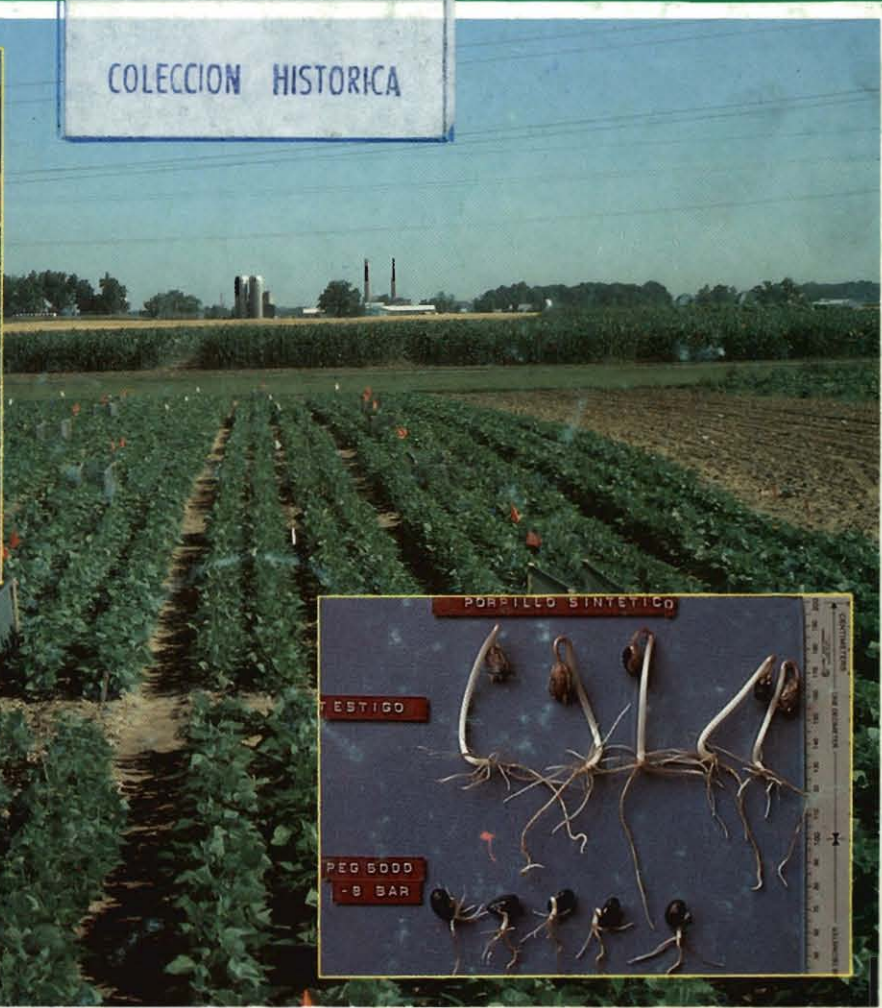


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TECHNICAL COOPERATION NETWORK ON FOOD CROPS PRODUCTION

DRY BEAN: Physiology of Yield Potential and Stress Tolerance



Phaseolus vulgaris L.

TECHNICAL COOPERATION NETWORK ON FOOD CROPS PRODUCTION



DRY BEAN: PHYSIOLOGY OF YIELD POTENTIAL AND STRESS TOLERANCE



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Santiago, Chile
FAO Regional Office for Latin America and the Caribbean
1989

PED. EXTERIOR

100-58072

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This manuscript was prepared originally by Messrs. Jeffrey W. White, Ph.D., Plant Physiologist, Bean Program, Centro Internacional de Agricultura Tropical (CIAT), Apartado Aéreo 6713, Cali Colombia, and Juan Izquierdo, Ph.D., Crop Physiologist, Regional Plant Production Officer, FAO Regional Office for Latin America and the Caribbean, P.O. Box 10095, Santiago Chile, as one chapter of the book Bean Production and Improvement in the Tropics which was intended to be published by CIAT. Very long delays in preparation of other chapter manuscripts are precluding the production of the book, so in order to make the information available to bean researchers and extensionist that are participating at the FAO/RLAC Food Crops Technical Cooperation Network and to CIAT Bean Program cooperators, it was decided to publish this document through a joint effort of CIAT and FAO.

As of July, 1989, it is expected that the book, now entitled Common Bean: Research for Crop Improvement will be available in 1990.

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I. INTRODUCTION

The common bean (*Phaseolus vulgaris*) has a poor reputation both in terms of yield potential and tolerance to physiological stresses such as drought, flooding, and saline soils. It is imperative and necessary then to increase bean productivity in view of its agricultural importance and essential participation in the diet of millions of inhabitants of Latin America and the Caribbean as well as of other regions in the world. While agricultural research progresses without being able to make a breach in the barriers that restrain the yield of this crop, particularly under stress conditions, regional bean productivity has decreased over the last 40 years. In Brazil, the main producing country, bean productivity in the poorer regions is 405 kg ha⁻¹. (Alves, 1987).¹

Various research programs have reported experimental yields over 5 ton/ha in bush beans, and genetic variability for yield potential and stress tolerance have been demonstrated.

Although these findings have not lead to dramatic increases in bean productivity as has occurred with other crop species, physiological studies of beans, and other grain legumes such as soybean (*Glycine max*) and cowpea (*Vigna unguiculata*), have generated useful information for guiding agronomic management and suggesting strategies for varietal improvement of beans, and as our knowledge increases, further practical benefits will certainly be forthcoming.

Traditional varieties of beans respond poorly, in general, to the two agronomic management elements recommended by the green revolution, and which have made it possible to obtain high yields in other crops: high plant density and fertilization. In spite of these constraints, traditional varieties contain a valuable genetic variability which is useful for plant breeders in the search for resistance to pests and diseases or other characteristics associated to high yield. New varieties of beans and appropriate crop management technologies suitable for the conditions of the small farmers in developing countries, are essential in the next years. In this context, biotechnology can provide, in support to genetic improvement, new alternatives to achieve this objective. However, adaptation of these future innovations to the traditional farming practices of the small farmers and to the ecological context in which they will be introduced, must be specifically considered. Genetic improvement and plant physiology must converge in results expressed as new varieties of beans, more "rustic" and adapted to marginal conditions. These can initiate the expected "new revolution" in this crop. A clear understanding of the processes and physiological phenomena that determine and regulate the expression of yield, is basic for this new stage.

Due to the diversity and complexity of physiological events determining yield potential, the authors have presented both a descriptive and integrative look at the physiology of the bean plant. The chapter first discusses basic physiological processes which determine bean yields, and then applies this information to yield potential and stress tolerance. Many unpublished results obtained at research work conducted in Latin America were included to illustrate physiological phenomena not considered in previous studies.

¹ Alves, E. 1987. Os desafios de extensao rural brasileira. Mimeograph. (Unpublished).

Texts and journals on plant physiology contain many studies on the role of growth regulators in bean plants, but we shall only refer to such work when evidence exists for effects on specific physiological processes. Although there are many unknowns concerning plant growth regulators, their overall role appears to be one of transmission of regulatory information from one tissue to another. In relation to crop growth problems, studies of growth regulators are generally of only indirect use, as expressed by Wit and Penning de Vries (1983): "A hormonal system is a communication system. Such systems may be analysed either in terms of means of the hardware used or in terms of purpose of the messages transferred. In dynamic models of crop growth, interest should be focused on the latter, whereas the existence of the hardware, the hormonal systems, may be taken for granted".

Space limitations preclude a complete literature review on the physiology of this crop but interested readers can find pertinent and complementary information in Graham (1978), Laing, Jones and Davis (1984), Tanaka and Fujita (1979), and Wallace (1985).

II. BASIC PROCESSES

Physiological processes in a plant may be classified into metabolic events such as photosynthesis and respiration which have a direct effect on growth, and morphogenic ones which affect the change in form or development of the plant. The two groups of processes interact strongly, but are best discussed separately.

A. Growth Processes

Growth may be measured in many ways (stem elongation, accumulation of nodes, leaf expansion, etc.), but emphasis is given here to the processes which affect dry weight accumulation and its partitioning since yield is the ultimate expression of these processes. Accumulation of dry weight in bean plants is a direct consequence of the balance among photosynthesis, respiration, and losses due to senescence and abscission. Partitioning, on the other hand, establishes an equilibrium between vegetative and reproductive growth integrated over the development of beans, resulting in an end product of yield.

1. Photosynthesis:

As in other grain legumes, beans have a C_3 photosynthetic pathway. Estimates of maximum leaf photosynthetic rates (AP) at ambient CO_2 concentrations have ranged from 12 $mg\ CO_2\ dm^{-2}\ h^{-1}$ to 35 $mg\ CO_2\ dm^{-2}\ h^{-1}$ (Table I). Recent estimates have been relatively high, presumably reflecting improved measurement techniques, but are still well below rates of soybeans, which can reach 45 to 60 $mg\ CO_2\ dm^{-2}$ (Shibles *et al.*, 1975).

AP varies greatly with leaf age and environmental conditions. Leaves increase in photosynthetic capacity as they expand, maintain a maximum for a highly variable period depending on cultivar and leaf position, and then decline as the leaf senesces (Fraser and Bidwell, 1974). This decline in AP appears to result primarily from loss of photosynthetic capacity, but also involves increased stomatal resistance (Davis and McCree, 1978). Tanaka and Fujita (1979) detected a significant positive correlation between nitrogen content and AP in leaves at ages past the time of maximum rate, suggesting that loss of photosynthetic capacity is related to nitrogen remobilization. Similar conclusions were reached in soybeans (Lugg and Sinclair, 1981), with the clarification that the linear relation only holds below a critical leaf protein concentration levels (12 $g\ protein.m^{-2}$ of leaf in their study).

Table I. Reported values of maximum leaf photosynthetic rate at near-ambient CO_2 concentrations.

	Photosynthetic Rate	
	$mg\ CO_2\ dm^{-2}\ h^{-1}$	$g\ CH_2O\ m^{-2}\ h^{-1}$
Austin & MacLean, 1972a	24	1.6
Fraser & Bidwell, 1974	19	1.2
Gaastera, 1962	22	1.4
Hesketh & Moss, 1963	12	0.8
Izhar & Wallace, 1967	15	1.0
Louwerse & Zwerde, 1977	22	1.4
Kueneman <i>et. al.</i> , 1979	31	2.1
Tanaka & Fujita, 1979	35	2.3
Laing <i>et. al.</i> , 1984	34	2.2

Maximum photosynthetic rates in beans are reached at irradiances of 300 W.m^{-2} , the same level reported for soybeans (Shibles *et al.*, 1975). Burga (1978) found evidence in beans that AP varies with the position of the leaf within the canopy, and reaches its maximum at the time of initial pod filling. Laing *et al.* (1984) cite unpublished work of El-Sharkaway demonstrating differences in response of AP in two bean cultivars, with optima varying from 21°C to 31°C. No effect of water vapour pressure deficit (VPD) on AP was detected by Hesse and Lenz (1982) using 50 klx illumination at 22°C, but El-Sharkaway *et al.* (1984) found that beans had an intermediate level of sensitivity as compared to other crops. A possible explanation for the different conclusions lies in interacting effects of irradiance, temperature and relative humidity on stomata opening, as reported in other species (Larcher, 1975).

Louwerse and Zweerde (1977) found that maximum AP was obtained from plants under high radiation regimes, and that AP was positively correlated with leaf thickness, specific leaf weight and number of chloroplasts, but not with chlorophyll content. Different sources of nitrogen affect AP too, apparently through effects on photoreactions affecting nitrogen metabolism (Marques *et al.*, 1983). Even simple differences in container size can affect leaf photosynthetic rates as in the study of Carmi *et al.* (1983) where plants which had been stunted by being grown in small pots showed higher AP.

Further complications result from the possibility that other parts of the bean plant may regulate photosynthesis independent of effects of water or nutrients. Carmi and Koller (1978) detected root effects on photosynthesis in primary leaves of beans. Research in soybean suggests that if demand from growing tissues is insufficient (e.g. as induced by artificial depodding), photosynthesis may be inhibited. Starch accumulation in chloroplasts may play a key role (Chatterton and Silvius, 1979), although Carmi and Shoemaker (1979) found that bean mesophyll cells appeared able to accumulate large amounts of starch without disrupting the chloroplasts. Leaf starch in soybeans has been found to be negatively correlated with the activity of the sucrose-P synthetase (Huber and Israel, 1982). These findings support the postulate that sucrose-P synthetase is key in legumes in regulating photosynthetic formation of sucrose, and hence, starch. The role of this enzyme, strongly related to nitrogen content, appears to be critical in legume metabolic processes.

Green bean pods fix CO_2 at lower rates than adjacent leaves, and the rate decreases with pod age (Tanaka and Fujita, 1979). Bean pods recycle substantial amounts of internally-released CO_2 , but are not an important photosynthetic source of dry matter to developing seeds (Crookston, O'Toole and Ozbun, 1974a).

Under conditions of high mesophyll O_2 concentrations, such as occurs when stomata close under high light intensities but limited water availability, O_2 competes with CO_2 in reacting with RuDP carboxylase, with the important difference that chemical energy is expended and CO_2 evolved. It was first thought that photorespiration, as it is termed, was either a waste process or permitted production of compounds essential for plant growth. No such function has been demonstrated, and most researchers now favor the idea that photorespiration serves to dissipate light energy when photosynthesis is blocked due to low CO_2 concentrations (Powles and Osmond, 1979; Tolbert, 1980) or to maintain CO_2 levels relatively constant within mesophyll tissues (Leopold and Kriedeman, 1975). Nevertheless, Ogren (1984) considered that occurrence of photorespiration in anaerobic bacteria disproves the protection function, and concluded that lower photorespiration rates still may be attainable. Rates in beans have been shown to vary with environmental conditions (Martin *et al.*, 1971). Wallace *et al.* (1976) felt that this variability would make detection of genetic differences in beans difficult.

Efficiency of the photo-assimilative process is severely affected by microclimate at the crop level. The distribution of radiation within a bean plant community is one of the most important elements of microclimate of the crop. Interception of light can be approximated by the exponential decay function,

$$I = I_0 \exp(-k \cdot L),$$

where I_0 is net radiation above the canopy, I is radiation at a level corresponding to L units of leaf area index, and k is the extinction coefficient, a characteristic depending on leaf orientation and distribution (Milthorpe and Moorby, 1979). The review of the values of extinction coefficients for various crops by Monteith (1969) indicates that k ranges from 1.05 (horizontal leaves) to 0.24 (grasses with vertical leaves). Data from Gardiner *et al.* (1979) for two varieties planted at 46 and 91 cm row spacings (Figure 1) gave values of k of 0.48 at 46 cm and 0.56 at 91 cm, suggesting that bean leaves are oriented in a relatively horizontal manner, and confirming the expectation that leaves are more erect at narrower spacings. The same tendency was found by Burga (1978), who also reported a highly significant negative correlation between k and leaf angle, this reflecting the ability of the bean plant to orient their leaves with the position of the sun in the sky to increase canopy light interception. Wien and Wallace (1973) and Sato and Gotoh (1983) showed that leaf orientation responds to light, that sensors are contained both in pulvinules and leaflets, and that varietal differences in patterns of orientation exist.

2. Respiration:

Although it is biochemically not a realistic separation, respiration is most easily considered as composed of two components. One is termed "maintenance respiration", and represents respiration attributable to activities associated with maintenance of tissue function. Growth respiration is the other component, and represents respiration associated with transport and biosynthesis in the construction of new tissues during growth.

Maintenance respiration is similar to basal metabolism in animals, and is thought to vary with tissue composition and temperature. Austin and McLean (1972a) found that roots of bean plants in the primary leaf stage had rates approximately twice those of leaves and stems, and that rates doubled with a 10°C increase in temperature. Sale (1975) detected a similar level of sensitivity for dark respiration of bean leaves.

Assuming varietal differences in plant structure and temperature adaptation, there is every reason to expect as much variability in maintenance respiration rates as is found for photosynthesis. Genotypic variation in several grain legumes was detected by Pandey *et al.* (1976). This point appears unexplored in beans except where differences in dark respiration of leaves have been detected in studies of photosynthesis (Izhar and Wallace, 1967).

Estimates of growth respiration rates are obtained from costs of biosynthesis (Penning de Vries *et al.*, 1974; de Wit *et al.* 1978). Using data on tissue composition of beans from various sources (Table 2), approximate respiration costs for roots, leaves, stems and pods have been calculated (White, 1981). Pods are the most costly due to their high protein content, while roots and stems require much less due to their relatively high carbohydrate content (Table 2).

Since growth respiration is directly related to energy requirements for specific chemical reactions, it is believed relatively temperature insensitive. Biosynthetic pathways are similar among many species, so genetic variability is supposed low beyond expected differences due to variability in plant composition. However, estimates of efficiency of carbohydrate use in nitrogen fixation (which is normally accounted for in assumptions about costs of protein synthesis) indicate major varietal differences (Kipe-Molt, personal communication), and environmental effects and genetic variability in beans need additional research.

Penning de Vries and van Laar (1977) used sequential tissue analyses to estimate respiration costs of beans during germination and early seedling growth under different temperature regimes.

