD OF COMMON BEAN, *Phaseolus vulgaris* L.

J. Ariel Gutiérrez, James García and Shree P. Singh

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

In two crosses of common bean, *Phaseolus vulgaris* L., selection for yield was practiced at three planting densities: low (4 pl/m), medium (8 pl/m), and high (16 pl/m) from the F_2 to F_7 generation. From each cross and each density six lines were selected. The 36 selected lines and their 13 parents were then evaluated at four densities: low, medium, high, and very high (24 pl/m), in a study layed out in strips with a 7 x 7 lattice design in three repetitions.

Results of the first semester of evaluation indicate that selection for yield was effective only in a cross between parents of small-by-medium-sized grain. In this cross the lines derived at high density were superior to those derived at low density. Low density is not adequate to evaluate yield since the two crosses presented yields statistically inferior to the other three densities.

35681

STATUS OF THE WORLD COLLECTION OF *Phaseolus* BEANS

Rigoberto Hidalgo

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

In 1975, CIAT was designated as the depository for the preservation of the world collection of beans of the genus *Phaseolus*. To fulfill this responsibility, CIAT created the Genetic Resources Unit with the necessary installations and specialized personnel to manage the collection. The bank was formed with a working collection of the Bean Team, and later, with contributions from the majority of known collections in countries of Latin America, North America and Europe. Up to the present, donations of germplasm have been received from 63 countries, from which approximately 40.000 accessions have been introduced, corresponding to four cultivated species and 28 wild species.

The principal responsibilities for the management of bean germplasm of the genus *Phaseolus* are: acquisition, multiplication, characterization-evaluation, documentation, and open distribution of said germplasm to agricultural investigators in national programs. Emphasis has been given to *Phaseolus vulgaris* as a consequence of the high priority of CIAT in the conservation of this species.

Of all germplasm introduced, about 23.000 accessions have been increased and are ready for distribution. Of this material, 90% is *P. vulgaris*, 7% corresponds to other domesticated species, 2% are wild ancestral species, and less than .5% are wild non-ancestral species.

Porcentual distribution of available P. vulgaris germplasm as seed color and growth habit (1987)

Growth habit	Seed color (%)								
	White	Cream	Yellow	Brown	Pink	Red	Purple	Black	Total
I	7.2	3.7	4.9	1.2	1.2	2.0	1.7	1.6	23.5
II	1.6	1.1	0.4	0.4	0.3	0.4	0.5	7.2	11.9
III	6.3	8.0	3.2	1.5	1.9	6.7	2.0	6.9	36.5
IV	5.3	5.8	3.0	1.6	1.4	2.3	1.7	6.2	27.3
Total	20.4	18.6	11.5	4.7	4.8	11.4	5.9	21.9	100.0

Status of the world collection of Phaseolus beans in the Genetic Resource Unit at CIAT until December 1987

Species	No. of accessions	
	Introduced	Multiplied
P. vulgaris	34.665	20.743
P. vulgaris wild ancestrals	410	357
P. lunatus	2.835	844
P. lunatus wild ancestrals	97	41
P. coccineus subsp. coccineus	928	439
P. coccineus subsp. polyanthus	460	246
P. coccineus wild ancestrals	102	24
P. acutifolius	143	116
P. acutifolius wild ancestrals	57	57
wild not cultivated P. angustissimus, P. leptostachyus, P. esperanzae, P. filiformis, P. glaucocarpus, P. pauciflorus, P. glabellus, P. grayanus, P. jaliscanus, P. macrocarpus, P. macrolepis, P. maculatus, P. pedicellatus, P. polystachyus, P. plufiflofus, P. pachyrrhizoides, P. polymorphus, P. scabrellus, P. ritensis, P. ovalifolius, P. tuerckheimii, P. wrightii, P., anahuacensis, P. floribundus, P. neglectus, P. striatus, P. canthotrichus, P. parvulus	307	61
Total	40.005	22.928

EVIDENCE FOR ISOZYME ALLELE DIFFERENCES BETWEEN THE TWO MAJOR GENE POOLS IN *Phaseolus vulgaris*

Susan L. Sprecher and M. Wayne Adams

Crop and Soil Sciences Department, Michigan State University
East Lansing, MI 48824, USA
Bean Cow Pea CRSP

The two major gene pools recognized in *Phaseolus vulgaris* on the basis of seed size differences, region of domestication, phaseolin markers, etc., tend to differ in the alleles which they carry at six to eight enzyme or protein loci. Among bean landrace lines sampled from Malawi, the two most numerous isozyme genotypes consisted of alternate allozymes at six loci, and were associated with large and small seed size. From isozyme and growth habit evidence it appears that extensive recombination between the gene pools has not occurred in Malawi, due to genetic, rather than geographic barriers. In addition, among lines carrying Dwarf Lethal and phaseolin variants already associated with the two gene pools, and among dry bean cultivars in use in the USA, there is high homogeneity for isozyme genotype within pool. The presence of strong recombination barriers, indicated by the isozyme differentiation and by male sterility associated with allozyme heterozygosity, has implications for the future improvement of common beans via intermating between the gene pools. It also supports the conclusion that incipient speciation is occurring in *Phaseolus vulgaris*.

ISOZYME VARIANTS AT TWO BETA-NADH DIAPHORASE LOCI IN DRY BEANS (_Phaseolus_ _vulgaris_ L.) AND THEIR CORRELATIONS TO THE GENE POOLS

Susan L. Sprecher and M. Wayne Adams

Crop and Soil Sciences Department, Michigan State University
East Lansing, MI 48824, USA
Bean Cow Pea CRSP

Isozymes of beta-NADH Diaphorase (DIAP: a general term for certain oxidoreductase flavoproteins), were identified as gene products of two closely linked loci in cultivated _Phaseolus_ _vulgaris_. The locus _Diap-1_ was shown to have three alleles, termed Fast, Slow, and Intermediate from their mobility in the starch gel electrophoresis buffer system used, and a Null, or no activity, allele. Fast, Slow and Null alleles have been found at the _Diap-2_ locus. The banding pattern produced in electrophoresis indicates that the most active DIAP enzyme in beans is a tetramer, the holoenzyme being made up of four subunits, and that subunits produced by alleles at _Diap-1_ and _Diap-2_ interact to form multimers. In a homozygous plant with active alleles at both DIAP loci, five tetrameric isoenzymes are produced, and consequently five bands are visible on the electrophoretic gel.