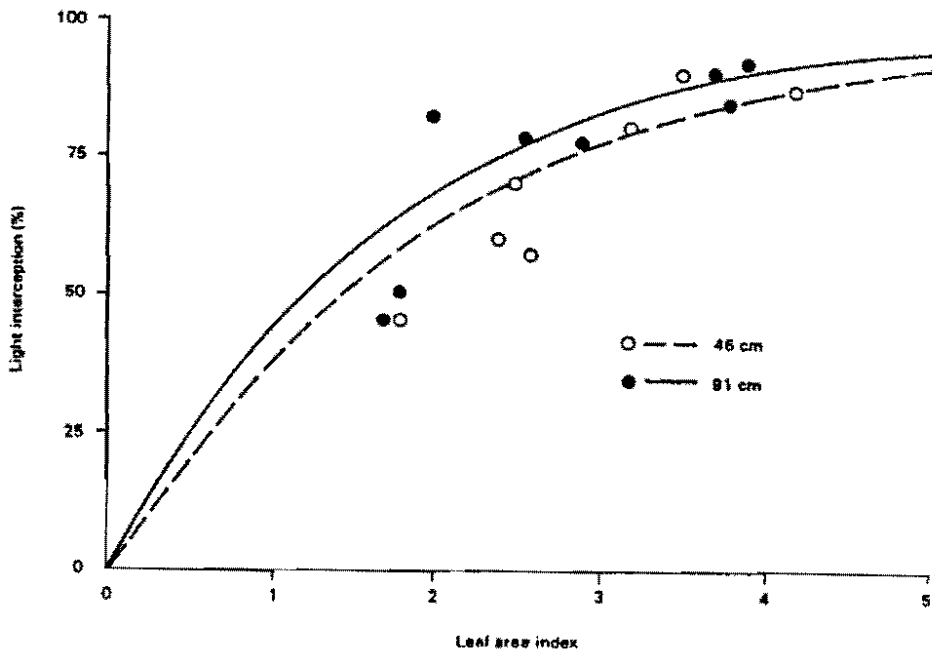


Fig. 1 Relation between leaf area index and light interception at 46 cm and 91 cm row widths. Estimated from data of Gardiner *et al.*, 1977.

Table 2. Composition of bean plant tissues and costs of biosynthesis. Data for compositions compiled from Piper and Morse (1923), Jordan and Chibnall (1933), McKee *et al.* (1955) and Sinclair and de Wit (1976).

	Leaf	Root	Stem	Pod
-----% of dry weight-----				
Carbohydrate	61.7	78.9	77.4	60.9
Protein	20.8	9.5	11.9	30.2
Lipid	7.7	0.9	0.6	1.5
Lignin	4.0	7.0	7.0	4.0
Ash	5.8	3.7	3.2	3.4
-----g CH ₂ O g ⁻¹ tissue-----				
Cost of biosynthesis*	1.50	1.28	1.32	1.52

* Source: White, 1981.

3. Nitrogen Metabolism:

The high protein content of legume seeds explains the particular importance of nitrogen metabolism in grain legume physiology. In bean seeds, a protein content of 20% to 24% implies a nitrogen content of approximately 4%, which in turn means that every 1,000 kg of yield implies a need for 40 kg of N, not including amounts needed to replace losses due to leaching or residual N in other tissues. It was found that up to 80% of the foliar N is reallocated to other plant parts before the onset of leaf abscission (Izquierdo, 1981). And it will be remembered that N content of leaves is high, that content varies with ontogeny (Table 3), and that it can show a direct correlation with AP.

Although N may be introduced through the foliage, the normal route of uptake is through the roots, either as nitrate or N_2 , which is converted in root nodules to ammonium ions. For our purposes, it will suffice to observe that once fixed as ammonium, N is in a form readily convertible to amino acids. In the case of N absorbed as nitrate, the nitrate is first converted from nitrate to nitrite by nitrate reductase, and then from nitrite to ammonium by nitrite reductase. The different metabolic pathways required with different N sources appear to effect efficiency of N-partitioning (Westermann *et al.*, 1985).

In beans, nitrate reductase activity is greatest in leaf tissue. This permits the reduction reaction to be coupled to energy directly available from photosynthesis, and this should reduce the apparent energy cost as compared to crops which have greatest reductase activity in roots (Hunter *et al.*, 1982). Nitrate reductase activity varies greatly with leaf age and crop growth stage (Franco *et al.*, 1979), and some level of activity is maintained even when nitrate is excluded as a nitrogen source (Timpa and Meyra, 1983). In other crops, considerable effort has gone to determining whether nitrate reductase activity is yield limiting, but no clear positive results have been obtained (e.g. Fakorede and Mock, 1976). The great plasticity of nitrogenase activity in bean plants suggests the same would be true for beans.

B. Developmental Processes

As a bean plant grows, it undergoes not only a change in size, but changes in form which are associated with formation of flowers and pods, and eventually, yield. These changes are the result of developmental processes such as stem elongation, flower bud differentiation, and pod growth. The processes are closely linked to growth, but are here considered independently for clarity. Rates of development are sensitive to photoperiod and temperature.

1. Germination:

During the drying phase associated with pod maturation, a bean seed enters a state of reduced metabolic activity characterized by changes in dehydration of cellular membranes and a severe reduction in respiration rate. This condition is maintained as long as the seed moisture content remains low. Upon contact with a medium of sufficiently high water availability, the seed imbibes water and respiration rates increases dramatically. Cultivars seem to vary in the proportion of water taken up through the micropyle or the raphe and hilum, while uptake through the seed coat is negligible (Korban *et al.*, 1981). Some bean seeds present a condition of "hard seededness" such that water uptake is extremely restricted. This appears to be due to a combination of factors including restrictions of the micropyle (Kyle and Randall, 1963). Austin and Mac Lean (1972b) noted that under cool (12°C) temperatures, large seeded cultivars germinate more rapidly than small seeded ones.

2. Vegetative Growth:

Although growth analysis (the use of sequential samples of crop dry weight and leaf area to describe crop growth) requires approximations inherent in considering the dry weight accumulation and

distribution as the sum of the various growth and developmental processes, such studies have proven useful in describing crop plastic response to environment and effects of differences among cultivars.

Table 3. Mean organ values for nitrogen for nine dry bean genotypes at four reproductive stages*, East Lansing.

Plant organ	Reproductive stage			
	Anthesis	Mid-pod elongation	Mid-seed filling	Physiological maturity
	-----g m ⁻² -----			
Root	.23 ab*	.28 a	.27 ab	.24 ab
Stem	1.50 ab	3.21 a	3.30 a	1.73 b
Petiole	.68 a	.76 a	.81 a	.26 b
Leaf blade	6.36 b	7.83 a	5.46 b	.87 c
Pod wall	-	-	5.60 a	2.64 b
Seed	-	-	5.16 b	13.10 a

* Means followed by the same letter in rows do not differ significantly Duncan multiple range test at 5%.

* Source: Izquierdo, 1981.

After seedling establishment, bean crops under non-stress conditions generally follow a near exponential growth phase until onset of rapid pod growth. Growth then slows, some crops reaching zero crop growth and then declining in weight, and others obtaining their maximum weight very near maturity (Figure 2).

Maximum crop growth rates (CGR) reported for bush beans range from 14 to 18 g m⁻².day⁻¹ (Table 4). Climbing beans on trellises have reached rates of 20 g m⁻², the greater rates presumably reflecting better canopy structure and less investment in support tissues. These values are less than half of values reported for other C₃ crops (Monteith, 1978).

Net assimilation rate (NAR, calculated as CGR/LAI) usually declines with crop age. Typical values during flowering are from 4 to 7 g m⁻².day⁻¹. High values of NAR may reflect compensation for restricted leaf area (e.g. due to a determinate growth habit) rather than high photosynthetic efficiency since NAR during flowering and LAD from emergence to onset of flowering may be negatively correlated among different cultivars (Figure 3).

LAI increases with crop growth, and as with CGR, often reaches a peak around time of onset of rapid pod growth, the halt in leaf production presumably reflecting increased demand for nitrogen in growing pods (Figure 2). LAI in determinate beans may stop increasing at a relatively early stage due to lack of nodes to produce additional leaves. Most bean crops undergo nearly complete leaf senescence before maturity, but some "non-senescent" crops do occur. At CIAT-Pamira, non-senescent crops usually involve cultivars with poor pod or seed set, thus the lack of senescence probably reflects weak sink demand. In temperate regions, such a pattern may involve problems of photoperiod-temperature adaptation, particularly slowed growth with cooler temperatures (Wallace,

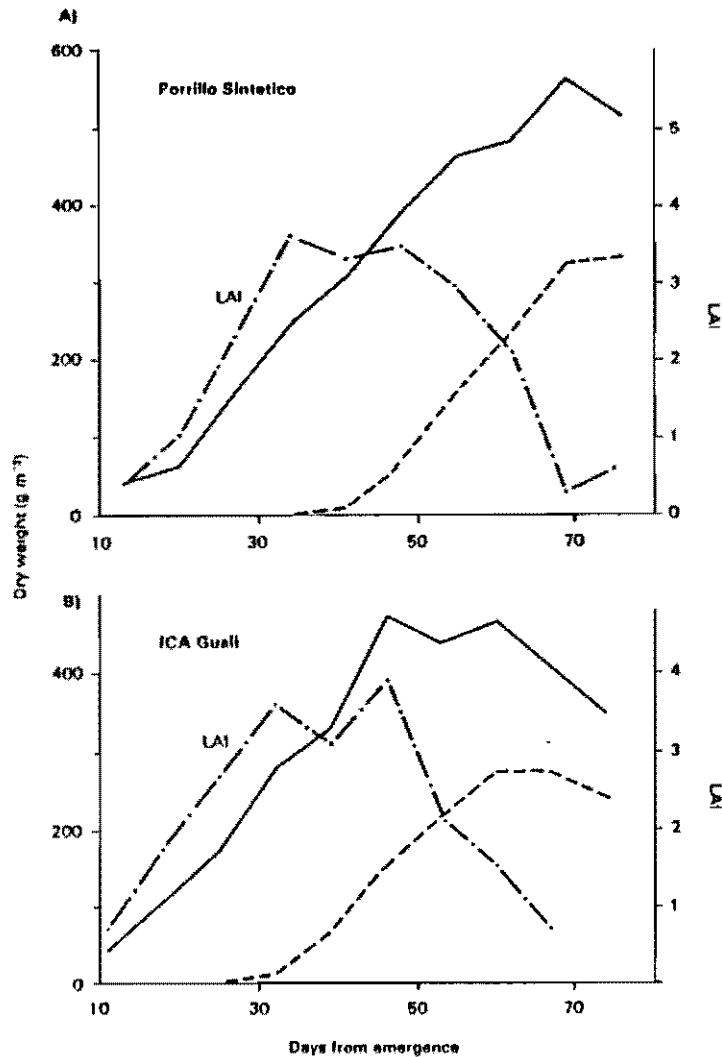


Fig. 2 Change in reproductive and total crop dry weights in relation to LAI in two bean cultivars: A) Porrillo Sintetico; B) ICA Guali.

Table 4. Reported maximum crop growth rates (CGR) and leaf area index leaf area index (LAI) at time of maximum CGR.

Cultivar	Growth habit *	Maximum CGR	LAI	Source
$g\ m^{-2}\ day^{-1}$				
Hawkesbury Wonder	-	18	5.0	Sale, 1974
Michoacan 12-A-3	3	17	5.0	Aguilar <i>et al.</i> , 1977
Porrillo Sintetico	2	14	3.2	Laing <i>et al.</i> , 1984
Porrillo Sintetico	2	17	3.3-4.4	CIAT, unpublished
JU 84-7	2	16	-	Rodriguez, 1986
Flor de Mayo X-16441	4	21	7.0-8.0	Fanjul <i>et al.</i> , 1982

* CIAT classification.

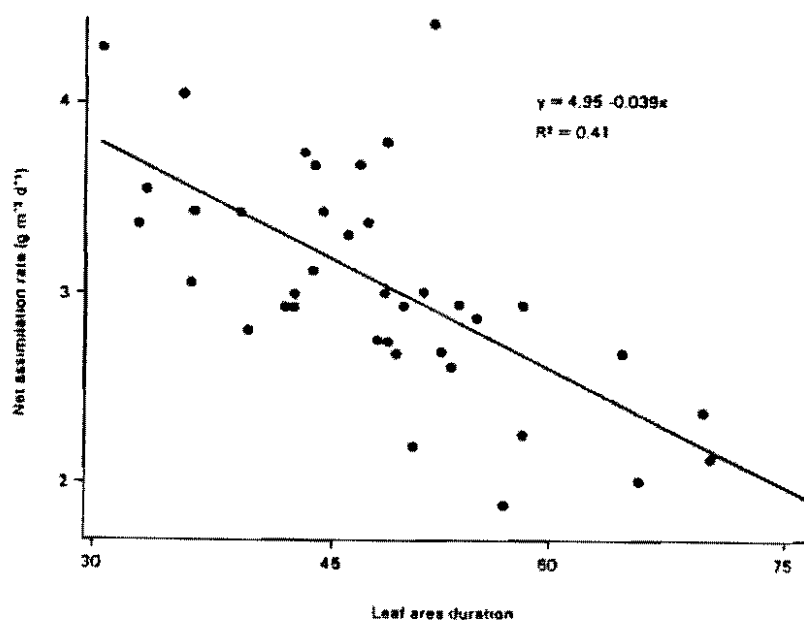


Fig. 3 Relation between leaf area duration from emergence to flowering and mean net assimilation rate from flowering to flowering plus 10 days for 38 bush bean lines. CIAT-Palmira, 1978.

Maximum LAI's are often in the range of 3 to 4 units. These are frequently below optimal LAI's estimated as LAI at maximum CGR (Table 5).

Table 5. Comparison of maximum LAI and optimal LAI calculated as LAI estimated maximum CGR for 11 sets of data for cv. Forrillo Sintetico at CIAT.

Maximum LAI	Optimal LAI	Yield
		g m ⁻²
3.1	3.0	219
3.3	3.1	227
3.1	2.8	277
3.4	4.8	277
2.0	2.2	295
3.0	3.7	298
3.4	2.6	312
3.5	5.1	347
4.1	3.3	355
2.7	2.6	365
4.6	5.4	412
Mean 3.2	3.5	308

Specific leaf area (SLA = leaf area/leaf dry weight) usually starts low, increases to a maximum around flowering, and then declines toward maturity (Figure 4). Determinate varieties often have comparatively high SLA, again presumably reflecting compensation for restricted LAI.

Under non-limiting conditions, main stem leaf initiation and expansion proceeds at near linear rates (Figure 5). Leaf initiation and expansion rates differ greatly among cultivars (Table 6). Flower initiation has been detected as early as 10 days after planting (Wallace, 1985).

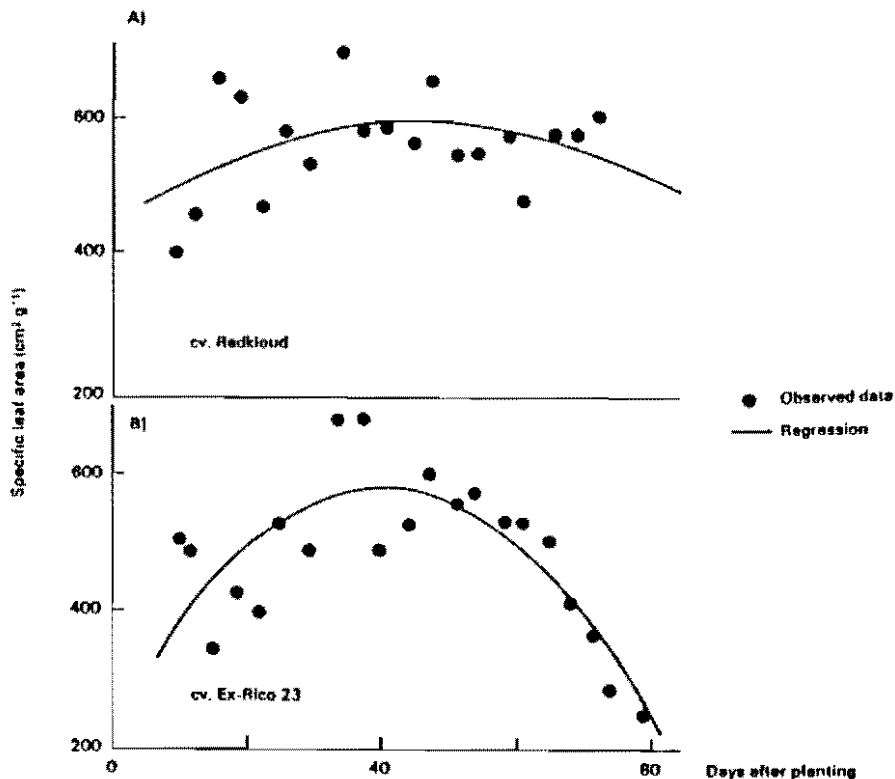


Fig. 4 Change in specific leaf area over time in two bean cultivars: A) Redcloud; B) Ex-Rico 23. Source : White, 1981

3. Reproductive Growth:

Beans usually self-pollinate. Patterns of flowering opening are well known. Anther dehiscence occur just before bud opening, usually at night. In *P. acutifolius* dehiscence is preceded by appearance of stigmatic secretions, composed primarily of carbohydrates and lipids, and the secretions rupture the stigma cuticle (Lord and Kohorn, 1986). Pollen tubes grows down the hollow style and fertilisation occurs within 12 hours, ovules nearest the style being fertilised first.

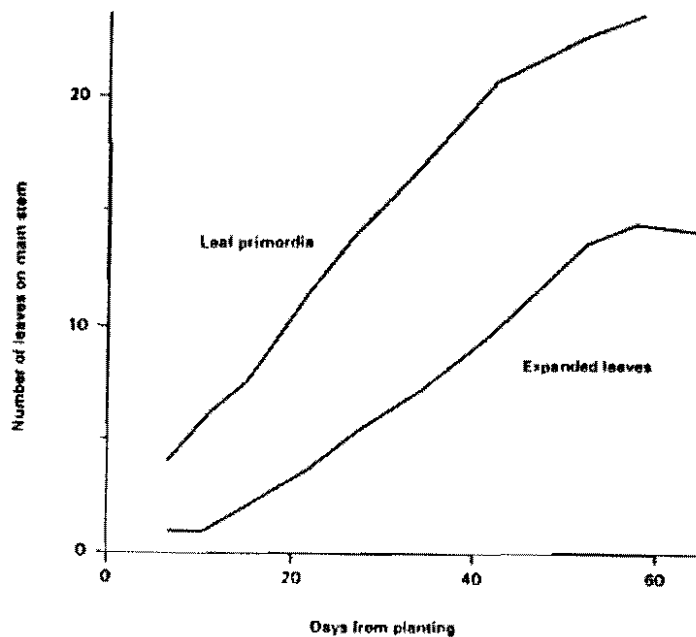


Fig. 5 Comparison of main stem leaf initiation and leaf expansion rates of cv. ICA Fijao grown under field conditions. CIAT-Palmira, 1977.

Table 6. Main stem leaf initiation and expansion rates for cultivars of differing growth habit. Palmira, 1977.

Cultivar	Habit	100	Leaf	Leaf
		seed	initiation	expansion
		weight	rate	rate
		mg	primordia day ⁻¹	leaves day ⁻¹
G 3807	I	18	0.45	0.30
G 4498	I	16	0.42	0.32
G 3816	I	60	0.20	0.21
G 1540	I	27	0.25	0.18
G 1995	II	18	0.54	0.32
G 3645	II	17	0.56	0.33
G 4495	II	15	0.48	0.27
G 4525	II	19	0.48	0.26
G 3046	III	22	0.50	0.33
G 2006	III	23	0.43	0.29
G 3353	III	27	0.50	0.32
G 4122	III	22	0.45	0.26
G 1093	IV	30	0.52	0.31
G 2327	IV	23	0.60	0.29
G 2540	IV	19	0.65	0.33
G 2525	IV	20	0.60	0.37
Mean			0.48	0.29

Overall pod growth patterns in legumes are reportedly so similar that they may all be summarized as involving three distinct phases: pod wall growth, seed growth, and desiccation (Dure, 1975). In bean pods reaching maturity 48 days after flower opening, maximum pod length was reached in 24 days, and pod fresh weight dropped only in the last 6 to 8 days, although seed weight continued to increase during the last phase (Oliker *et al.*, 1978). Figure 6 illustrates these events for black beans. The growth pattern of individual pods appears relatively insensitive to source-sink manipulations (Figure 7). As would be expected in a crop with such diversity in phenology and seeds size, pod development rate varies greatly among cultivars (Table 7), but is not strongly correlated with other variables (Table 8). Temporal changes of pod composition vary significantly among snap bean cultivars (Stark and Mahoney, 1942; Guyer and Kramer, 1952).

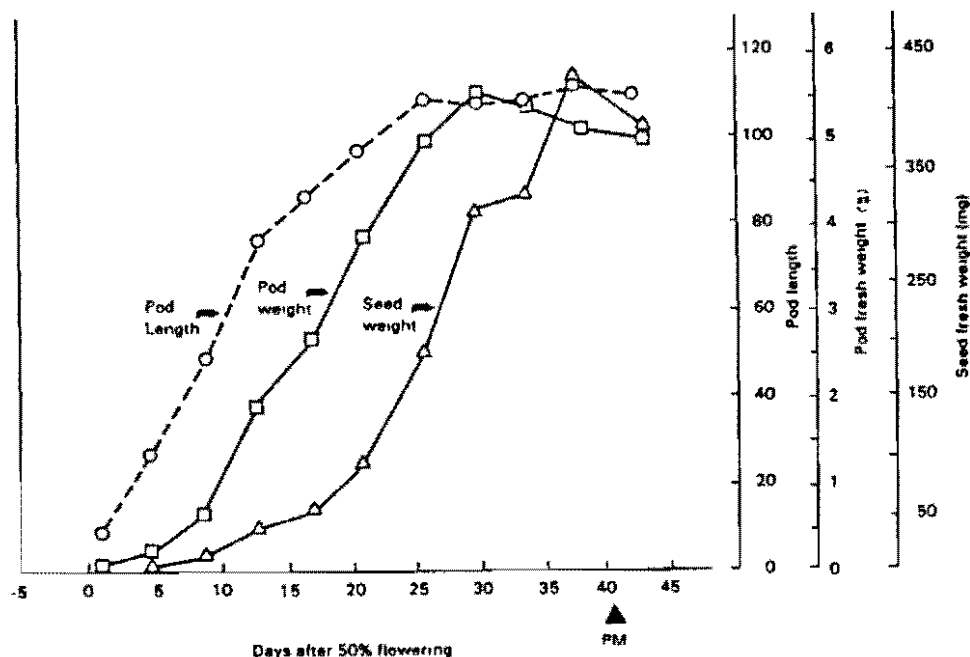


Fig. 6 Pod and seed growth of cv. "Black Turtle Soup" bean. Source: Izquierdo 1981.

Genetic differences exist within cultivars and breeding lines for both rate and duration of seed filling in rice (Jones *et al.*, 1979), soybeans (Kaplan and Koller, 1974), maize (Daynard *et al.*, 1971; Duncan, 1980; and Johnson and Tanner, 1972), and cowpea (Wien and Ackah, 1978). Several studies have shown that the duration of seed filling was more closely related to yield than was the rate of filling. Other works (Egli and Leggett, 1976; Sofield *et al.*, 1977) agreed that the rate of seed filling were related to cultivar differences in final grain weight. In beans, negative non-significant correlations between the linear filling rate and yield was reported by Izquierdo and Hosfield (1983). However, the same work, significant positive correlations were found between the linear filling duration and effective filling period to yield, number of seed per pod, seeds.m⁻², and 100 seed weight among cultivars and lines with differing architectural forms. Some correlation was found among linear filling duration and bean yields (Faredes 1986).

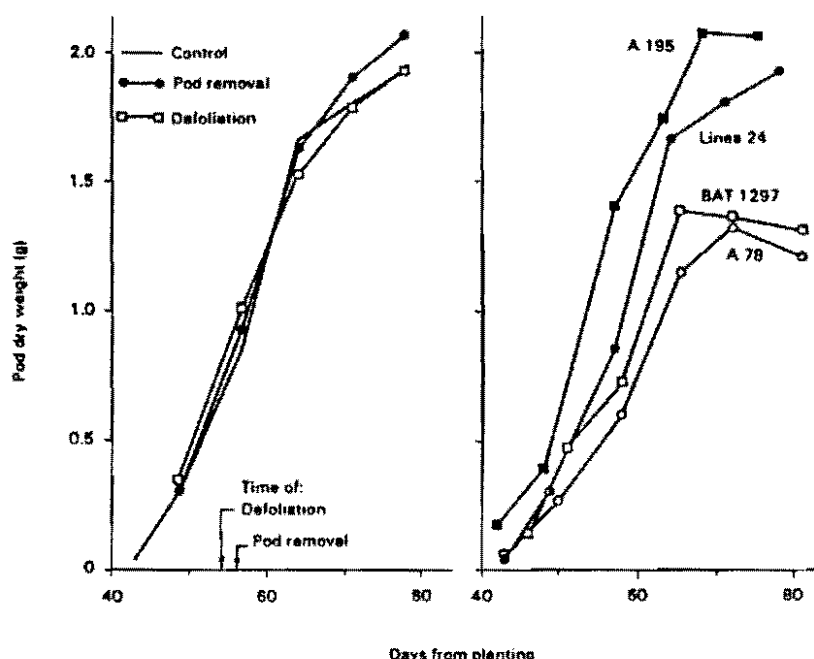


Fig. 7 Growth pattern of individual pods: A) as affected by defoliation and pod removal in line ICA Linea 24; B) under normal conditions for four bean lines.

Table 7. Yield, maximum pod growth rate, and other parameters of 20 lines. Palmira, 1985a.

Line	Yield	Days to flower.	Days to maturity	Daily yield	100 seed weight	Mean pod dry wt.	Pod growth rate
	$g\ m^{-2}$			$g\ day^{-1}$	g	$g\ pod^{-1}$	$g\ m^{-2}\ day^{-1}$
G 4495	2400	40	78	30.8	19.6	1.33	.0125
RAB 24	2370	42	82	29.1	21.0	1.04	.088
BAT 477	2360	45	77	30.6	20.0	1.16	.119
A 149	2350	48	84	27.8	36.3	1.30	.083
BAT 271	2290	42	81	27.8	19.1	1.21	.092
G 4000	2200	44	83	26.6	17.0	1.05	.097
G 5059	2190	40	80	27.4	19.2	1.13	.105
BAT 85	2020	42	79	25.6	20.0	1.26	.130
G 4446	1830	44	84	22.1	22.7	0.93	.091
A 54	1830	43	83	22.0	21.2	1.27	.106
G 13922	1820	45	82	22.2	38.9	1.44	.093
BAT 304	1810	37	70	25.7	14.3	1.04	.110
G 4498	1760	40	74	23.8	18.1	0.93	.078
BAT 41	1740	33	68	25.6	15.2	0.89	.094
G 3807	1650	31	71	23.5	14.4	0.72	.077
XAN 146	1570	38	73	21.6	22.5	1.04	.107
G 76	1510	38	70	21.6	39.4	1.39	.117
G 4494	1410	40	74	19.1	41.9	1.30	.102
G 3017	1110	38	58	19.0	14.8	0.79	.113
G 1540	850	36	68	12.2	17.1	0.78	.064
Mean	1850		76	24.2	22.6	1.10	.101
S.E.	150		1	2.0	3.3	0.12	.015

Considerable research has been done on aspects of bean seed growth related to seed biochemistry (Loewenberg, 1955; Carr and Skene, 1961; Sussex and Dale, 1979), but such works have shed little light on factors affecting overall pod growth and maturation.

Table B. Correlations among yield, pod growth rate, and other parameters measured in 20 lines. Palmira, 1985a.

	Yield	Days to maturity	Daily yield	100 seed weight	Pod weight
Days to maturity	.74**				
Yield/day	.95**	.50†			
100 seed wt.	-.03	.26	-.15		
Pod weight	.45†	.53†	.33	.71**	
Pod growth rate	.26	-.04	.37	.06	.50
Pod growth rate (excluding G 1540)	-.02	-.20	.08	-.02	.39

†, ** p < .05 and p < .01 respectively.

4. Senescence and Abscission:

After photosynthesis and respiration, the processes of senescence and abscission play the most important roles in determining plant growth. Any tissue may undergo senescence, and in stem borne tissues, especially leaflets, petioles, flower and pods, this process is usually accompanied by an apparently programmed pattern of abscission. However, the tissues where senescence appears to be of greatest importance are in leaves, flowers and pods. Hypotheses concerning the role of senescence and abscission usually follow three lines.

The most frequently cited hypothesis for legumes is that tissues which are at a disadvantage in competition among sources and sinks are eliminated, thus maintaining the overall efficiency of the plant. Leaves are dropped which no longer fix sufficient CO₂ (are too near the CO₂ compensation point). This might result from loss of N due to remobilization to growing pods, or leaves losing efficiency due to shading by leaves higher in the canopy.

Abnormal flower buds (Yañez *et al.*, 1984), and failures of pollination or fertilization can result in abortion of flowers and young pods. However, it has been reported that only one ovule needs to be fertilized to prevent pod abscission, and stress enhanced bean pod abscission was stated not to be caused by failure in fertilization (Harterlein *et al.*, 1980). This data is supported by findings in soybean reproductive shedding (Abernathy *et al.*, 1977; Wiedbold *et al.*, 1981). Studies of timing of bean flower and pod abscission have shown that pod abscission can continue up to 45 days after anthesis (Izquierdo and Hosfield, 1981b). It has been stated that older pods may drop if adequate carbon assimilate is not available (Tanaka and Fujita, 1979). Since legumes have a particular high nitrogen demand during podfill, senescence resulting from competition for N usually results in legume crops "self-destructing" (Sinclair and de Wit, 1976).

A second hypothesis is that senescence, defined by Leopold, (1980) as deteriorative processes conducive to plant death, is a programmed process of that occurs irregardless of the source-sink balance of the plant. This mechanism is most easily imagined as functioning in perennial plants in

the process might persist as a relictual characteristic in annual crops, having been reported in pea (Lockhart and Gottschall, 1961), bean (Wareing and Seth, 1967) and soybean (Lindoo and Noodén, 1977).

Such a process would still show relations with pod set if growing pods produced a senescence signal (which could be either an inhibitor or stimulator, depending on the pod growth stage).

The last group of hypotheses consider senescence as a physiological disorder triggered by imbalances of endogenous growth regulators. The reported rise in abscisic acid (ABA) levels during senescence makes ABA an attractive candidate as a general inducer of senescence, but not all studies support this. In the case of beans, widely varying levels of ABA were found during and before leaf senescence (Colquhoun and Hillman, 1975). On the other hand, if leaf senescence at maturity is triggered by ethylene production in maturing pods, rapid leaf fall might reflect nothing more than an excessive sensitivity of leaves to ethylene.

The strongest arguments for source-sink relations come from studies of effects of depodding and defoliation. Continual depodding, whether through artificial means or physiological stresses causing flower and pod drop, generally result in delayed leaf senescence (Tanaka and Fujita, 1979). The fact that senescence ultimately does occur (an observation used to support the second hypothesis; Noodén, 1980) may be ascribed to eventual depletion of nutrient reserves (particularly with artificial depodding), accumulation of diseases and pests, changes in agronomic conditions such as cooler temperatures or failures to maintain irrigation treatments, or deleterious effects of large accumulations of starch in leaves.

A second line of evidence comes from studies of carbohydrate and nitrogen remobilization and leaf photosynthetic rates, where patterns of senescence and relations between nitrogen content and AP are in full agreement with the idea that source sink balances determine patterns of senescence. Although the balance of evidence appears to favor a relation between source-sink balance and senescence, the question is far from resolved. Thimann (1980) and Noodén (1980) have written lengthy reviews defending other mechanisms.

C. Integration of Processes

1. Carbohydrate and Nitrogen Partitioning:

Studies on ^{14}C distribution in beans (Seth and Wareing, 1967; Lukas *et al.*, 1976; Tanaka and Fujita, 1979; Water *et al.*, 1980) have provided a fairly complete picture of qualitative patterns of carbohydrate distribution during crop growth. Young leaves are their own sink, incorporating all fixed carbon into leaf tissues, but as the leaf expands, up to 80% of fixed carbon may be exported from a leaf. As a leaf approaches senescence, exports fall with declining photosynthetic capability and increased respiratory costs. A source-sink unit has been defined, consisting of a leaf, any branch or raceme in the axil of the leaf, and the internode below. The degree to which this unit exports assimilate to other parts of the plant varies with growth habit, leaf position, and growth stage. Stephenson and Wilson (1977), studying soybean with ^{14}C analysis, showed that this unit was able to account for up to 70% of the assimilate distribution. This unit, initially termed a "nutritional unit" (Adams, 1967), was subsequently named the "phytoeric unit" (Adams, 1981) due to its great physiological significance in carbohydrate source-sink balance.

Although the phytoeric unit is a useful approximation, it simplifies differences among leaves. Lower leaves export a large proportion to roots, while leaves at the highest nodes of indeterminate plants export relatively large proportions to lower nodes. Removing racemes at one node results in greater exportation to adjacent nodes both above and below. Vegetative tissues can serve as sites of accumulation of assimilate reserves. Removing pods will augment reserves, while defoliation and water stress triggers assimilate and N remobilization (Izquierdo and Hernandez, 1984, unpublished; Table 9).

Table 9. Water stress and 33% defoliation* mean effects on dry matter N stem remobilization of sixteen black bean genotypes, Chillan. (Hernandez, 1984).

Treatment	Stem remobilization (-)*	
	Dry matter	Nitrogen
	g plant ⁻¹	mg g ⁻¹
33% defoliation	21.63	2.27
Drought	20.32	2.55
Control	18.86	1.83
Bayes LSD5%	-	0.42

* The water holding (drought) and 33% defoliation were applied at 50% flowering.