This study shows that DIAP is genetically differentiated between the large and small seeded gene pools in beans, and that it displays specific allelic variation within sub-groups of domesticated types. Several combinations of those alleles specific to different gene pools have not been found to date, and this suggests that recombinational barriers exist within the species.

MITOCHONDRIAL RESTRICTION FRAGMENT LENGTH POLYMORPHISMS IN BEAN LANDRACES FROM MALAWI

M.M. Khairallah and M. Wayne Adams

Crop and Soil Sciences Department and B.B. Sears (Botany and Plant
Pathology) Michigan State University, East Lansing, MI 48824, USA
Bean Cow Pea CRSP

The concept of genetic diversity has been a salient issue for plant breeders for decades. With the advance of molecular techniques, we can now estimate the genetic diversity at the basic hereditary level: the DNA molecule. In addition to the nuclear genome, plant cells contain two organelle genomes of much smaller size, that of the chloroplasts (cp) and of the mitochondria (mt). Both genomes are non-Mendelian in their inheritance, with the mt genome being strictly maternal in most angiosperms. Organelle genomes have been used to estimate the diversity within and between species, to draw phylogenies and maternal lineages, and to solve unanswered questions in the evolution of plant species.

In this study, the mitochondrial genomes of 23 bean lines and two Phaseolus species are being examined for diversity using the restriction fragment length polymorphism (RFLP) technique. Twenty of these lines were collected from Malawi, and show differences in morpho-agronomic characters and in isozyme patterns. The other lines are pure bred cultivars, 'Mecosta', 'Sanilac' and 'Tendergreen'. One accession of Ph. coccineus and Ph. acutifolius are used in order to compare the amount of intra- versus interspecific variation.

The RFLP technique consists of isolating mtDNA, digesting it with various restriction endonucleases that recognize different palindromic sequences, and separating the fragments generated by agarose gel electrophoresis. A polymorphism is seen as a difference in migration of a band(s) or as the absence/presence of band(s), and indicates a base-pair mutation or an insertion-deletion event. The bean mt genome is large and the restriction patterns it generates are quite complex. Therefore, in order to detect RFLP's, the DNA has to be transferred to a membrane (Southern transfer) and is hybridized with radioactively labelled probes. The probes used in this study are large random cosmid clones (34-48 kb) of the bean mt genome, kindly provided by Dr. C. Chae (Univ. of Florida, Gainesville).

To date, 4 probes x 8 endonucleases combinations have been examined. Restriction patterns of Ph. coccineus and Ph. acutifolius are quite distinct from the Ph. vulgaris ones. Three intraspecific RFLP's have been detected which differentiate the small and large-seeded Malawian lines. The 3 cultivars examined were alike and similar to the small-seeded lines. Two other RFLP's differentiated 'Mecosta' from all the other bean lines. More data is needed before it can be concluded that the mt genomes of the two gene pools of beans (large and small seeded) are distinct. The percent sequence divergence among the Phaseolus species will be calculated by the shared fragment method as more probes are screened.

METHODOLOGY TO EVALUATE F_5 PROGENIES DERIVED FROM F_4 INDIVIDUAL PLANT SELECTIONS OF CLIMBING BEAN (Phaseolus vulgaris L.) IN THE RELAY SYSTEM WITH MAIZE (Zea mays L.)

Alberto Román Vélez

Grain Legume and Annual Oil Crops Program
Centro Regional de Investigación "La Selva"
A. A. 100, Rionegro, Antioquia, Colombia

In the Regional Research Center, ICA "La Selva", situated in the municipality of Rionegro, Antioquia, Colombia, eight trials were planted in 1986 and 1987 with the purpose of defining a new methodology to evaluate F_5 progenies of climbing bean (Phaseolus vulgaris L.) in the relay system with Maize (Zea mays L.). A system of small plots (.84 m^2) served to evaluate and screen large quantities of materials with respect to yield, 100 seed weight, days to physiological maturity, and days to flower, utilizing four repetitions. Thus, 77.76% of planting area was saved, in comparison with planting of plots in hills and three repetitions, and research costs were reduced.

PATTERN ANALYSES OF GENOTYPES WITHIN YEARS AND OF LOCATION OVER YEARS, FROM REGIONAL NAVY BEAN TRIALS

R.J. Redden and I. DeLacy

Department of Primary Industries
D.P.J. Hermitage Research Station
Warwick, Qld. 4370, Australia

Grain yield data from six years of regional trials grown at a wide range of locations in Queensland, Australia were examined for trends in genotype x environment interaction using pattern analyses. A total of 21 genotypes were entered in more than one year, with a maximum of 14 in any one year. Up to 4 locations were used with a maximum of 10 in any one year. Matrices of dissimilarity estimates within years for locations, were combined over years for nine locations to provide a complete matrix despite absence of particular combinations in particular years. Locations were classified into groups reflecting geographic proximity and a separation between irrigated and rainfed management. Within years genotype classification was influenced by: responsiveness to irrigation; reaction to rust; common blight and zinc deficiency; erect vs spreading plant habit (type II); and maturity.

SCREENING *Phaseolus vulgaris* GERMPLASM FOR GENERAL NODULATION ABILITY

R.J. Redden, A. Diatloff and T. Usher

Department of Primary Industries
D.P.J. Hermitage Research Station
Warwick, Qld. 4370, Australia

An initial germplasm collection of 1462 accessions was rated for ability to nodulate with indigenous rhizobia, in plots split for nitrogen fertilizer. A secondary screening of the upper 6% in a replicated trial identified 19 promising accessions. These plus CIAT and local checks were compared over four locations for nodule formation, a) with indigenous rhizobia, b) inoculated with one rhizobial strain, and c) in the presence of nitrogen fertilizer. Ability to nodulate generally across sites and treatments was shown by ICA 21573, Epicure and to a lesser extent Amarillo 155. Some accessions were specifically responsive to inoculation, one was mainly responsive to indigenous rhizobia, and others including CIAT checks showed site/treatment specific responses.

COMPONENTS OF NITROGEN FIXATION IN Phaseolus vulgaris

J.A. Kipe-Nolt and H. Vargas

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

In 1985 experiments to evaluate components of nitrogen fixation were initiated, with the objective of selecting the most promising lines and incorporating their characters in breeding programs for improved nitrogen fixation.

Greenhouse and field trials with African and Central American indigenous genotypes and some agronomically promising materials from CIAT were conducted. The genotypes varied in growth habit.

The number of nodules/plant was determined at different stages during the plant growth cycle, from which the parameters early, maximum, late, and total nodulation were derived. Specific nodule activity, use of carbohydrates and sensitivity to mineral N were also evaluated.

The genotypes varied widely according to these characteristics, and the differences did not appear to be related to growth habit. This variability can be used to select superior genotypes for each parameter and include them in breeding programs for improved nitrogen fixation.

35682

BEAN IMPROVEMENT IN THE GREAT LAKES REGION OF AFRICA

Pierre Nyabyenda

ISAR, B.P. 138, Butare, Rwanda

The regional bean program has as its goal to develop minimum input technology for the benefit of poor farmers, based on improved disease and pest resistant varieties, together with bean based cropping systems for soil conservation and improvement. The work is done by a network of collaborating scientists in the national programs of Zaire (PNL), Burundi (ISABU) and Rwanda (ISAR), in partnership with regional scientists of IRAZ and CIAT. The long-term sustainability of the program is obtained through training and workshops, which build on the research capability of individual scientists, and develop stronger collaborative ties between scientists of neighbouring countries. The sustainability of the technology generated is ensured by encouraging national programs to involve the farmer in the research process, and by working with development projects in on farm research aimed at combining improved productivity with soil conservation. The mechanisms for achieving collaboration in technology generation are the regional variety improvement nurseries, and the sub-projects.

Introductions include the VEF and EP nurseries from CIAT each year. Other introductions include the international disease nurseries, especially for angular leaf spot (BALSIT), anthracnose (IBAT), halo blight (IBHBN) and ascochyta. These are the most important diseases of beans in the region. Early generation hybrid material is also introduced from CIAT for selection locally. A line developed by the Rwanda program from the hybrid of Rubona 5 x G 7480 (Wulma) has been coded as RWR 221, and has proved exceptionally promising in on farm trials. It will shortly be released for seed multiplication and distribution to farmers.

The regional nurseries are formed every year out of the materials in the three national program variety testing schemes. They form the nucleus of all collaborative research projects between countries, and also serve to encourage collaboration between disciplines within national programs. Finally, at the level of the AFBYAN, they serve to bring together the efforts of all three African regional programs through a systematic interchange of the best varieties.

The 'Pepiniere Regionale de Lignées Avancées de l'Afrique Centrale' is formed every year in September from the varieties entering the preliminary yield trials ('Essais Comparatifs') of each country. It forms the nucleus of the regional testing scheme, and is the basis of the regional sub-projects. The varieties in the PRELAAC are evaluated for the individual traits which are studied in the sub-projects, including tolerance to bean fly, ascochyta, resistance to anthracnose, halo blight and angular leaf spot. By bringing expertise from neighbouring countries to bear on the same group of materials, much more information can be generated than would otherwise be possible by any individual national program. Out of 100 bush bean and 49 climbing bean varieties in the 1988 PRELAAC, 14 of each were selected for the 1989 regional yield trials (ERGL).

For halo blight there was generally excellent agreement between the results in the glasshouse in England (NVRS) with race 3 and the field observations in Kisozi (Burundi), where race 3 is known to predominate, as in the rest of the region. The situation for anthracnose was more complex. A 321, AND 303 and ZAV 83052 were resistant in all four test sites, but most lines showed differential reactions at the sites, indicating considerable pathogenic variation. For angular leaf spot, there was mostly good agreement between the results at Rubona (Rwanda) and Mulungu (Zaire). The best were A 364, A 74, Ecuador 299, G 2858, XAN 68 and ACV 83031. For bean fly, there were significant differences in wilting among varieties. Some of the varieties in the nursery suffered up to 98% wilting. The best were A 364, AND 10 and RWV 78. For the first time, combined resistance to BCMV, halo blight and anthracnose was obtained in a climbing bean line, ZAV 83052.

The priority regional sub-projects in plant protection are: anthracnose and bacterial blights, as the major seed-borne diseases which cause several problems in seed multiplication programs; angular leaf spot, as the most widespread and yield-reducing foliar disease; bean fly, as the most widespread and devastating insect pest. Of local importance are: ascochyta, floury leaf spot and root rots.

The anthracnose sub-project is based at ISAR in Rwanda. Anthracnose is probably the most important seed-borne pathogen in the region. Studies on the variability of the anthracnose pathogen in Burundi and Rwanda have shown the presence of four and seven different races respectively. In both countries Cornell 49-242, which has the much used ARE gene, was susceptible in the field. The sub-project includes a breeding program whose objective is to develop stable resistance in well adapted local germplasm. G 2333 offers excellent resistance to all known races, and preliminary findings indicate that this is based on several genes.

The halo blight sub-project is based in Burundi (ISABU) and field work is carried out at Kisozi. From work done in England (NVRS), it is known that race 3 predominates in the region. Race 1 is also present but does not seem to be very important. Race 2 is not known to occur, but it is found in the neighbouring SADCC region. Resistance to race 3 is much less common than resistance to race 2. The first objective of the halo blight project, therefore, is to incorporate resistance to race 3 into improved germplasm, and the second longer-term objective is to develop race non specific resistance. Most varieties currently available to farmers are susceptible to halo blight, and this poses a serious problem especially for seed multiplication. One line in the 1988 PRELAAC showed race non specific resistance to halo blight, A 204, and this should be used as a parent in future crosses. A race 3 resistant line has already been developed from Kilyumukwe, a promising but susceptible Rwandan variety.

The objective of the BCMV sub-project is to develop germplasm resistant both to the mosaic and black-root symptoms. Crosses, backcrosses and early generation screening are done at CIAT with a mixture of Florida and NL-3 strains. Materials are then screened in the field at Rubona (ISAR) under natural infection, using spreaders of infected seed. The problem of BCMV has been most severe in climbers. New resistant lines have been developed. For example GLB 1 is a resistant line descended from a cross with C 10, a well known Rwandan climbing bean variety. GLB 6 is a mosaic resistant version of G 2333.