* Change in dry matter and N content at stems from 50% flowering to physiological maturity.

Studies on nitrogen distribution have not provided as complete a picture due to the lack of techniques as convenient as those used with ¹⁴C. However patterns of nitrogen accumulation and remobilization determined through analyses of tissue N suggest patterns similar to carbon with necessary differences due to N entering the plant through the roots, and to the relatively high N requirements of leaves and pods (Westerman *et al.*, 1985).

Basic patterns both of carbon and nitrogen distribution are probably identical to those found in other grain legumes (Shibles *et al.*, 1975; Pate, 1975), and are consistent with the idea that much of bean plant growth and development is regulated by competition among sources and sinks. The size, metabolic activity, and proximity of a sink to sources seem to be primary determinants of the ability of a given sink to compete among other sinks.

While this qualitative model is of great use in understanding crop growth, more quantitative data are needed to determine whether allocation processes limit bean yield. Adams *et al.* (1978) showed differences in accumulation of starch-like substances among different cultivars, but did not establish whether the differences were due to variability specifically related to remobilization, or to other factors such as overall plant vigour which could indirectly control the amount of assimilate available for remobilization. However the technique they used is appropriate only for very gross genotypic separation, and was found to have a low correlation with quantitative starch analyses (Izquierdo, *et al.*, 1985).

2. The Source-Sink Model:

Having reviewed the various component processes of bean crop growth and development, there remains the task of integrating the components into an overall model of how a bean plant functions. The most satisfactory model available assumes that basic processes are integrated by competition among sinks for limited resources, and that the relative proportions of resources allocated to different organs depends on what Brouwer (1963) described as "functional balance". Reduced availability of water or nutrients reduces partitioning to leaf growth, but increases partitioning to roots (Figure 8). Defoliation results in excess root capacity in relation to leaf area (too high a root to shoot ratio), and partitioning will favor leaf growth until the functional balance is

restored. Central to the model is the assumption that resources, usually carbohydrate or nitrogen, are limiting. However, this premise is not universally accepted, and the doubts merit discussion.

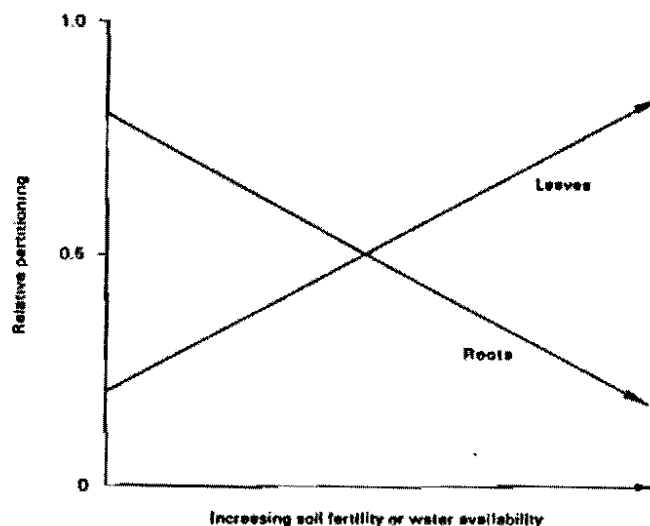


Fig. 8 Illustration of "functional balance" (Brouwer, 1963) between relative partitioning of growth in leaves or roots as affected by soil fertility or water availability.

Inhibition of photosynthesis due to insufficient sink strength is one argument. If this condition occurs, then it follows that resources are not limiting. Evidence for the effect comes primarily from experimental manipulations creating abrupt changes in source-sink relations (e.g. through depodding), so while sink limitation of photosynthesis may occur, one might argue that it is not a major factor under most field conditions. In opposition, up to 35 g m⁻² of unremobilized total nonstructural carbohydrates were found in stems of Type II beans in monoculture with a normal plant stand at physiological maturity (Izquierdo, 1981). This could indicate lack of use of available reserve resources due to small sink size and/or to delayed senescence with relatively high AP.

Another line of criticism comes from work primarily of Lambers (1979, 1982, and 1984) on cyanide resistant respiration. This respiration utilizes pathways independent of those mentioned previously, and seems to produce no products considered essential to growing crops. Indeed, its principal effects are a depletion of carbohydrate and generation of heat. The process appears widespread in plant species, and occurs in beans (Azcon-Bieto and Lambers, 1983). As Lambers (1983) has argued, such apparently "waste" respiratory activity is inconsistent with any theory assuming that resources are limiting. At the moment, perhaps the best arguments against this criticism are that models assuming limited resources are remarkably good at predicting crop growth (e.g. SOYGRD by Wilkerson *et al.*, 1983), and that research on cyanide resistant respiration is sufficiently new and the techniques involved are difficult enough that its function may remain to be discovered.

A third line of criticism stems from findings that roots can release large amounts of carbohydrates and amino acids into the soil where they stimulate microbial activity (Russell, 1977). Under conditions of nutrient stress or in the presence of soil pathogens, such activity might benefit the plant via stimulation of beneficial organisms such as mycorrhizal fungi or bacteria which inhibit pathogens. However, conditions might occur where such secretions would serve no function.

III. YIELD POTENTIAL

A. Introduction

Maximum yields for bush beans are on the order of 5 to 6 ton ha⁻¹ (Table 10). Occasional reports of higher yields are found, but are usually attributable to small plot sizes with strong border effects. Climbing beans on trellises have yielded 8 tons ha⁻¹ (Fanjul *et al.*, 1982), but comparisons with bush beans are of limited meaning since trellises eliminate lodging while reducing the need for allocation of assimilate to tissues for mechanical support. Although yields of 5 to 6 ton ha⁻¹ are impressive (over 10 times the mean yield in Latin America), they are so infrequently obtained that considerable research has gone into finding ways to maximize yields in beans.

Table 10. Maximum bush bean experimental yields reported from the Bean International Yield and Adaptation Nurseries, 1976-1984.

Year	Location	Variety	Yield	Crop duration
			kg ha ⁻¹	days ⁻¹
1976	Santiago, Chile	Puebla 158	3705	113
1977	Graneros, Chile	Pinto Dorado	5500	94
1978	Graneros, Chile	ICA Pijao	4400	95
1979	Palмира, Colombia	BAT 85	4600	75
1980	Graneros, Chile	Jamapa	4400	-
1981	Graneros, Chile	BAT 58	5100	101
1982	Graneros, Chile	Jamapa	4900	90
1983	Graneros, Chile	XAN 109	5000	93
1984	Popayan, Colombia	ZAV 8306	5100	108

Work on "yield potential", as it is termed, generally assumes that for a given climatic regime, soil fertility and water availability are managed to provide good growing conditions, and that effects of pests and diseases are minimal, if not completely absent. Theoretically, agronomic practices should be "optimal", but since this might include use of CO₂ fertilization, supplementary radiation, or artificial supports, most researchers have studied yield potential in the context of existing cropping systems, either for bush or climbing beans. We follow this precedent, emphasizing bush beans in monoculture, but not assuming limitations on practices such as plant density, row spacing, irrigation, and fertilizer applications.

1. Estimates of Yield Potential:

As mentioned above, maximum yields for beans (Table 10) provide one estimate of yield potential in beans. Yields of over 5 ton ha⁻¹ from IBYAN's in Chile illustrate the importance of considering production environment. The Graneros site has fertile soil, high radiation (little cloud cover, and daylight of up to 15 hours at its 34°S latitude), cool nights (10°C to 13°C minimum), and little disease or pest pressure. Photoperiod effects may provide additional benefits, since long days delay flowering and maturity. While high yields can be obtained in beans, one should not expect that a tropical site with longer, warmer nights, lower radiation, and a myriad of other problems will yield over 6 ton ha⁻¹.

Considering maximum yields of other legume crops (Table 11), bean yields are similar on a per day basis. Data for non-legume crops suggest a considerable "yield gap" (Table 11).

Various indirect estimates of bean yield potential are available. Assuming that greater lodging resistance and delayed maturity are obtainable, yields of climbing beans might approximate the potential of bush beans. Flowering and maturity have been delayed in Forrillo Sintetico through use of photoperiod effects provided by a gradient of artificial light giving a 18 hour photoperiod. Yields increased 48 kg ha⁻¹ for each day of delay in maturity (Table 12).

Studies of heterosis effects might provide another source of estimates. Gutierrez and Singh (1985) obtained F1 yields 28% to 47% over percent the mid-parent value, but no cross yielded significantly better than the best parent.

Table 11. Estimates of yield potential of grain legumes and other crops.

Crop	Yield (kg/ha)	Crop duration (days)	Reference
Legumes			
Chickpea	4000		Saxena, 1984
Cowpea	4200		Wien and Summerfield, 1984
Groundnut	5900		Ashley, 1984
Pigeonpea	4500	110	Sheldrake, 1984
Soybean	5600		Shibles <i>et al.</i> , 1975
Non-legumes			
Corn	12000	132	Milthorpe and Moorby, 1979
Rice	12000	190	Milthorpe and Moorby, 1979
Sorghum	7300		Miller and Kebede, 1984
Wheat	14100		Evans <i>et al.</i> , 1975
Potato	19000		Milthorpe and Moorby, 1979
(tuber dry wt.)			
Sugar beat	29000	300	Milthorpe and Moorby, 1979

Cruder estimates of yield potential come from studies of flower and pod abscission. For a crop producing 250 pod m⁻², each pod containing 1.2 g of seed (6 seeds weighting 200 mg each), a 20% increase in pod set with no change in yield pod⁻¹ must, by simple algebra, give a yield increase of 20%, from 3 to 3.6 ton ha⁻¹. Considering that flower and pod abortion rates are frequently on the order of 60% to 80%, yield potential would be around 5.4 ton ha⁻¹. Further details and data on estimates of yield potential considering reproductive abscission are discussed under the topic of increasing sink strength as a strategy to increase seed yield.

Before reviewing strategies for yield potential, the role of agronomic management merits attention. Although proposals usually assume "near optimal" agronomic conditions, one may question whether present agronomic practices truly approach those needed to obtain maximum yield. If four independent factors (e.g. planting density, water management, fertilizer applications and soil compaction) are at 95% of their optimum, this results in a 19% yield reduction (100(1 - .95⁴)), enough to reduce a hypothetical potential of 6 ton ha⁻¹ to 4.6 ton ha⁻¹.

Table 12. Yield of cv. Porrillo Sintetico under four photoperiod regimes provided by a gradient of light intensity given an 18 hour photoperiod. CIAT-Palmira.

Distance from lamps	Days to flower	Days to maturity	Seed yield	Total biomass	LAD
			-----kg ha ⁻¹ -----		
3	51	95	4100	7000	23
9	43	84	3500	5600	16
15	36	71	3000	4700	12
21	36	69	2800	4100	11

B. Yield Potential vs Agronomic Management

Before reviewing strategies for yield potential, the role of agronomic management merits attention. Although proposals usually assume "near optimal" agronomic conditions, one may question whether present agronomic practices truly approach those needed to obtain maximum yield. If four independent factors (e.g. planting density, water management, fertilizer applications and soil compaction) are at 95% of their optimum, this results in a 19% yield reduction ($100(1 - .95^4)$), enough to reduce a hypothetical potential of 6 ton ha⁻¹ to 4.6 ton ha⁻¹.

C. Physiological Strategies for Increasing Yield

In the discussions that follow, specific strategies for increasing yield potential are reviewed, starting with strategies for increasing source and sink capacities. As a conclusion, the authors propose an ideotype for maximum yield. The problems of earliness and seed size, and for some unconventional strategies are also discussed.

1. Source Limitations:

Many strategies are based on the assumption that increasing yield potential requires an increase in source size. Support comes from the observation that in comparisons of varieties, greater yield is closely associated with greater growth, whether measured as crop dry weight, leaf area duration, or other size parameters (Table 13). Reductions of yield under shading (Escalante, 1980) and yield increases with CO₂ fertilization (Laing, *et al.*, 1984) also support the assumption that source size limits yield.

The simplest strategy for increasing source strength is simply to increase the length of the growth cycle. In varietal trials managed for high yields in tropical areas, yield is usually correlated with time to maturity (Table 13).

Table 13. Correlations of yield with harvest index, biomass, days to maturity and leaf area duration from various studies.

Trial	Harvest index	Biomass	Days to matur.	Leaf area durat.	Source
10 lines					
Habits 1 and 2	.51	.94**	.75**	.88**	White, 1981
38 lines					
Habits 1,2, and 3	.46**	.87**	.41**	.42**	White, 1981
Porrillo Sintetico					
12 experiments	.28	.96**	.85**	.87**	Laing <i>et al.</i> , 1984
9 species of grain legumes	.50	.91**	.86**	.93**	Laing <i>et al.</i> , 1984

Length of growth cycle

Table 14. Seed yields of 8 lines grown under 3 daylengths, with and without trellises. Palmira, 1985b.

Cultivar	Day length (hr)		
	12.5	13.5	14.5
	-----kg ha ⁻¹ -----		
	NO TRELLISES		
JU 78-12	2185	1985	1692
G 17648	1550	1236	873
BAT 450	2338	2439	2413
JU 80-13	2046	2225	2154
DOR 49	2335	2398	2649
XAN 112	2038	1686	2041
G 2959	2333	2307	2178
G 3807	1590	1785	1992
Mean	2052	2008	1999
	WITH TRELLISES		
JU 78-12	2694	3200	3168
G 17648	1882	2913	1556
BAT 450	2324	2598	2190
JU 80-13	2073	2121	2444
DOR 49	2304	2381	2841
XAN 112	2043	2106	2446
G 2059	1912	2800	2538
G 3807	1731	1562	2144
Mean	2115	2460	2416

The previously mentioned work with photoperiod treatments to delay maturity demonstrated this as did a yield trial of 6 lines grown under 3 photoperiod regimes (Table 14). Wallace (1985), reported that at higher latitudes, yield is negatively correlated with lateness, apparently because late materials mature poorly as a result of growth limitations with cooler temperatures. Although there has been considerable work done on genetic control of time to flowering and maturity (Wallace, 1985), and there have been efforts to select for late maturing lines, expected yield increases have not been obtained. A major problem has been that selection for lateness resulted in selection of materials which are late because of poor photoperiod-temperature adaptation, not greater vigor or source capacity.

Photosynthesis

Another strategy for increasing source capacity is to increase the photosynthetic capacity of the crop. As in most crops, consistent positive correlations between supposed maximum photosynthetic rates and yield have not been found (Kueneman *et al.*, 1979). This failure probably results from interactions of factors determining the efficiency of photosynthesis at the crop level. Comparisons of photosynthetic rates in 20 lines of mung bean (Chandra, *et al.*, 1985) supported this assumption. While maximum rates were not correlated with yield, rates during podfilling (which were only 50 to 60% of maximum rates) had a correlation of 0.66 with yield (significant at the 0.01 probability level). Given that photosynthesis rates during pod filling usually decline rapidly due to nitrogen remobilization from leaves to pods, the most critical problem relating photosynthesis to yield potential may be nitrogen partitioning during reproductive growth, as discussed later.

Respiration

Reducing respiration implies both a direct increase in availability of assimilate, and a possible indirect increase through higher optimal LAI. Assuming that growth respiration depends on plant composition, selection for decreased growth respiration would probably prove difficult, and might result in lower protein content in seeds. Selection for low maintenance respiration appears more promising. Work in perennial ryegrass and fescue (Wilson and Jones, 1982; Volenec, *et al.*, 1984) have resulted in successful identification of lines with reduced respiration in warm temperatures, and these differences were associated with increased yields. Gifford and Evans (1981), in a review of relations among photosynthesis and partitioning, concluded that such results represent the only known cases where selection for a photosynthetic or respiratory characteristic were successfully related to yield. However, to date, research on respiration costs has received minimal attention as compared to photosynthesis.

In beans, as in other crops, considerable effort has been expended in identifying lines combining reduced photorespiration and greater yield, (Wallace, *et al.*, 1976). Results have been negative, supporting the conclusion that photorespiration is an unavoidable consequence of increased O₂ concentrations in the presence of RBP-carboxylase (Powles and Osmond, 1979; Tolbert, 1980).

Light utilization

Since crop photosynthetic rates depend on light interception patterns, yield potential should vary with canopy structure. The relatively horizontal leaf orientation detected in studies of light interception in bean canopies imply loss of efficiency due to excessive illumination of upper leaves and shading of lower ones. As in many other crops, ideotypes for beans often suggest selecting for more erect leaf orientation. Wien and Wallace (1973) and Sato and Gotoh (1979 and 1983) detected varietal differences in leaflet movements, but the results were not extended to effects on canopy structure.

Simple geometric arguments suggest that for a given LAI, both smaller leaves and greater vertical separation of leaves will result in better penetration of light in the canopy (Loomis and Williams,

1969). Reducing leaf size should not prove problematic, but the Principle of Similitude (Thompson, 1942) dictates that the taller the plant, an increasingly great amount of resources must be invested in tissues with support functions (e.g. in stems and petioles). One concludes that for a given set of growth conditions, there is an optimal bean plant height. Quantitative estimates of optima are lacking, but in cereals reduced plant height has been associated with higher yields (Chandler, 1967).

Lodging is commonly seen in bush beans, and often reduces plant growth severely (Fig. 9). Some of the damage is usually attributable to mechanical damage and subsequent disease infections, but loss of plant height reduces efficiency of light interception. Thus, lodging resistance is another mechanism for photosynthetic efficiency. Although, use of trellises can reduce plant partitioning for support tissues, freeing additional assimilate for pod growth, it is instructive to consider data for yields with and without artificial supports in relation to other experimental manipulations. Delayed maturity through photoperiod extension resulted in increased yields when trellises were provided, but the yield effect was not detected in plots without support. Stofella *et al.* (1979) reported morphological variation in roots strongly associated with lodging resistance and seed yield in black bean lines, indicating that a larger root size may reduce lodging and increase seed yield.

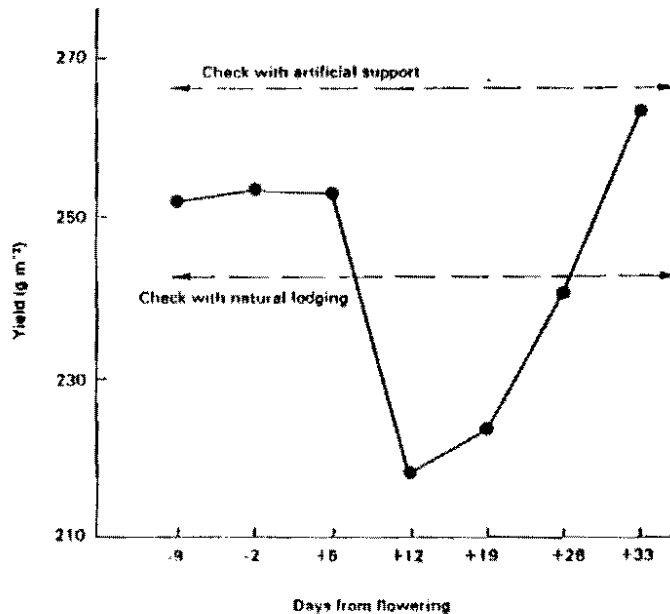


Fig. 9 Effect of artificial lodging at different dates from flowering on seed yield of cv. Porrillo Sintetico. Lodging produced by rolling a bamboo pole over the crop. CIAT-Palmira, 1975.

Higher maximum LAI is not necessarily beneficial since greater leaf area alone results in greater respiratory costs and a reduction in light intensities in the lower canopy. However, if respiration is reduced or efficiency of light interception improved, greater maximum LAI's would be beneficial.

Increasing LAD is desirable if achieved without exceeding optimal LAI, but achieving higher LAD's seems difficult. Agronomic practices favoring rapid canopy establishment (narrower row spacings and higher plant populations) might help. Another possibility is to reduce the rate of leaf senescence during pod filling. Supposedly non-senescent bean lines are known, but their yields are low enough that this characteristic was probably achieved through reduced reproductive growth.

2. Sink Limitations:

Although most studies on the relative importance of source and sink strengths in determining yield potential conclude that source limitations are more important, possible sink limitations, most notably "excess" flower abortion, are often reported. Furthermore, sink inhibition of photosynthesis would make source strength appear limiting while actually resulting from insufficient sink strength.

Possible causes of low sink strength may be classed as either insufficient numbers of sinks or low strength of individual sinks.

Flower, seed and pod abortion

Fruit setting and pod retention proceeds acropetally in legumes. Abscission of flowers or small pods occurs on practically every raceme of the plant. There is evidence that the basal and older pods regulate the abscission of new flowers and small pods in several species of grain legume. This has been substantiated in cowpea (Djehomon, 1972), lupin (Van Steveninck, 1957), lima bean (Cordner, 1933), faba bean (Jaquier and Keller, 1980), soybean (Wiebold *et al.*, 1981), pigeon pea (Ariyanayagan, 1980), and dry bean (Subhadrabandhu, 1976 and Tamas, 1976).

The abscission of reproductive organs during flowering and fruiting period in the grain legumes is often greater than 50%. Binkley (1932) showed shedding of flowers of six garden bean up to 76% while a range of 42% to 54% of reproductive abscission on nine genotypes comprising four differing plant architectures were found (Izquierdo, 1981a). Pod drop accounted for up to 82% of the total reproductive structures abscised, with the shedding of small pods less than 10 mm in length accounting for most of this (Izquierdo, 1981b).

Several lines of evidence suggest that if the shedding of reproductive parts in beans could be prevented or decreased, the yields might be increased (Subhadrabandhu *et al.*, 1978 and Tucker *et al.*, 1975). A bean yield potential up to 6200 kg ha⁻¹ has been estimated if the yield loss due to abscission was added to the actual yield (Table 15). Patterns and rates of flower and pod shedding significantly differed among genotypes with contrasting plant architecture and growth habit (Figure 10). Since pods abscised at such an early stage of development one might suggest that the lack of fertilization is mainly responsible for abscission but evidence is contradictory. Yañez and coworkers (1984) found that flower buds with a high probability of abscising showed a wide range of abnormalities including large numbers of ovules with necrosis and 15% of buds lacking the embryo sac.

Most researchers have assumed that self pollination proceeds at a high enough rate in beans that pollination is not a limiting factor, but the fact that pollination does occur in the absence of pollinators does not establish that it is of sufficient efficiency to maximize yield potential. Artificial tripping of bean flowers, which mimics the effect of bee visits, have increased seed set per pod and number of pods per inflorescence, but effect varies with genotype and season (Table 16). This variation probably explains why artificial manipulations resulted in yield increases in some, but not all lines when flowers opening in the first 7 days after flowering were artificially tripped (Table 17). Unfortunately, these results still do not establish that pollination limits yield potential. Inefficiency of pollination may be a character of lines with low yield potential, while the highest yielding materials already achieve sufficient pollination.

Halterlein *et al.* (1980) stated that only one fertilized ovule was needed to prevent pod drop. Fechan and Webster (1986) also found that abscission occurred primarily in fertilised flowers of Red Kidney beans. And similar results have been found in soybean (Abernathy *et al.*, 1977; Wiebold *et al.*, 1981).

Table 15. Estimated losses in yield due to abscission, actual yields yield potential of nine dry bean entries comprising four architectural forms, East Lansing, 1981.

Architectural form and entry	Estimated	Actual yield	Yield potential ^y
	yield loss due to abscission ^x		
-----kg ha ⁻¹ -----			
Archetype			
61380	2661	3577 a*	6239
61356	3185	3076 ab	6262
61618	3188	2949 b	6137
Classic II			
BTS	2904	2589 bcd	5494
Nep-2	2798	2845 b	5644
Small bush			
Seafarer	3496	2569 bcd	5066
Sanilac	3443	1823 e	5266
Tuscola	3822	2162 de	4984
Erect small bush			
C-14	3027	2366 cd	5394

* (reproductive abscission/m²) . (seed/pod) . (seed weight).

^y Yield potential = Estimated yield loss due to abscission + actual yield.

* Mean separation in columns by Duncan's range test, 5%.

Source: Izquierdo, 1981.

Perhaps the best way to reconcile these different reports is to assume that causes of abscission vary greatly with growing conditions and cultivar. Abscission may result from water stress or from competition among developing pods for nitrogen, other nutrients and carbohydrates. Another cause of abscission is probably related to hormonal regulation of abscission of younger developing structures in a raceme, mainly by the older fruit. Regulatory control also could be exerted through hormone availability, hormone balance or hormone inhibition of assimilate mobilization to developing seeds. Differences between bean cultivars for ethylene production by reproductive structures has been reported (Izquierdo and Hosfield, 1980) and related to levels of reproductive abscission. El-Beltagy and Hall (1975) suggested ethylene as the cause of abscission in broad beans, and specific response to ethylene by target cells located at pod peduncles has been described (Osborne, 1977 and Webster, 1975).

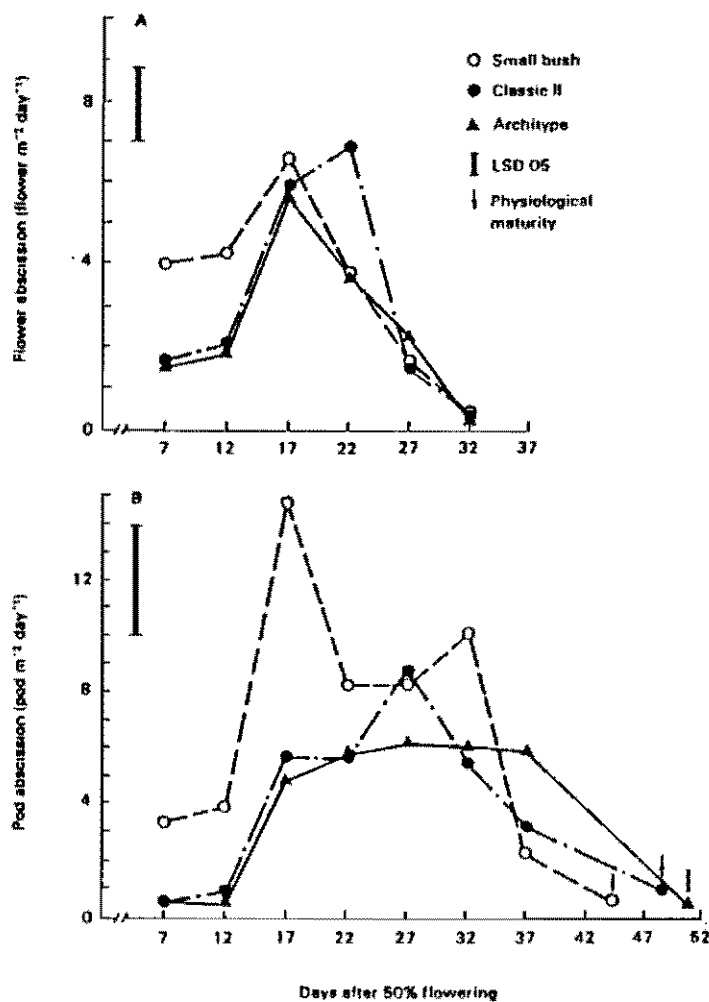


Fig. 10 Patterns and mean rates of reproductive abscission (Flowers:a and pods:b) of dry bean genotypes with differing plant architecture and growth habit. Small bush: cvs. "Seafarer", "Sanilac" and "Tuscola" (navies, growth habit I); classic II: cvs. "Black Turtle Soup" and "Nep-1" (growth habit II); and archetypes (erect, reduced branching and narrow profile canopy): breeding lines 61380, 61356, and 61618 (growth habit II). Source: Izquierdo, 1981.

Table 16. Effect of artificial tripping of bean flowers on pod and seed set in ten bean cultivars. Palmira, 1984.

	Pods/Inflorescence		Seeds/Pod	
	Control	Tripped	Control	Tripped
A 120	1.30	0.75	4.2	4.4
A 200	1.31	1.22	4.9	4.6
A 227	0.84	0.93	3.1	4.1
A 429	0.87	1.68	4.5	4.8
A 463	0.32	0.55	2.8	6.4
A 488	0.22	0.41	5.0	5.9
BAT 202	0.14	0.37	2.9	3.8
BAT 1061	1.42	1.70	5.9	5.8
BAT 1281	0.96	0.92	5.0	5.0
BAT 1670	0.98	0.87	2.9	2.5
Mean	0.84	0.94	4.1	4.7

Table 17. Effect of artificial tripping of bean flowers on seed yield four cultivars. Palmira, 1985.

Cultivar	Yield		Seeds Pod ⁻¹		Pods m ⁻²	
	Control	Tripped	Control	Tripped	Control	Tripped
	----ton ha ⁻¹ ----					
BAT 477	2.43	2.45	5.4	5.4	210	250
BAY 1481	2.51	2.89	5.3	6.2	280	260
Calima	1.36	1.57	2.0	2.0	95	103
G 1540	1.40	1.39	4.2	4.1	164	191
F Treatment	7.8†		0.9		1.2	
Cultivar x Trt.	2.9		1.2		0.8	

† Significant at p = 0.5 level

Another explanation for poor pod set assumes that the other organs or older pods are competing successfully with the flowers and small pods for assimilate. Wiebold (1981) speculated that increased abscission in canopy regions receiving low irradiance might be a consequence of non-availability of photosynthates in soybean racemes. Localized competition among older and younger developing pods, at each bean "phytomecric unit" could cause a localized abscission. Carbohydrate availability and level were studied as regulatory agents in abscission. Subhradrabandhu (1976) reported that carbon dioxide enrichment and long days during the reproductive phase decreased pod abscission due to a high accumulation of carbohydrates in the stems of the cv. "Black Turtle Soup". Higher IKI-starch score values have been associated with higher pod retention and yield of cvs. Nep-2 and Black Turtle Soup than the navy cv. "Tuscola" (Izquierdo *et al.*, 1980).

In the same line, a model based on vascular limitations has been postulated for pigeon peas (Rawson and Constable, 1981). This explanation assumes that the carbon-assimilates can not be moved to the flowers and small pods rapidly enough because the vascular system of the pedicel is not fully operational. Axillary flowers with short pedicles and a large cross section with large leaves close to the sink could increase the potential yield by reducing the resistance to the movement of assimilates. In wheat, phloem capacity appeared to be quite plastic, different species varying 10-fold in cross-sectional area of phloem. The variation was associated with sink strength, thus leading to the conclusion that translocation was probably not limiting (Evans *et al.*, 1970). However, measurements of translocation rates are difficult to make, and the problem has not been resolved (Evans, 1975).

Emphasis is usually given to losses in sink strength due to flower and pod abscission, but abortion of individual ovules or developing embryos would also reduce sink strength. Unfortunately, data on embryo abortion is rare since determination of ovule numbers requires tedious dissections of individual ovaries. Table 18 compares number of seeds per pod at harvest, and the maximum number of seeds per pod found in the harvest sample. Assuming ovule number indicates potential seed number, a 20% or more loss in yield potential could be ascribed to embryo abortion. But again, it remains to be demonstrated whether such abortion reflects defects in development, or is simply due to insufficient assimilate.

Table 18. Embryo abortion rate, mean and maximum number of seeds per mean number of ovules per pod and seed weight in 5 lines (from White, 1981).

Line	Embryo ¹ abortion rate	Mean No. seeds/pod	Maximum No. seeds/pod	Mean ovules/pod	Seed weight mg
G 122	44%	3.5	6	6.3	290
G 1540	42%	3.1	5.8	5.3	270
G 6729	41%	2.3	4.8	3.9	440
G 4495	27%	5.9	8.5	8.1	180
G 4459	46%	4.0	7.3	7.4	120

¹ Calculated as 100(1 - seeds per pod/ovules per pod)

Pod growth rates

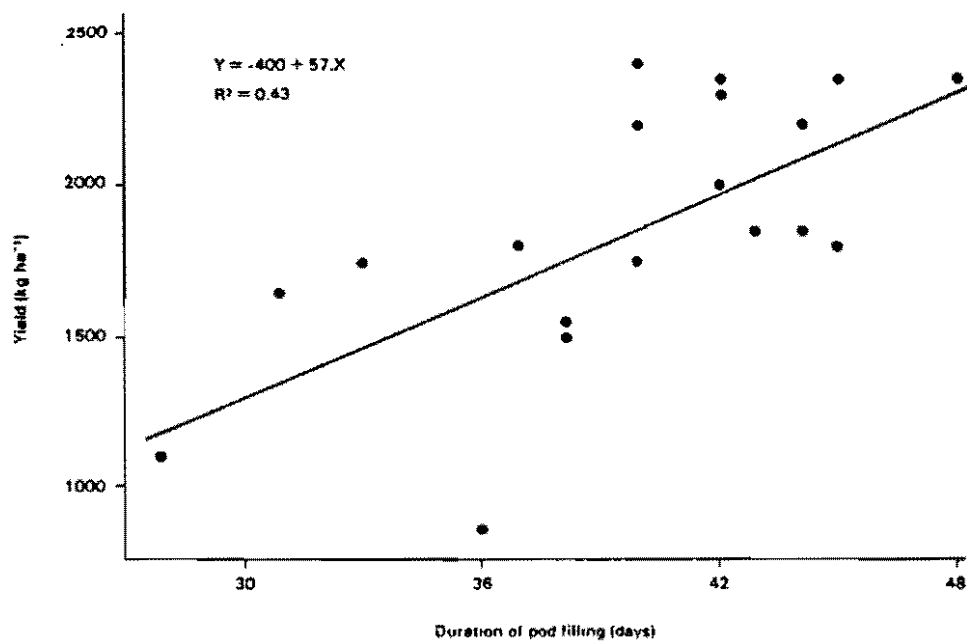


Fig. 11 Relation between seed yield and duration of pod filling in 20 bean lines. CIAT-Falmira, 1984.