Root rots are caused especially by _Fusarium_ _solani_ and _Rhizoctonia_. Screenhouse screening in soil from problem sites indicates that resistance is available.

Surveys indicate that poorer farmers frequently have to buy in seeds, while the richer farmers can keep seed from household stocks. This indicates that it would be possible to target new bean varieties to poorer farmers by ensuring the availability of seed at critical times of the year. For consumption, farmers go to the market or to a local store, but do not generally buy from neighbours. By contrast, when buying beans for seed, farmers mostly go to their neighbors. They mostly do not trust market merchants who may mix seed from different regions. There is a need, therefore, to stimulate decentralized multiplication of improved seed by small farmers themselves, and identify more effective channels for distributing seed.

35683

DISTRIBUTION OF COMMON BEAN AND SOIL CHARACTERISTICS IN PRODUCTION AREAS IN LATIN AMERICA

J.N. Fairbairn

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Introduction

This series of posters is to show in a very general way, a part of the work of the Agroecological Studies Unit, which has as its principal objective to collect, organize and analyze information over areas of interest to CIAT's programs. The highest level of definition of these areas is shown here as a continental study of the geography of bean production, and, upon combining this distribution with information on soils and climate, a catalogue of existing production environments is compiled.

Data Collection

Information on the bean production areas was obtained from all countries of Latin America and the Caribbean, from several available sources. These sources included agricultural censuses, annual agriculture statistics, regional reports and personal information:

1) The most recent information for each country was utilized.
2) Information was utilized by placing points in the smallest possible political or natural region.
3) Consistency was checked with other sources, as well as with local experience.

Construction of the Map

Points representing 1000 ha of beans were placed on the map, using as the topographical base the O.N.C. maps on a scale of 1:1,000,000, and were localized using topographical information within the political divisions. Land utilization maps were also used, as well as LANDSAT images, and in some cases CIAT's climatological data base (SAMMDATA).

Soil Characteristics

Points were digitalized using an ALTEK table and were drawn on a scale of 1:5,000,000, and on the same projection as the World Soil Maps of the FAO. Each point was then marked with a soil unit that includes several types. Characteristics of soil types were taken from descriptions of representative profiles and laboratory analysis of the FAO publication. The maps show the production areas which are limited by low pH and low levels of available phosphorous. It seems that in the case of phosphorous almost half (47%) of the area planted has adequate levels of phosphorous (>10 ppm), 20% is deficient (<5 ppm) and 33% would benefit from phosphorous fertilization or the introduction of varieties that are more efficient in the utilization of phosphorous (at levels from 5 to 10 ppm).

35684

ARE THE SOUTHERN ANDES A BROADER AREA OF DOMESTICATION OF THE COMMON BEAN Phaseolus vulgaris L.?

J. Tohme, J. Vargas, W. Roca, and D.G. Debouck

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Recent biochemical analyses have provided additional evidence that the southern Andes have been a centre of bean domestication. In the traditional large seeded cultivars, several phaseolin types different from the ones found in Colombia and Mesoamerica were identified but their wild counterparts have not been yet fully characterized. Twenty-four wild common bean accessions from recent germplasm explorations in southern Peru and Bolivia were analysed by SDS/PAGE. All the phaseolin types reported in cultivated landraces from the southern Andes have now been found in the wild relatives of P. vulgaris from that area, with the exception of 'A' phaseolin. Worth mentioning is the high frequence of 'H' phaseolin in the wild populations of Cuzco. Moreover new phaseolin types have been found in southern Peru ('K') and in Bolivia ('To' and 'Ta'), not identified so far in landraces, thus suggesting a "founder effect" in bean domestication in that area. The most frequent phaseolin types in landraces 'T', 'C', 'H', were also found in wild populations over a broad geographic range, roughly over 2300 km from Junin to Tucuman. Our results suggest that the beans in the southern Andes were domesticated in more than a single place, but perhaps repeatedly in different places of that range. Definitive evidence would have to be looked for in isozymes profiles studies or mt DNA analysis.

35685

BIOCHEMICAL EVIDENCE FOR TWO DIFFERENT GENE POOLS IN LIMA BEANS

A. Maquet, C.E. Posso, and D.G. Debouck

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Samples of Phaseolus lunatus L. (82 cultivated and 14 wild forms) from different tropical countries were analysed by SDS/PAGE technique for the total seed storage protein. Two major families of electrophoretic patterns can be identified among the cultivated materials and traced back to two different wild ancestors, one distributed from Jalisco, Mexico up to Salta, Argentina along the eastern slopes of the Andes, and another one in Cajamarca, Peru. Furthermore, there is an intermediate pattern displayed by a wild form present in Panama. These results confirm the existence of at least two groups of wild forms and support the idea of separate domestications, also in accordance with archeological evidences. The variability as judged on seed storage protein patterns is higher in Peru and surrounding highlands, since the Big Limas and their wild ancestors display more variable patterns in comparison to Mesoamerica. The Big Lima seed morphotype is frequently associated with the Peruvian pattern, while the Sieva and Potato morphotypes are associated with the Mesoamerican pattern. Although it is not a strict correlation, a larger seed size is usually associated with the Peruvian pattern; apparently there is no correlation between the type of pattern and seed shape or color. The lack of correlation is further evidenced by a landrace of Nariño, Colombia (DGD-1336), a Big Lima-like type segregating for seed color and displaying the 3 patterns (Peru, Panama and Mesoamerica). This case of natural introgression would indicate that the two well separate gene pools overlapping in Southern Colombia are still genetically compatible. These preliminary results should be confirmed by testing more materials, especially wild forms, since the later also show resistance to the bruchid Acanthoscelides obtectus (Say).

35686

INTERSPECIFIC HYBRIDIZATION FOR THE IMPROVEMENT OF Phaseolus vulgaris

V. Schmit

CIAT/University of Gembloux Collaborative Project
Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Objective

To introduce interesting characteristics of other Phaseolus species to P. vulgaris with emphasis on resistance to Ascochyta and bean fly.