In addition to effects on number of sinks, low strength of individual sinks might limit yield. If this were true, pod growth rate might be correlated with yield. For 19 bean cultivars, maximum pod growth rate was only slightly correlated with yield (Fig. 11). As discussed in the introduction to the section on yield potential the results only demonstrate a relation, not cause and effect. Pod or seed growth rates and duration may reflect availability of assimilate as much as sink strength. However, if this were the case, treatments which alter the source-sink balance, such as depodding and defoliation, should alter pod growth rates. Pod growth patterns under such treatments are very similar as compared to differences among cultivars (Figure 7), supporting the possibility of sink strength effects. When the pod elongation rate of 25 lines within an international replicated trial for drought tolerance (BIDYT-CIAT) was measured, both under post-flowering unirrigated (stress) and irrigated conditions, a reduction up to 17% in the linear elongation rate was observed (8.96 irrigated and 7.47 mm day⁻¹ under stress) (Izquierdo and Huepe, 1986, unpublished).

Harvest index

If sink strength is limiting, one would expect a relatively large proportion of crop weight at maturity as vegetative growth instead of seed yield. To evaluate this possibility, a "harvest index" is usually calculated as:

$$HI = \text{Seed yield} / \text{Biological yield},$$

where biological yield is simply total crop dry weight at maturity. While yield increases in many crops have been linked to increased harvest index (Wallace *et al.*, 1972), data showing correlations among yield and harvest index must be judged with caution if not complete skepticism. Since harvest index is calculated in part from yield data, any correlation will include this artifact and be artificially inflated (Charles-Ewards, 1982). Simply using pairs of random numbers to calculate artificial values of harvest index, one can generate highly significant correlations. Calculating values representative for beans, a mean harvest index of 0.58 and mean "yields" of 2.0 tons ha⁻¹ generated with random numbers, 20 pairs of data gave a correlation of $r^2 = 0.77$ (Figure 12).

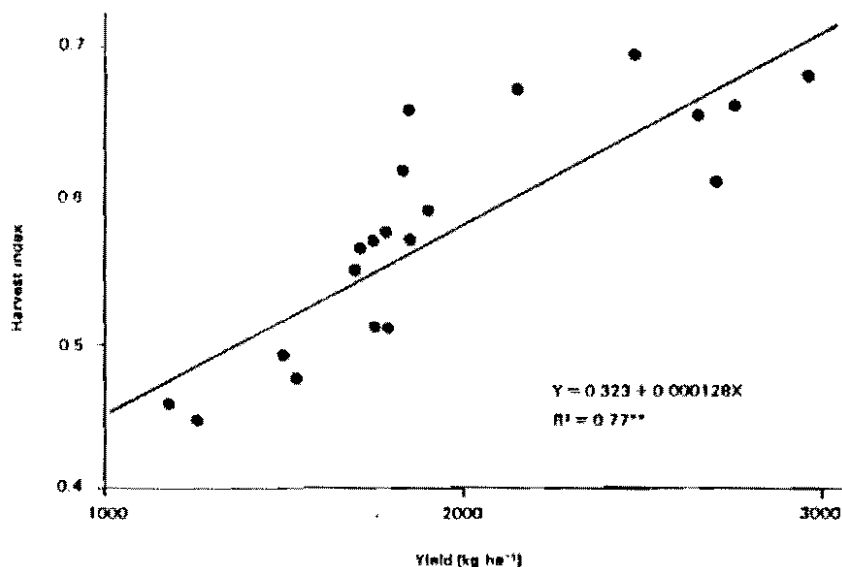


Fig. 12 Artificial correlation of yield and harvest index calculated from pairs of random numbers.

Adding to the problem of interpreting harvest index values in beans is that varietal differences in defoliation and stem senescence during maturation of beans make it difficult to decide which tissues to include in a sample. Difficulties are also encountered in deciding when to sample, and how to manage the sample subsequently. Harvesting at a single date will inflate values of early

maturing lines. Permitting samples to air dry after harvest might result in reduced differences since respiration can continue to cause weight loss.

To cope with some limitations due to cultivar differences in leaf abscission at maturity a modified harvest index (Kohashi-Shibata and da Costa, 1980) has been proposed as: $mHI = \text{seed yield} / \text{total cumulative biological yield at physiological maturity} + \text{dry weight of abscised organs (flowers, pods and leaves)}$. The collection receptable for field abscission studies described by Izquierdo and Hosfield (1982) is well suited for obtaining the dry weight of abscised components. Fig. 13 shows a highly significant correlation between the mHI and final yield, although this result is also an artifact.

Masaya (personal communication) compared harvest index to other parameters for individual plant selection in F_2 and F_3 populations, and found that it was essentially useless (Table 19). More research is needed to evaluate mHI as a tool to overcome the limitations found with the conventional harvest index.

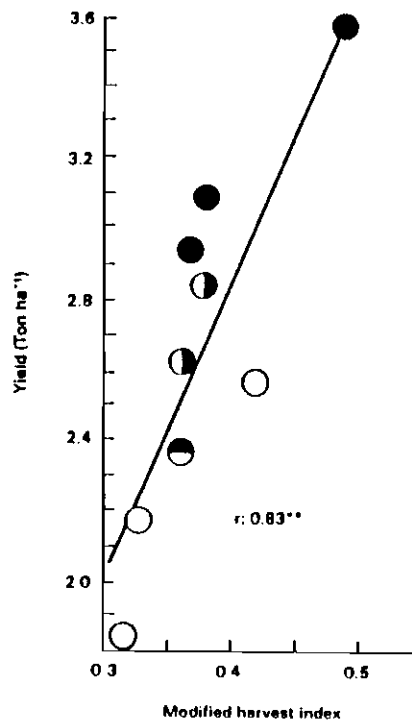


Fig. 13 Modified harvest index relationship to yield for 9 dry bean cultivars with differing plant architecture (O: architype; O: classic II; O: small bush; and O: tall erect bush). Source: Izquierdo, 1981a.

Table 19. Average seed yields of F₄ progenies derived from individual plant selections in the F₂ using various combinations of selection criteria: HI = harvest index; DW = plant dry weight DY = daily yield. Numbers in parentheses indicate F₂ plants in a given selection category. Masaya, personal communication.

Cross	Parental Yields		Selection criteria						
			1	2	3	4	Criterion 4 plus		
	Female	Male	HI	DW	YD	VS	1+2	1+3	2+3
-----g plot ⁻¹ -----									
A 429 x XAN 112	268	256	266 (20)	312 (10)	283 (3)	270 (62)	-	-	287 (13)
A 429 x Pata de Zope	268	259	258 (16)	286 (9)	-	269 (23)	-	258 (2)	317 (4)
A 429 x Pecho Amarillo	268	285	253 (21)	253 (9)	-	263 (128)	-	-	282 (9)

3. Assimilate Partitioning:

Rather than assuming that specific characteristics of the source or sink limit yield, an alternate hypothesis is that it is the partitioning process which is defective. Adams (1973, 1975, and 1981) has proposed a series of architectural models emphasizing the need for cultivars which are efficient in mobilizing both dry matter and N to the seed. If a cultivar accumulates assimilate and nitrogen during vegetative growth, and is able to remobilize it during podfilling, this should delay leaf senescence, and lead to higher yields. Combined with a more erect plant type to reduce lodging, such a plant-type should permit much greater efficiency during the podfilling period.

Modification in plant architecture does not necessarily have to lead to increased efficiency in translocation although yield advantages of the improved varieties over old standard cultivars has been associated with changes in physiological performance (Gay *et al.*, 1980). The morphological model characterized by the Adam's archetype has produced apparently not only a more desirable bean plant type from the agronomic standpoint (lodging resistance, and ease of mechanical harvest), but has lead to higher yields due to increased physiological efficiency involving filling duration, partitioning and remobilization of assimilates (Izquierdo, 1981).

The hypothesis of stress tolerance due to remobilization of reserves is attractive but has limitations. The ability to withstand a stress by assimilate remobilization is not necessarily linked to storage capacity. Partitioning and remobilization capacity are both needed and must be considered in a breeding program. This suggestion is consistent with the fact that bush type entries have been characterized by a short but rapid filling period, high partitioning, and high remobilization of dry matter. However, these entries, as compared to the other types, are susceptible in different degrees to leaf area reduction due to physical and biological stresses. Once the photosynthetic mechanism becomes impaired in bush type plants, seed filling depends on remobilization. Evidence that water stress enhances assimilate remobilization (Samper and Adams,

unpublished) indicate the need for further research. Aspects of this problem will be discussed in a subsequent section.

4. Yield Components:

A special group of hypotheses concerning assimilate partitioning are those related to characteristics such as seed weight, seeds per pod or inflorescence, and pod number, which may be defined in such a way that when multiplied together, their product is equal to crop yield. Such "yield components", as they are termed, were first used by Engledow (1925) in studies of wheat yields, but analyses of yield components are frequently done in leguminous crops. For beans, components may be defined as:

$$\begin{aligned} \text{Yield} &= \text{SW} \times \text{SP} \times \text{NM}, \text{ where} \\ \text{SW} &= \text{weight of single seeds} \\ \text{SP} &= \text{seeds per pod} \\ \text{PN} &= \text{pods per node} \\ \text{NM} &= \text{nodes per m}^2 \end{aligned}$$

These components also serve to calculate others:

$$\begin{aligned} \text{SP} \times \text{PN} \times \text{NM} &= \text{seeds per m}^2 \\ \text{SW} \times \text{SP} &= \text{yield per pod} \\ \text{PN} \times \text{NM} &= \text{pods per m}^2 \\ \text{SW} \times \text{SP} \times \text{PN} &= \text{yield per node} \end{aligned}$$

Components may be subdivided to distinguish between components borne on branches or main stems (e.g. Bennett *et al.*, 1977).

The simplest strategies for increasing yield through selection for yield components observe that if certain components are increased without affecting the others, then yield must increase. This follows from simple algebra, and as theory is unimpeachable. In practice though, studies of variation in components measured in different genotypes generally show that for pairs of components whose product equals (eg. Seed Weight \times Number of Seeds per m^2), the correlation between the pair is negative (Table 20). This effect was termed "yield component compensation" by Adams (1967), and is attributed to compensatory growth as distribution of some yield limiting resource is affected by genetic and environmental factors. The principal implication of this process is that selection for high levels of one component will probably not result in yield increases.

Table 20. Correlations between pairs of yield components (whose product equals yield) for two trials of bush beans. Source: White, 1981.

		Trial with:	
		10 cultivars	38 cultivars
Seed weight	vs. Seeds m^{-2}	-.81**	-.86**
Yield pod^{-1}	vs. Pods m^{-2}	-.65	-.80**
Yield node^{-1}	vs. Nodes m^{-2}	-.21	-.77**

*,** Significant at the $p = 0.05$ and $p = 0.01$ levels, respectively.

However accepting that yield component compensation occurs does not eliminate the possibility of identifying an optimal combination of components. Graphs of varietal differences in two components whose product equals yield (Fig. 14) illustrates the overall trend of compensation, but deviations from the curves for constant yields show that there is much variation besides that explained by compensation. Thus one might expect higher yielding lines to represent some optimal combination of components.

5. Integrated Strategies:

As mentioned before, plant breeders have made no decisive breakthrough in yields of dry beans with the exception of developing disease resistant varieties which allow genetic potential to be expressed.

Integrated approaches considering plant morphology as well as physiological efficiency have been attempted by defining crop ideotypes adapted to specific environments. Donald (1968) emphasized that a plant ideotype must be a poor competitor. This break from traditional thinking comes from the understanding that the individual plant within a community will express its potential for yield most fully if it suffers a minimum of interference or competition from its neighbors. The crop ideotype is expected to make a minimum demand on resources per unit of dry matter produced, but the community as a whole must extract a maximum amount of the resources.

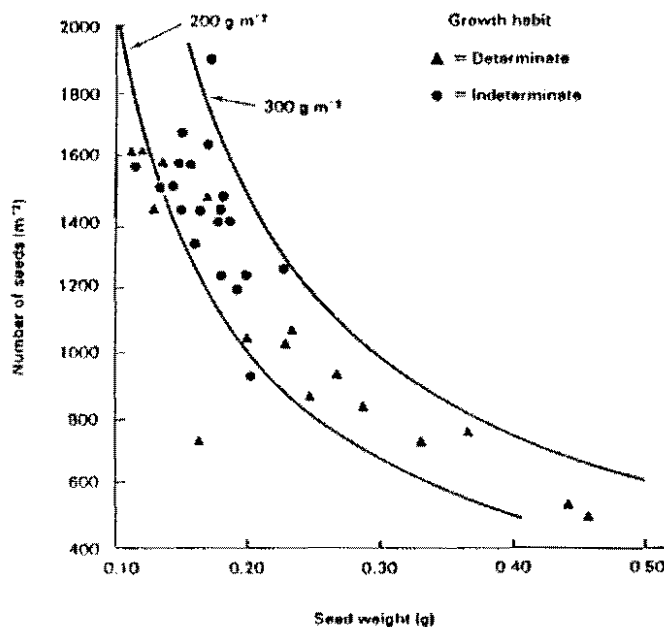


Fig. 14 Yield component compensation among 38 bean lines. Curves represent levels of constant seed yield. Source: White, 1981.

In beans, characteristics such as determinate habit, early maturity and small leaves have been considered to provide wide genotypic adaptation (Silvera, 1974). Adams (1973) suggested a bean ideotype for monoculture, and further hypothesized that only few changes needed to be made to adapt this ideotype to be a successful competitor when grown in mixed culture with maize. He suggested that the leaf size be medium to small, and that the sink capacity be increased by raising the number of flowers per raceme and number of seeds per pod. On the physiological side, he suggested it would be desirable to raise the net rate of CO₂ exchange, to increase the rate of translocation of photosynthate to sink, and to select for a high harvest index.

Tanaka (1974) suggested an indeterminate bean type which would produce many pods on the main stem for mixed culture with maize.

Adams (1973) mentioned the isogenic line, model building and factor analysis as three methods that had been used in construction of plant ideotypes, but very limited number of studies have been conducted in beans. Denis (1971) utilized a factor analysis of bean plant-type variables. With the same approach, more than 60% of total variance was attributable to the factor named "partitioning" under stress conditions (Samper and Adams, 1985, unpublished).

These theoretical, morpho-physiological plant models have been approximated in breeding efforts (Adams, 1981), and improved lines have appeared to show greater yield in monoculture.

6. A New Strategy:

Having reviewed various strategies for increasing yield potential, a logical conclusion is to provide a new strategy. Basic components of our strategy are not radically different from those described for cereals (e.g. Donald, 1968; Chandler, 1969), and also share components of previous proposals for grain legumes.

Our first premise is that the strategy must be developed in the context of appropriate agronomic management. We suggest narrow row spacings (e.g. 30 cm) at densities of 40 plants m^2 . The fact that these practices do not give maximum yields with existing materials is irrelevant since the interest is not in current cultivars, but rather a new type of bean crop. An abundant nitrogen supply will be required. For a 1 ton ha^{-1} yield increase approximately 80 to 100 kg ha^{-1} of additional nitrogen are needed, assuming 50% losses to non-seed tissues and leaching or volatilization. Achieving such levels may require split applications of nitrogen or special management to maximize N-fixation. Recent work on flood culture of soybeans has produced 40% increases in growth over conventional irrigation, suggesting that water management may require further improvement (Nathanson *et al.*, 1984).

A specific morphology (e.g. determinate stems and no lateral branches) is less important than crop response to high fertility. As in changes introduced in to rice cultivars (Chandler, 1967), plants which show limited N response of stem elongation and leaf expansion are needed. This response will probably be correlated with reduced branch growth and smaller maximum leaf size. Root or stem strength will have to be increased to improve lodging resistance.

The demonstration that photoperiod response is often closely related to yield performance establishes the need for assuring proper climatic adaptation. Reduction of maintenance respiration at high temperatures may prove useful. Nitrogen partitioning should permit storage in non-leaf tissues for remobilization during podfill. This may also require a reduction of pod sink strength in early stages of podfilling.

Specific combination of yield components should not be sought, besides maintaining smaller seed sizes (180 to 250 μg per seed). It is possible that number of seeds per pod should be monitored in relation to ovules per pod to assure that seed formation is efficient.

In the first 15 to 20 days after emergence, the growth curve of the crop may actually be slower than with existing cultivars, reflecting less allocation to leaf growth. Early reproductive growth may also be reduced, this being associated with longer leaf life during pod-filling stage. Greater leaf life will assure maintenance of high seed-filling rates toward maturity.

While this crop will have a higher yield potential, competitive ability will have been sacrificed (Jennings and Jesus, 1968). The crop should perform poorly in mixtures with traditional cultivars

or other crops, and in the presence of heavy weed competition. Variability in individual plant yields will be low. The crop will have a poor tolerance to defoliation, whatever the cause.

The most efficient way to develop cultivars satisfying these requisites is first to yield test a wide range of climatically adapted materials under the agronomic conditions specified above. Maturity date should be recorded to correct yields for length of growth cycle. Screening for specific characters should begin with lodging resistance, nitrogen response, and reduced maximum leaf size. Reduced maintenance respiration is desirable, but because of the equipment needed for screening it is not suggested as a primary selection criterion.

For sites where late maturity may be exploited, selection for lateness should prove useful, but only if combined with strict control to eliminate materials with low reproductive sink strength ("poor adaptation" or low pod set). Selection strategies might include selection for late flowering and high node position of the first mainstem inflorescence (not node of first flower). Exclusive reliance on parents known to be well adapted might help.

Other desirable characteristics described for the ideotype should emerge through direct selection for yield. Resources should not be invested on seeking them individually.

7. Special Problems:

The preceding sections have discussed yield potential with little reference to specific cropping systems or limitations of seed type. However, maximization of yield potential is often sought with specific limitations. Problems associated with mixed cropping and mixtures of bean cultivars are particularly difficult. Increasing yield potential in medium to large seeded and in early maturing lines has also proven troublesome. These two topics are discussed here.

Medium to large seeded cultivars

For conditions permitting yields of 2.5 to 3 ton ha⁻¹, medium to large seeded lines (hereafter referred to as "large seeded" for simplicity) typically yield 0.5 ton ha⁻¹ less than small seeded ones. Comparing mean yields over three trials of 57 lines varying from 170 mg to 470 mg seed weight, seed size explained approximately 47% of variation in yield (Fig. 15). This would suggest that for maximum yields, small seeded lines are needed, but this has to be balanced against consumer preferences for larger beans. Thus, there is considerable interest in identifying causes of this difference in yield potential.

The most persuasive set of hypotheses derive support from the recent finding that small and large seeded cultivars represent two genetically distinct groups, reflecting different origins. The small seeded lines are predominantly Mesoamerican in origin, while large seeded ones have an Andean origin (Gepts *et al.*, 1984). The groups are sufficiently different that progenies from inter-group crosses usually produce dwarf F1 plants (Singh and Gutierrez, 1984).

Accepting that the groups have different origins and are difficult enough to intercross that there has been little introgression among the groups, the difference in yield potential simply reflect differences in adaptation of the cultivars. The small seeded, Mesoamerican types are adapted to pests, diseases, soil and climatic conditions typical of middle altitude sites (roughly 800 m to 1600 m) typical of Mesoamerica, while the larger seeded types are adapted to conditions found at higher elevations (1000 m to 3000 m) along the Andes. Although many cultivars are now grown outside the regions they were originally adapted to, the difficulty of crossing among groups has limited the possibilities of transferring components of adaptation which would improve yield performance.

Evidence supporting differences in adaptation is found in comparisons of photoperiod response in different seed size groups (Table 21).

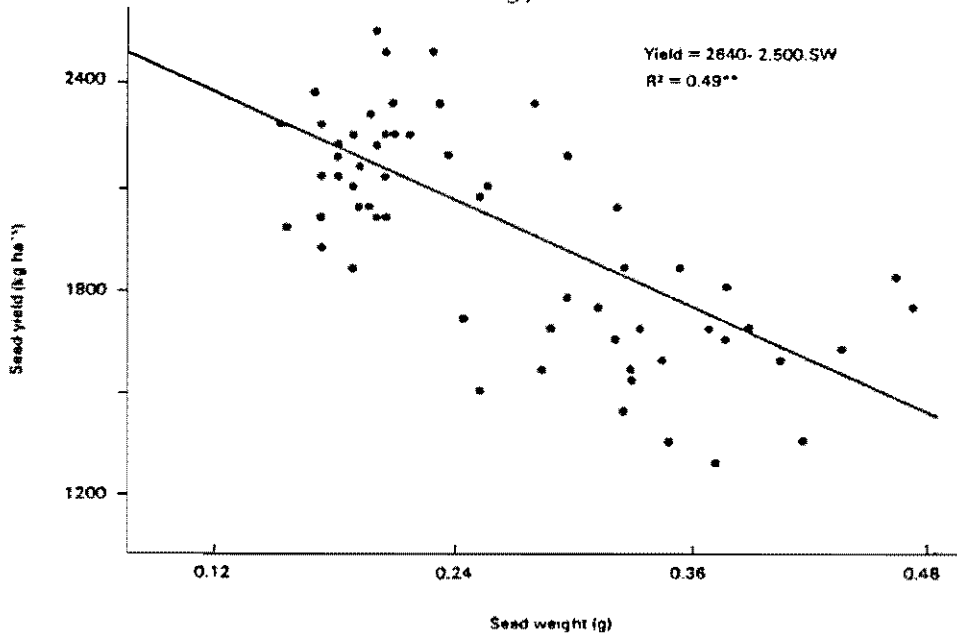


Fig. 15 Comparison of mean of seed yields over three trials at two locations and individual seed weight for 57 bean cultivars. CIAT, 1984 and 1985.

Table 21. Photoperiod response of flowering for different germplasm accessions at CIAT grouped according to seed size.

Seed size	Number of accessions with given photoperiod response of flowering†		
	Day neutral	Intermediate	Sensitive
Small (less than 28 mg)	53	27	20
Medium (28 to 35 mg)	24	36	52
Large (greater than 35 mg)	16	24	59

Chi² = 47, p < 0.001

† Based on delay in flowering in 18 hr artificial photoperiod as compared to natural 12 daylength at Palmira, Colombia.

Large seeded materials are predominantly photoperiod-sensitive and small seeded ones, day-neutral. In yield trials performed at different elevations within Colombia, large seeded materials yielded poorly at the warmer sites, but were superior at the coolest site (Fig. 16). Austin and MacLean (1972b) also noted that large seeded materials germinated faster at cooler temperatures (12°C) than small seeded ones, suggesting this might provide a useful screening characteristic.

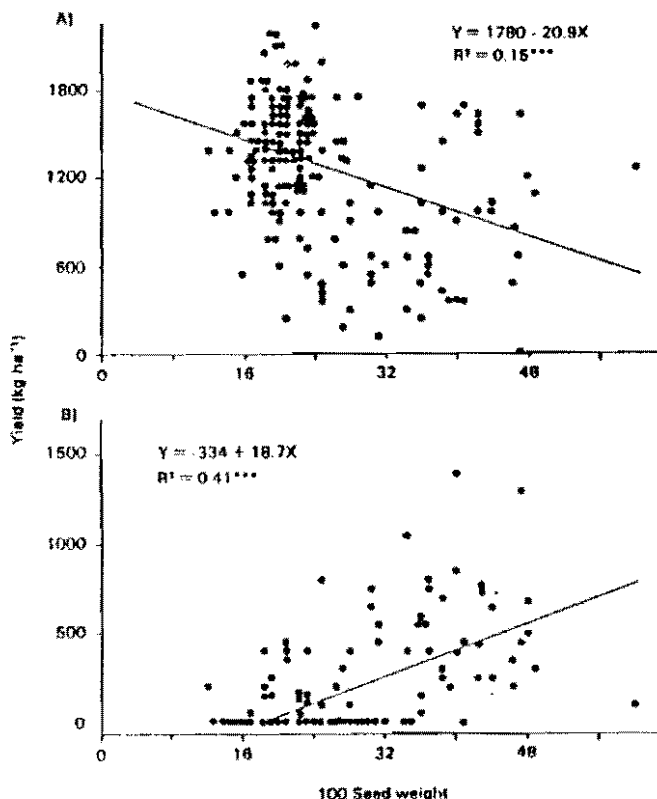


Fig. 16 Relation between seed yield and 100 seed weight at two locations in Colombia : A) Santa Fe de Antioquia (27°C); B) Pasto (13°C mean temperature). CIAT, 1978 and 1979.

A second line of arguments revolves around the assumption that if the developmental processes which determine seed size share genetic control affecting other developmental processes, then large seed size may be obligatorily linked with larger size of other organs or tissues. And these size effects may be disadvantageous. For example, in other crops, large fruit size results from larger cell size, and related effects are manifested in size of leaves, stomata, pollen grains and other tissues, this phenomenon being termed "gigantism" (Schwanitz, 1967). In beans, seed weight is often said to be positively correlated with leaf size and mean internode length, and has been found correlated with tissue cell sizes (Fig. 17).

Close associations have been noted between leaf size, pod size, and seed size in beans (Duarte and Adams, 1972) and between leaf size, lemma size, and seed size in barley (Hamid and Grafius, 1978). These relationships are explicable on the assumption of common genetic influences on homologous tissues. The assumption of homology between leaf and seed may be reasonable on grounds that each organ is initiated at the earliest primordial stage in a similar manner from an apical meristem.

Smaller cell size has been associated with higher photosynthetic rate and greater drought tolerance in other crops (Black *et al.*, 1976; Cutler *et al.*, 1977; Nobel, 1980).

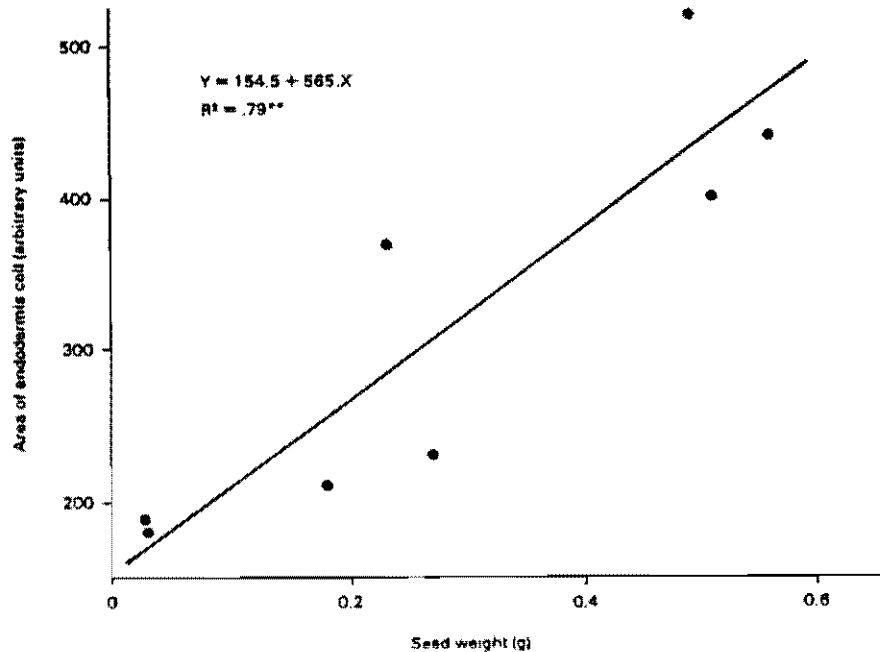


Fig. 17 Relation between endodermis cell size and seed weight in 6 bean cultivars. Cell size is measured as cross sectional area in arbitrary units.

Possible relations between seed size and pod growth rate also might influence yield potential. If larger seeds imply larger individual pod weights, and this in turn requires higher pod growth rates or longer filling periods, large seeds might result in excessive sink strength within a leaf-raceme unit. White (1981) found highly significant positive correlations of 0.86 and 0.85 among seed size and pod dry weight in comparisons of 10 and 38 lines, respectively. However, in studies of individual pod growth patterns, seed size and pod growth rate were not correlated (CIAT, 1985), differences in pod size primarily resulted from variation in duration of pod filling, not rate of filling. This is in agreement with observed differences in the linear seed filling period found between differing plant architectures and strongly related to final yield (Izquierdo and Hosfield, 1983).

Clearly, the causes of the difference in yield potential among seed size groups are not well established, although hypotheses abound. Adaptation differences are probably of major importance, but accepting this, one is still left with the possibility that characteristics obligatorily associated with large seeds are adaptive in cooler climates.

Early Maturity

For conditions where growth seasons are limited, there is a strong motivation for maximizing yields. Although many arguments for yield potential can be extended directly to early maturing lines, researchers have suggested that certain characteristics should be advantageous in early maturing lines.

Before considering some strategies for increasing yield potential in early maturing lines, we should consider the definition of earliness. Given the strong effects of climate and photoperiod on maturation rate, no rigid definition can be given, nor will specific lines be early under all conditions. However, as a rough guideline, we will assume in these discussions that if "normal" lines at CIAT, Palmira mature in 75 to 80 days, then early lines would mature in 58 to 68 days.

The importance of specialized agronomic management for early lines also merits note. Accepting that source limitations will be critical in early maturing materials, rapid establishment of leaf area should be critical. Besides seeking varieties with this characteristic, planting pattern and density may be modified for more rapid establishment of crop cover. For four early lines, Molina (1986) found that a 20 cm by 20 cm planting pattern resulted in greater canopy cover at 30 days, crop dry weight at 50 days, and seed yields than row spacings of 30, 45 or 60 cm with the same plant population per unit area (Table 22).

Table 22. Yields of four early maturing lines sown at four row spacings, but conserving a population of 20 plants.m⁻². Palмира, 1985.

Cultivar	Between_row_spacing_(cm)			
	60	45	30	20
	-----kg ha ⁻¹ -----			
RAB 60	2520	2100	2290	2700
XAN 145	2340	2060	2240	2610
BAT 41	2110	2180	2090	2300
G 3807	1640	1890	1870	1950
Mean	2150	2060	2120	2390

S.E. for difference of treatment means = 102

Large seed size is also frequently mentioned as a mechanism for achieving rapid establishment (Rodriguez, 1986), but in comparison of 40 early maturing lines, seed weight was not correlated with yield or yield day⁻¹ (Table 23).

Table 23. Correlations among yield and other parameters for 40 early maturing lines plus G 4525. Palмира, 1984b.

	Yield	Yield/day	Days to maturity
Yield/day	.99**	-	
Days to maturity	.90**	.72**	-
Crop dry weight	.87**	.85**	.77**
Harvest index	.18	.23	-.08
100 seed weight	.14	.14	.18
Seeds/pod	.28	.26	.23
Pods/m ²	.68**	.68**	.49**

** Significant at the p = 0.01 level

If a short growth cycle results in a limited number of sites for pod filling, relatively large pods or number of pods per node would increase sink size. In contrast, for a crop with a short period for pod filling, very efficient distribution of sink demand might be crucial. This, in turn, suggests an advantage for early materials with smaller pods distributed over a wide range of sites.

Arguments for either a relatively long or short duration of pod filling can also be given. Since duration of podfilling is positively correlated with yield, one might seek cultivars maximizing this period within the growth cycle of early lines. Alternately, if total vegetative growth determines crop yield, a line which flowered late, but filled pods rapidly would be preferred.

Many other strategies have been suggested for increasing yield potential in early maturing lines. The reader is referred to Rodriguez (1986) for details.

B. Potential of Biotechnology or other Strategies in the Future:

Previous discussions have adhered to what might be considered conventional strategies for increasing yield potential. However, with the advances in techniques for manipulating genes and propagating plants, there exists the possibility that advances will result from strategies considerably outside the scope of those outlines above.

Although exploitation of heterosis through use of hybrid seed has shown little promise in common beans (Gutiérrez and Singh, 1984), other strategies for exploiting heterosis exist. In some crops, seed is produced without the genetic recombination occurring in meiosis (Bashaw, 1980), the process being termed "apomixis" or more specifically "agamosperry" (seed formation without production of gametes). Apomixis occurs in very low frequencies in grain legumes (Sobolev *et. al.*, 1976), but with a more complete understanding of control of meiosis it might be possible to construct a apomictic cultivars much in the way as has been proposed for potatoes (Hermesen, 1980). Alternatively, apomixis might be sought through mutation breeding. Apomixis complicates breeding strategies, but combining a genetic propensity for apomixis with a requirement for chemical induction would minimize this drawback (Iwanaga, 1983).

Another avenue for exploiting apomixis is through vegetative propagation. A few areas of bean production already involve transplant of seedlings (Singh, personal communication), and introducing vegetatively propagated material should prove straight forward. Presently, it is difficult to propagate beans through tissue culture (Mroginski and Kartha, 1984), but if barriers are overcome, F1 hybrids might be propagated through tissue culture, and distributed as "somatic embryoids", that is, embryo-like propagules.

Although considerable work has been devoted to tissue culture with *P. vulgaris*, to date, there is no published and confirmed procedure available for *de novo* plant generation from either callus, cell suspension, or protoplast cultures. Regeneration of plants by *in vitro* culture has succeeded with apical meristems of zygotic embryos only.

Shoot apex, callus and cell suspension cultures are relatively easy to establish and were employed in several studies but results are very poor. In a report that has never been confirmed, 140 plants were regenerated from about 400 callus cultures when explants originated from leaves of *P. vulgaris* were cultured on a medium supplemented with bean seed extract (Crocomo *et al.*, 1976). An average of 15 regenerated buds per each explanted shoot apex was obtained from the cultivar "Palmital Frecoce" with full plants recovery after the third subculture with gibberellic (GA₃) and naftalen acetic acids (NAA) growth regulators (Martins and Sandhal, 1984). Very recent results of research in this area at CIAT have shown the induction of somatic embryo-like structures on bean callus cultures (Roca, 1986, personal communication). But, to realize any of these possibilities a complete breakthrough in regenerating bean plants from tissue cultures is needed.

Although current techniques for hybridizing legumes have permitted limited crosses between legume genera or species (Alvarez et al., 1981), investigation on the use of protoplast fusion to produce somatic hybrids suggest the possibility of producing grain legumes containing desirable features of distantly related genera (Schiefer, 1982). Thus, bean cultivars with the late maturity and architecture of soybean plants, might result from somatic hybrids of common bean and soybean. Considerable information exists on fusion of soybean protoplast with non-legumes, but in no case have plants been regenerated (Mroginski and Kartha, 1984).