Species to be crossed with P. vulgaris:

Phaseolus coccineus, P. polyanthus, P. purpurascens

Methodology

1. Collection and seed increase of P. coccineus and P. polyanthus.
2. Evaluation and selection of interesting P. coccineus and P. polyanthus accessions at CIAT.
3. Crossing between P. vulgaris elite lines and selected P. coccineus and P. polyanthus
4. Selection of interspecific hybrids resistant to pests and diseases
5. Integration of homogeneous resistant lines to the VEF, EP, and bean breeding program.

Type of crosses created at Gembloux:

Direct crosses: using P. vulgaris as female and P. coccineus or P. polyanthus as male parent.

Complex crosses: Cross between a wild *P. coccineus* or *P. purpurascnes* as female and *P. vulgaris* as male, backcross of the F_1 with *P. coccineus* or *P. polyanthus*, and backcross of the F_1 with *P. vulgaris*; or reciprocal.

Selection for resistance to:

	Ascochyta	Bean Fly
F_1	Seed increase at Popayan	
F_2 + F_3	Individual selection at Popayan	Selection at A.V.R.D.C. for bean fly resistance for agronomy
F_4	Individual selection at Popayan and Rionegro	Selection at A.V.R.D.C. for bean fly resistance
F_5	Selection for disease resistance and *P. vulgaris* plant type	Selection for agronomy Backcross with *P. vulgaris*
F_6 and further progenies	Continuation of the same selection scheme Selection of homogeneous and resistant lines to be integrated in nurseries of the Bean Program, in the VEF and the EP	

ELECTROPHORETIC STUDY OF PHASEOLIN IN AFRICA GERMPLASM COLLECTIONS OF COMMON BEAN

M. Triana, D.G. Debouck, H. Ramirez, and W. Roca

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Crosses made between the Mesoamerican gene pool of _Phaseolus vulgaris_ L. and the South Andean gene pool in order to combine their higher productivity and larger grain type respectively often failed because of two complementary dominant genes causing hybrid weakness. One can wonder however whether natural recombinants could exist where the two gene pools were in contact for a long period of time. One place to investigate with appropriate climatic conditions could be Eastern Africa, where beans were brought from their American centres of origin 2 or 3 centuries ago and where natural outcrossing has been reported. After a SDS/PAGE analysis on 275 homogenous bean accessions of 6 East African countries, it appears that 'T' phaseolin is dominant, followed by 'S' and 'C' types; no recombinants between the two gene pools were found. Germplasm from the Southern Andes form thus the major part of East African mixtures, perhaps because of their attractive larger seed size. Although some landraces are very close to their South American counterparts, they differ however by their frequencies specific selective pressures and/or adaptive characters.

VARIETAL DIFFERENCES IN COMMON BEAN CONDENSED TANNINS

L. R. Lareo

Centro Internacional de Agricultura Tropical (CIAT)
A.A. 6713, Cali, Colombia.

Strong varietal differences among the eight primary testa colors of common beans (Phaseolus vulgaris L.) were found with respect to the molecular size, inferred by the differences in absortivity of their procyanidins measured by the acidified BuOH method. No one relationship was found among the colors and the total tannins content either by the vanillin assay or acidified BuOH, either for crude or "true" tannins, by the PVP method. These differences will be due to the different polymeric fractions composition as can be visualized in the circular paper chromotograms. These findings imply clearly that the true quantification of the condensed tannins in common beans and perhaps in other foods and feeds requires the preparation of their own standards because is not possible to generalize with only one for all the materials evaluated and because the common references as catechin and tannin acid have a different behaviour and do not reflect the true composition and amount of the tannins in the evaluated material.

BREEDING FOR TOLERANCE TO DROUGHT IN BEAN

J.A. Acosta G., F.J. Ibarra P., A. Pajarito R., R. Ochoa M.,
R. Lépiz I. y M.W. Adams

Instituto Nacional de Investigaciones Forestales y Agropecuarias (INIFAP)
Apartado Postal 186, Durango, Durango, México

Of the approximately 2 million ha of beans planted annually in Mexico, 87% depends exclusively on moisture from natural rainfall for its development. The greater part of the area in rainfed conditions is planted in summer and is located in the semiarid region of the center-north.

The National Institute of Forestry and Agricultural Research of Mexico (INIFAP) initiated this breeding project in 1980, and in 1982 Michigan State University (Bean-Cowpea CRSP, Title XII) joined INIFAP to work collaboratively.

Among results obtained to date are the following:

Germplasm:

Of 8.700 genotypes evaluated in a systematic screening in three stages, a group of approximately 40 were identified that possess a notable degree of tolerance in relation to the mean.

Knowledge:

a) To date, no characteristic (nor gene) has been identified, which by itself can explain the drought tolerance observed in these bean genotypes.

b) The characteristics which seem to be associated with drought tolerance in bean are: an abundant and deep root system, stomatal sensitivity, pubescence, leaf movement, and the capacity to remobilize stored assimilates before the onset of drought (before pod filling).

c) Genotypes of an intermediate vegetative cycle present a marked phenological plasticity in response to drought.

Methodology:

a) Grouping of germplasm based on its morphology and phenology facilitates interpretation of results, and thus, the identification of the most promising genotypes.

b) It is necessary for the evaluation of drought tolerance to define first the level of drought which permits differentiation of susceptible and tolerant genotypes. Under very severe drought pressure, it is difficult to recognize genotypic differences.

PROJECTIONS

1) Breeding for drought tolerance and incorporation of disease resistance in a recurrent selection scheme, working with the most important commercial types separately.
2) In the process of recurrent selection, yield evaluation under drought conditions of segregating populations in early generations.
3) Continue trying to identify characteristics (morphological, physiological, and biochemical) which facilitate the identification of drought tolerant genotypes.

MEASURING THE GENOTYPE X ENVIRONMENT INTERACTION EFFECT ON TIME-RELATED ADAPTATION AND YIELD

D.H. Wallace

Cornell University, 402 Bradfield Hall
Ithaca, N.Y. 14853, U.S.A.

Multiple location yield trials involve large genotype x environment interaction. The G x E sums of squares from the ANOVA of such trials is divided using principal component analysis into plus and minus G x E effects. The negative G x E interaction represent the decrease in days to flowering (or consequent effects on days to maturity or yield) caused when a higher mean temperature decreases the time the cultivar needs to develop a node. The positive G x E interaction represents the increase in days to flowering (or consequent effects on days to maturity or yield) when the same high temperature and/or larger day length amplifies the photoperiod gene activity to thereby increase (delay) the node to flower. The photoperiod gene activity contests the rate of partitioning to the reproductive growth, which is control over the rate of accumulation of yield. A high growth rate of the flower buds gives days to flowering in a shorter time than slow growth. A continual high growth rate of the seeds leads to early maturity while slow growth leads to later maturity. The analysis likewise assigns negative G x E to the environments if they affect development and predominantly through the rate of node development, and assigns positive G x E if they affect the developmental rate primarily by controlling the photoperiod gene activity.

STRATEGIES FOR CULTIVAR SELECTION OF LEGUMES

H.P. Müller, Th. Büscher, C. Leonards, S. Pick and D. Schaefer

Institute of Genetics, Abt. Biochemical Genetics, University of Bonn
D-5300 Bonn 1, Kirschallee 1, West Germany

Different approaches for characterizing legume genotypes are shown, the use of which facilitate selection for desirable traits in specific crosses and backcross programmes. Favourable alleles of genes which control distinct characters are to be found. Therefore, field trials, phytotron experiments and electrophoretic investigations on cultivars and wild populations are compared with regard to their usefulness for establishing an efficient system for selection according to breeding objectives in legumes. The proposed strategies, shown for Phaseolus, Pisum and Vicia will accelerate the development of field and laboratory methods, using molecular genetic markers (isozymes, RFLP's) which aid selection work and have implications for further improvement of beans.

APPENDIX 1

LIST OF PARTICIPANTS

Africa

Tesfaye Beshir
Scientific Phytopathological Laboratory
P.O. Box 152
Ambo, Ethiopia, East Africa
Phone: 94

Teshome Girma
Junior Research Officer
Institute of Agricultural Research
Nazret Research Centre
P.O. Box 103
Nazret, Ethiopia, Africa

Charles Wycliffe Bakamwangiraki
Scientific Officer (Plant Breeder)
Kawanda Research Station
P.O. Box 7065
Kampala, Uganda, Africa

Osman Hussein Yusuf
Field Officer
Central Agricultural Research Institute
P.O. Box 6852
Mogadishu, Somalia, Africa
Phone: 80515

Peter Ramadhani Dimoso
Principal Agricultural Officer - Research
Department of Crop Science
Sokoine University
P.O. Box 3005
Morogoro, Tanzania, Africa
Phone: 056-3511
Telex: 55308 UNIVMO TZ

Elizabeth T. Marenge
Field Officer II
T.A.R.O. Lyamungu
P.O. Box 3004
Moshi, Tanzania, Africa
Phone: 4411

Catherine Sylvester Madata
Student in Plant Breeding and Genetics
Michigan State University
Uyole Agric. Centre
P.O. Box 400
Mbeya, Tanzania, Africa
Phone: 7011-255-65-2116

Pierre Nyabyenda
Department Head
Institut des Sciences Agronomiques du Rwanda
ISAR
B.P. 138
Butare, Rwanda
Phone: 250-30446
Telex: 250-30599

Argentina

Nicolás Carlos Dantur
Coordinador del Programa de Poroto
Estación Experimental Agroindustral Obispo Colombres
Casilla de Correo 9 - Las Talitas
4101 San Miguel de Tucumán, Argentina
Phone: 216561 / 225475
Telex: 61152 REYES AR

Australia

Robert John Redden
Senior Plant Breeder
Department of Primary Industries
D.P.J. Hermitage Research Station
Warwick, Qld. 4370, Australia
Phone: 076612944

Brazil

Joao Luiz Alberini
Fitomejorador
Hata, Genetica e Melhoramento
Rua 14 de Julho 1817 - 8o. Andar
Sala 81
Campo Grande, MS, Brasil
Phone: (067) 384-1792

José Eustáquio de Souza Carneiro
Pesquisador em Melhoramento de Feijao
EMBRAPA / CNPAF
Rodovia GYN 12, Km. 10
Caixa Postal 179
74.000 Goiania, Goiás, Brasil
Phone: (62) 261-3022
Telex: 062.2241 EBPA BR

María José de Oliveira Zimmermann
Coordinadora del Programa Nacional de Pesquisa de Fríjol
EMBRAPA / CNPAF
Caixa Postal 179
74.000 Goiania, Goiás, Brasil
Phone: (62) 261-3022
Telex: 062.2241 EBPA BR

Joaquim Geraldo Cáprio da Costa
Pesquisador - Melhoramento de Feijao
EMBRAPA / CNPAF
Rodovia GYN 12, Km. 10
Caixa Postal 179
74.000 Goiania, Goiás, Brasil
Phone: (62) 261-3022
Telex: 062.2241 EBPA BR

Pedro Antonio Arraes Pereira
Researcher Plant Breeding
EMBRAPA / CNPAF
Rodovia GYN 12, Km. 10
Caixa Postal 179
74.000 Goiania, Goiás, Brasil
Phone: 55 (62) 261-3022
Telex: 062.2241 EBPA BR

Paulo Miranda
Pesquisador
Empresa Pernambucana de pesquisa Agropecuaria - IPA
Avenida General San Martín, 1371 Bonji
Caixa Postal 1022
50.000 Recife, PE, Brasil
Phone: 227.0500
Telex: 0812286

Antonio Sidney Pompeu
Fitomelhoramento
Instituto Agronómico
Avenida Barao de Itapura 1481
Caixa Postal 28
13.001 Campinas, Brasil
Phone: (0192) 410511
Telex: (019) 1059

Leandro Oliveira e Silva
Pesquisador
EMGOPA
Caixa Postal 608
77.100 Anápolis, Goiás, Brasil
Phone: (062) 3212851

<u>Canada</u>

Soon J. Park
Field Bean Breeder
Agriculture Canada, Research Station
Harrow, Ontario
Canadá NOR 1GO
Phone: (519) 738-2251
Telefax: (519) 738-2929

Colombia

Gilberto Bastidas Ramos
Coordinador Nacional de Leguminosas de Grano
Instituto Colombiano Agropecuario (ICA)
Apartado Aéreo 233
Palmira, Valle, Colombia
Phone: 28167
Telex: 55749

Alberto de Jesús Román Vélez
Ingeniero Agrónomo
Instituto Colombiano Agropecuario (ICA)
Apartado Aéreo 100
Rionegro, Antioquia, Colombia
Phone: 2714875

Oscar de Córdoba
Gerente Investigación y Desarrollo
CARGILL COLOMBIANA S.A.
División de Semillas
Calle 56 Norte # 3-19 La Flora
Apartado Aéreo 4850
Cali, Valle, Colombia
Phone: 642271 / 655540
Telex: 55705 BARCO CO

CIAT
Apartado Aéreo 6713
Cali, Colombia
Phone: 675050
Telex: 05769 CIAT CO
Cables: CINATROP

Steve Beebe
Jeffrey White
Michael Dessert
Douglas Pachico
Julia Kornegay
Shree Singh
Cesar Cardona
Joe Tohme
Oswaldo Voysest
Willem Janssen
Michael Thung
Marcial Pastor-Corrales
Judy Kipe-Nolt
Jonathan Lynch
Daniel Debouck
Ariel Gutiérrez
Cesar Cajiao
Carlos Urrea
Albeiro Molina
Harold Patiño
Rigoberto Hidalgo
Yolanda López
Jairo Quiros
Iván Ochoa

<u>Costa Rica</u>

Adrián Morales Gómez
Jefe Sección Leguminosas de Grano
Ministerio de Agricultura y Ganadería
Sabana Sur, Antiguo Colegio "La Salle"
Apartado 10094
San José, Costa Rica
Phone: 552027 Ext. 19

James Michael Dessert
Coordinador, Programa Regional de Fríjol en
Centro América y el Caribe
CIAT/IICA
Apartado 55, 2200 Coronado
San José, Costa Rica
Phone: 290222 Ext. 390 - 454
Telex: 2144 IICA CR

Cuba

Evelio Juan García Sánchez
Director del Area Experimental de Granos Velasco
Ministerio de la Agricultura
C. Recreo # 21
Velasco, Holguín, Cuba
Phone: 42109

Benito Faure Alvarez
Fitomejorador
Estación Experimental de Granos "El Tomeguín"
Avenida 85 # 6811 entre 68 y 70
Alquízar, La Habana, Cuba
Phone: 2829 y 2949

Dominican Rep.

Eladio Arnaud Santana
Encargado Estación Experimental de Arroyo Loro
Secretaría de Estado de Agricultura
Apartado # 145
San Juan de la Maguana, República Dominicana
Phone: (809) 557-3114

Ecuador

Mario Caviedes Cepeda
Jefe, Programa de Leguminosas
INIAP, Estación Experimental Santa Catalina
Panamericana Sur Km. 17
Apartado 340
Quito, Ecuador
Phone: 629-691 / 629-693
Telex: 2560 INIAP ED

El Salvador

Carlos Atilio Pérez
Coordinador, Programa de Leguminosas
CENTA
Km. 33 1/2 Carretera a Santa Ana
Nueva San Salvador, El Salvador
Phone: 28-2066

France

Hubert Bannerot
Directeur de recherches
Station de Génétique et D'Amélioration des Plantes
INRA
Centre de Recherches de Versailles
Route de Saint-Cyr-78026 Versailles-Cedex
France
Phone: (33) 1.30.83.32.85
Telex: 695269 INRAVER F

Germany

Hermann P. Müller
University Professor
Institut fur Genetik, Universität Bonn
Abt. Biochemische Genetik
Kirschallee 1
5300 Bonn, Federal Republic of Germany
Phone: 0228-735518

Guatemala

Porfirio Masaya
Coordinador del Programa de Fríjol
ICTA
Apartado 231-A
Guatemala, Guatemala
Phone: 312195

Samuel Ajquejay
Fitomejorador del Programa de Fríjol
ICTA
Apartado 231-A
Guatemala, Guatemala
Phone: 312195

Honduras

José Antonio Jiménez Torres
Jefe del Programa de Fríjol
Secretaría de Recursos Naturales
Danlí - El Paraíso, Honduras
Phone: 93-2112 Ext. 50

Juan Carlos Rosas
Profesor Asociado / Fitomejorador
Escuela Agrícola Panamericana - El Zamorano
P.O. Box 93
Tegucigalpa, Honduras
Phone: (504) 332717 / 333173
Telex: 1567 EAPZAM HO
Telefax: (504) 328543

México

Rafael Atanacio Salinas Pérez
Experto "B" Red de Leguminosas Comestibles Zona Norte
INIFAP
Campo Agrícola Experimental del Valle del Fuerte
Apartado Postal 342
Los Mochis, Sinaloa, México
Phone: 91 (681) 6-03-20 ó 21

Rogelio Lépiz Ildefonso
Fellow CIAT
INIFAP
Apartado Postal 77 Suc. A
Zapopán, Jalisco, México
Phone: 330508/330738

Francisco Cárdenas Ramos
Director del CENID - Recursos Genéticos
INIFAP
Apartado Postal 10
Chapingo, México
Phone: 5-361513

Jorge Alberto Acosta Gallegos
Experto "A" Red de Leguminosas
INIFAP
Apartado Postal 186
34.000 Durango, Durango, México
Phone: (181) 21133/21155/21044

Ernesto López Salinas
Investigador del Programa de Fríjol
INIFAP
Apartado Postal 429
Veracruz, México
Phone: 350418

Peru

Vidal Ortiz Arriola
Coordinador, Programa de Investigación de Leguminosas de Grano - CUSCO
INIAA
Avenida Huascar 226
Cusco, Perú
Phone: 227351 ó 222031

Juan Risi Carbone
Director del Programa de Investigación en Leguminosas de Grano
INIAA
Apartado Aéreo 248
Avenida Guzmán Blanco 309
Lima 100, Perú
Phone: 360849

Angel Valladolid Chiroque
Coordinador-Costa, Programa de Investigación de Leguminosas de Grano
INIAA
Panamericana Sur Km. 203
Apartado 115
Chincha, Perú
Phone: 262351

Guillermo Gálvez
Coordinador del Programa de Fríjol, Zona Andina
CIAT
Apartado 14-0185
Lima 14, Perú
Phone: 229623
Telex: 25672 PE
Telefax: (51-14) 424554

Venezuela

Orangel L. Borges F.
Profesor de Genética
Universidad Central de Venezuela
Facultad de Agronomía
Maracay, Estado Aragua, Venezuela
Phone: (043) 545252

United States

Donald H. Wallace
Professor of Plant Breeding and Vegetable
Cornell University
Plant Breeding Department
Emerson / Bradfield Hall
Ithaca, New York 14853-1902
U.S.A.
Phone: (607) 255-1657

Susan Louise Sprecher
Postdoctoral Research Associate
Michigan State University
Crop and Soil Sciences Department
East Lansing, Michigan 48824
U.S.A.
Phone: (517) 353-3954
Telex: 650-264-1762 MCI

Mireille M. Khairallah
Graduate Student (Ph.D.)
Michigan State University
Crop and Soil Sciences Department
Plant and Soil Sciences Building
East Lansing, Michigan 48824
U.S.A.
Phone: (517) 355-2248
Telex: 650-264-1762 MCI

Catherine Sylvester Madata
Student - Plant Breeding and Genetics
Michigan State University
Plant and Soil Sciences Building
East Lansing, Michigan 48823
U.S.A.
Phone: (517) 355-0766

John Giles Waines
Professor Genetics, Director Botanic Garden
University of California, Riverside
Department of Botany and Plant Sciences
Riverside, California 92521
U.S.A.
Phone: (714)-787-3706

Fred J. Muehlbauer
Research Geneticist
USDA-ARS
Grain Legume Genetics and Physiology Research
215 Johnson Hall
Washington State University
Pullman, WA 99164-6421
U.S.A.
Phone: (509) 335-9521

Richard L. Cooper
Soybean Breeder
USDA/ARS
Agronomy Department
OARDC-OSU
The Ohio State University
1680 Madison Ave.
Wooster, Ohio 44691
U.S.A.
Phone: (216) 263-3875

APPENDIX 2

PROGRAM OF THE WORKSHOP

7 November

08:00	Registration/Coffee	
09:00	Welcome, Introduction	D. Pachico/Confer. Coord.

Advances in studies of genetic resources in common bean

	Moderator	R. Lépiz
09:30	Introduction	R. Lépiz
09:45	Implications for bean breeders of studies on the origins of common beans, *Phaseolus vulgaris* L.	D. Debouck/ J. Tohme
10:15	Discussion	
10:30	The bean germplasm bank of Mexico	F. Cárdenas
11:00	Discussion	
11:15	Coffee	
11:30	Races of common bean, *Phaseolus vulgaris* L.	S. Singh/P. Gepts/ D. Debouck
12:00	Discussion	
12:15	Lunch	
13:30	Use of wild *Phaseolus vulgaris* to improve beans for resistance to bruchids	C. Cardona/ J. Kornegay
14:00	Discussion	
14:15	Potential of biotechnology in germplasm evaluation and the genetic improvement of *Phaseolus* beans	W. Roca/H. Ramirez P. Chavarriaga/ L.C. Muñoz
14:45	Discussion	
15:00	Coffee	
15:15	The potential of hybrid beans	H. Bannerot
15:45	Discussion	
16:00	Use of interspecific crosses to improve common bean (*Phaseolus vulgaris* L.)	G. Waines
16:30	Discussion	
16:45	General discussion	

8 November

08:00	Welcome from the directors	D.R. Laing

Breeding for early maturity

	Moderator	J. White
08:15	Introduction	J. White
08:30	A socio-economic perspective on earliness in beans	W. Janssen
09:00	Discussion	
09:15	Physiological aspects of earliness in common bean	J. White
09:45	Discussion	
10:00	Coffee	
10:20	Visit to demonstration plots	
12:30	Lunch	
14:00	The development of early-maturing varieties for Central American agricultural systems	P. Masaya
14:30	Discussion	
14:45	Round table discussion with audience participation	
15:30	Coffee/Refreshments/Presentation of posters	
17:00	Cocktail	

9 November

07:30	Field trip to Santander

10 November

Approaches and progress in breeding for quantitative traits in common beans

	Moderator	J. Kornegay
08:00	Introduction	J. Kornegay
08:30	Discussion	
08:45	Quantitative genetics in *Phaseolus vulgaris*: the example of resistance to *Xanthomonas campestris* pv *phaseoli*	S. Beebe
09:15	Discussion	
09:30	Development of appropriate breeding strategies for resistance to *Empoasca kraemeri* in common bean	J. Kornegay/ C. Cardona
10:00	Discussion	
10:15	Coffee	

10:30	Breeding for yield in common bean of Middle-American origin	S. Singh
11:10	Discussion	
12:00	Lunch	
	Moderator	A. Pompeu
13:30	Breeding common bean (<u>Phaseolus</u> <u>vulgaris</u> L.) for yield in intercrop	M.J. Zimmermann
14:10	Discussion	
14:25	Breeding for yield in soybeans: early generation testing and specific adaptation to high versus low yield environments	R. Cooper
15:05	Discussion	
15:20	Breeding for yield in other legumes	F. Muehlbauer
16:00	Discussion	
16:15	Coffee	
16:30	Round table discussion with audience participation	
17:15	Discussion with Brazilian breeders over formation of a nursery of sources of resistance - Quimbaya Room	S. Singh/S. Beebe/ M. Thung

<u>11 November</u>

Forum: Bean production in the year 2000

	Moderator	D. Pachico
08:00	Dry bean production and consumption in the year 2.000: projections thoughts and guesses with emphasis on Latin America and Africa	W. Janssen
08:30	Discussion	
08:45	The future of small bean producers in Mexico and their relation with commercial farming	R. Lépiz
09:15	Discussion	
09:30	Bean production in the year 2.000: Commercial production	J. Alberini
10:00	Discussion	
10:15	Coffee	
10:30	General Discussion	
11:30	Closing remarks	D. Pachico
12:00	Lunch	
13:30	Free for consultations	
13:30-16:30	Breeders of C. America and Caribbean: Discussion and planning of crosses Tayrona Room	
18:30	Dinner	

12 November

08:30	Trip to Popayán
12:30	Lunch in Popayán
13:30	Return to CIAT