Assuming that beans will be grown in environments where a C_4 photosynthetic pathway are advantageous, one might reconsider the possibility of converting beans to a C_4 pathway. Screening of over 60000 plants of soybean, oats and wheat failed to detect a single individual with a low CO_2 compensation point (Evans, 1975), and identical failure rates in other crops suggest that such a change will not be achieved using current breeding techniques. However, with improved ability to identify and manipulate specific genes, the complete set of genes required for the C_4 pathway might be transferred.

Genetic modification of plants by genetic manipulation of the DNA level are still far in the future. Most of this research currently uses model plants and genes. However, recombinant DNA technology may, on a medium term basis, be used to develop molecular genetic markers which in turn can be use to built genetic linkage maps for economic important traits (Vallejos et al., 1986). The availability of this procedure would help bean breeding by accelerating the introgression of foreign genes into commercial cultivar and is under study at CIAT (Roca, 1986, p.c.).

Other strategies are easily envisioned, but the above examples should serve as warning that while "standard" strategies hold the greatest promise for the immediate future, one should not be blind to other strategies. Perhaps the best recommendation comes from Ralph W. Emerson in the 19th century "A foolish consistency is the hobgoblin of little minds".

IV. PRODUCTIVITY UNDER STRESS

For the vast majority of bean production regions, yield potentials are never realized because of combined effects of edaphic, climatic, disease and pest problems. In most cases, there is genetic variability for responses to stresses, and considerable effort has gone to the study of tolerance or resistance to different stresses. The discussions that follow emphasize abiotic stresses such as drought and excess water. The last section discusses general stress tolerance or "rusticity" in beans.

A. Drought

The importance of water deficits in limiting crop yields can ultimately be traced to the fact that for most field conditions, water vapor diffuses out of a plant more easily than CO_2 , and that soil water is not sufficient to permit the plant to continually replace lost water. Conservation of water through stomatal closure or other mechanisms reduces photosynthesis, thus crop growth is limited. This results in a close relation between water availability and yield (Fig. 1B).

A high relationship between leaf area index and evapotranspiration has been observed in snap beans by Bonanno and Mack (1983) in agreement with the linear function described in Fig. 19 between evapotranspiration and yield of two black cultivars of beans differing in their response to drought stress.

Considerable literature exists on effects of drought in beans, and on possible mechanisms of drought tolerance, but although our understanding continues to improve, enough questions remain that practical benefits of such work are difficult to identify. Many of the difficulties arise from the inherent complexity of drought, but errors in planning and interpretation of experiments often underly contradictory findings. The most serious errors may be summarized as:

1. Failure to use relevant stress conditions. In particular, greenhouse conditions using container grown plants often result in stresses developed too rapidly, yet under conditions of low radiation and high humidity.
2. Failure to quantitatively characterize the stress. Published reports often fail to mention parameters such as soil water content ($g\ H_2O\ g^{-1}\ soil$), soil water or leaf potential, leaf canopy temperature, and yield reduction which help indicate levels of stress obtained.
3. Failure to account for acclimation to stress conditions.
4. Failure to study genotypes representative of those of interest to agronomists and plant breeders.
5. Failure to distinguish between drought responses and drought tolerance mechanisms. The mere fact that a parameter such as leaf size or proline or abscisic acid content is severely affected by drought stress, does not establish that its drought response reflects a mechanism of tolerance.

1. Effects of Drought:

While the ultimate effect of drought is limitation of growth and yield, specific physiological effects of water stress vary depending on the previous history of the crop (e.g. possible acclimation), and timing and intensity of the stress. Kramer (1983) noted that interactions of these factors probably explain a large number of conflicting results from studies of effects of drought. Thus while this review considers different effects of drought, ranging from near instantaneous effects to long term growth effects, specific conclusions are not always given.

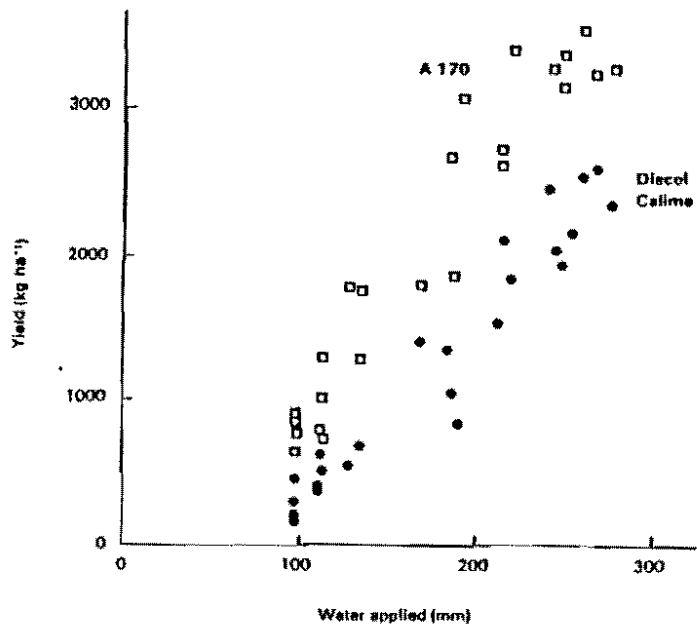


Fig. 18 Yields of A 170 and cv. Diacol Calima at different levels of applied water using a line source sprinkler installation. CIAT-Palmira, 1985.

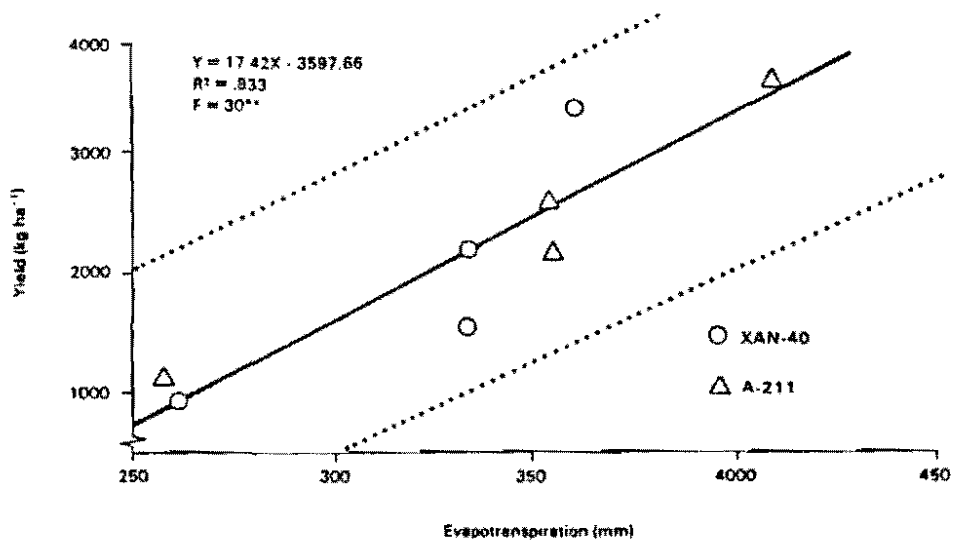


Fig. 19 Linear relationship of evapotranspiration on seed yield of two black bean genotypes. (95% confidence limits are indicated by dotted lines). Source: Jara, Izquierdo, y Matta 1988.

Rapid responses

Rapid onset of drought causes interruptions both in photosynthesis and in tissue expansion.

Effects on photosynthesis may be ascribed to two components (O'Toole *et al.*, 1977b). One is reduced gas exchange due to stomatal closure. In beans, full closure may be reached in a few minutes after an application of a stress (Fig. 20). With stomatal closure, CO₂ uptake is minimal and O₂ accumulates, causing decreased CO₂ fixation, but increased photorespiration (Powles and Osmond, 1979). There is still considerable argument as to what actually triggers stomatal closure. Abscisic acid (ABA) levels increase under drought and can trigger closure (Aspinall, 1980), but closure in beans was detected well before increases in ABA (Walton *et al.*, 1977). Stomatal closure has also been correlated with decreasing leaf water potential, Ψ_l (Moldau, 1973) and increased leaf temperature (Fig. 21). Recent work suggests that in beans as well as many other crops, rapid responses under field conditions may reflect sensitivity to decreasing atmospheric humidity, measured as increased of vapor pressure deficit (El-Sharkaway *et al.*, 1985). Beans appear intermediate in stomatal sensitivity to humidity (El-Sharkaway, *et al.*, 1985), suggesting that they follow a strategy intermediate water conservation (drought avoidance).

The other component reducing photosynthesis is loss of efficiency in the physiological processes of photosynthesis, reflected as an increase in mesophyll resistance (r_m). Under desiccation regimes similar to field conditions such effects occur only at low water potentials. Moldau (1973) found no increase in r_m resistance at leaf water potentials down to -1.3 MPa.

Attempts to determine which photosynthetic processes are responsible for increased r_m are inconclusive. O'Toole *et al.* (1977b) found that the decline in RuBPCase was actively greater than the increase in r_m . Desiccation of chloroplasts and associated disruption of the chlorophyll-thylakoid membrane complex may also be involved. Osmond *et al.* (1980) proposed that, in beans, internal cycling of CO₂ through photorespiration plays a major role in protecting against stress associated damage, and that much of reported damage under stress is due to rapid stresses applied in laboratory experiments.

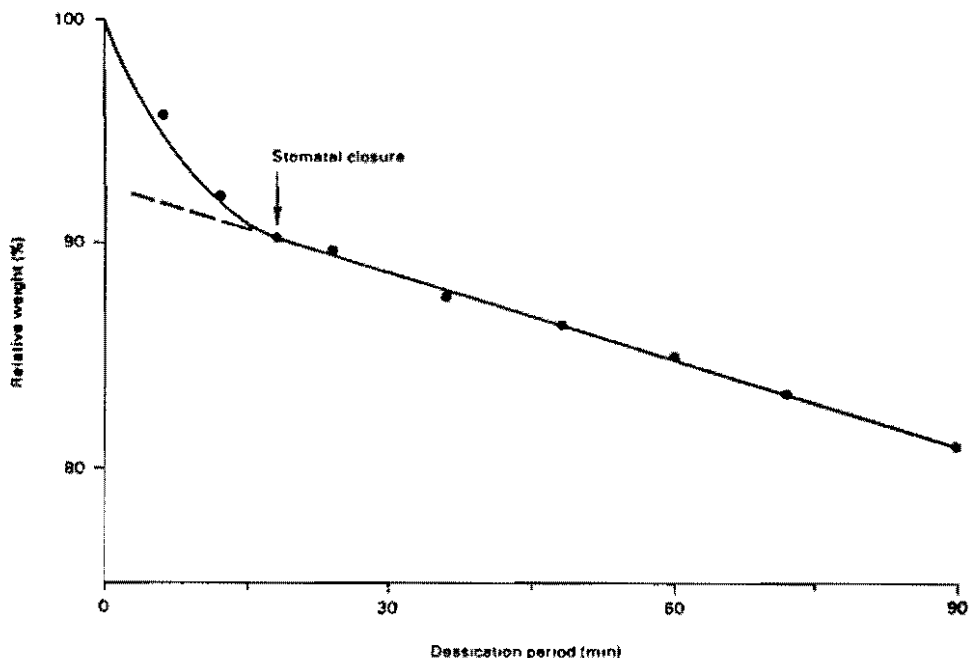


Fig. 20 Time needed to reach stomatal closure in a detached leaf of BAT 477 as indicated by onset of linear phase of water loss. CIAT-Palmira, 1986.

Drought stress may affect tissue expansion both through reduced cell expansion and division. Using sodium chloride concentrations to generate different water potentials in culture solutions, Brouwer (1963) concluded that interruption of cell expansion was more important than effects on cell division in limiting leaf growth. Bunce (1977) found a linear relation between soybean leaf elongation rate and turgor pressure, and further noted that plants grown in drier conditions required less turgor to achieve a given amount of elongation. However, more recent work has led to a consensus that reduced turgor pressure is not the primary cause of cessation of tissue expansion under drought.

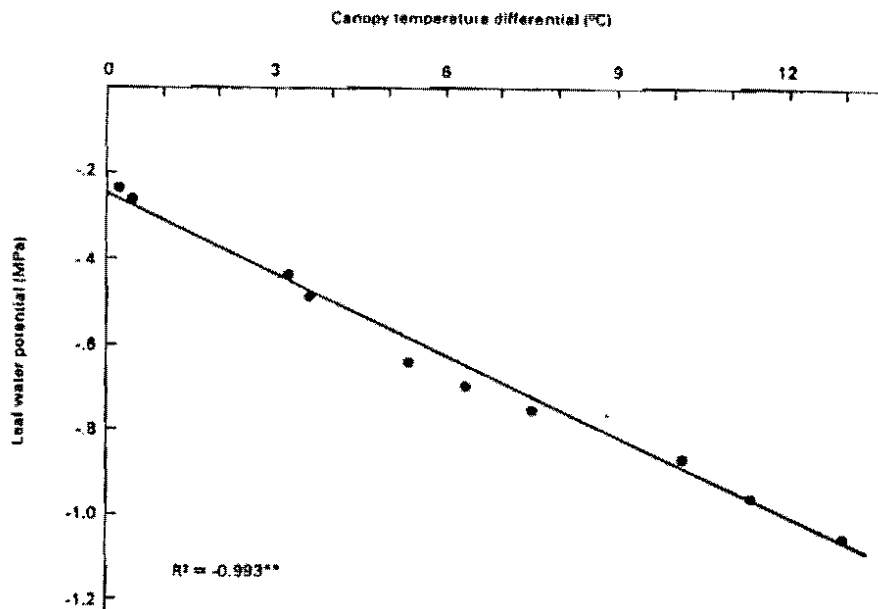


Fig. 21 Relation between leaf water potential and canopy temperature differential measured between stressed and irrigated plots from 4 bean lines.

Responses within hours

As a stress continues to be applied, plant water potential declines, reflecting combined effects on turgor pressure and osmotic potential as water is lost. Extreme reductions in turgor pressure result in wilting including loss of ability to orient leaves. Estimates of permanent wilting points in field grown beans are variable. Sponchiado (1985) obtained sufficient stress to induce "burning" of leaf margins, but P_s was never lower than -1.1 MPa. Jara (1985) obtained values of -1.2 MPa as the leaf potential of stressed plants at 82 days after planting.

Both ABA and proline accumulation have been detected in drought stressed beans (Stewart, 1972). ABA appears involved in stomatal function under drought, but since it accumulates in other tissues, additional functions may be involved. Accumulation of proline, and nitrate and ammonium ions may contribute to osmotic adjustment and reflect inhibition of protein synthesis (Stewart and Hanson, 1980; Frota and Tucker, 1978).

Response over longer periods

The previously discussed effects ultimately result in major changes in overall plant growth. Reduced growth is usually detectable soon after onset of stress, with reduction in leaf area being particularly marked. For a stress applied before flowering and sustained to maturity, Sponchiado

(1985) found that final biomass and LAD were reduced to 50% of levels in control plots, although yield reductions were approximately 40% and 80% for drought tolerant and susceptible lines, respectively (Table 24).

Studies in other crops have shown that stress during early reproductive growth usually has particularly severe effects (Slatyer, 1969), and the same holds in beans. Stoker (1974), using lysimeters to provide equal stresses at different stages, obtained 20% yield reductions with stress during early or late vegetative growth, 50% reduction in early podfill, and no reduction in late podfill. In soybeans, effects on yield components were easily interpreted in terms of timing of drought stress (Shaw and Laing, 1966). In beans, the same would appear to be true although the relations have not been tested as carefully. For a stress sustained to maturity, all yield components showed reductions, while a stress terminated by rains during podfilling caused seed weight to increase relative to the irrigated control (Fig. 22).

Drought stress in beans is usually associated with accelerated maturity (Fig. 23), although late season release from stress may trigger recuperative growth resulting in delayed maturity.

Comparison of drought response of other legumes

Drought response of other legumes vary greatly. Within the genus *Phaseolus*, *P. acutifolius* is often cited as being more drought tolerant than *P. vulgaris* (Cory and Webster, 1984), but its small seed size has limited its commercial acceptability.

Table 24. Comparison of growth parameters of two drought tolerant and drought susceptible materials grow drought (D) and irrigated (C) plots at Palmira, Colombia (Sponchiado, 1985).

Variable	Treatment	Tolerant		Susceptible	
		BAT 85	BAT 477	BAT 1224	A 70
Yield (kg ha ⁻¹)	D	1460 a ¹	1460 a	550 b	550 b
	C	2520 a	2540 ab	2340 a	2770 b
Biomass (kg ha ⁻¹)	D	2600	2500	2200	1900 ab
	C	5200	5300	5700	5400 a
LAD	D	92 a	83 b	74 ab	80 a
	C	170 b	161 b	170 b	186 a
HI (%)	D	55 a	58 a	25 b	29 b
	C	48 a	48 a	41 a	51 a

¹ Values followed by the same letter within a row are not different at p = .05 level of Duncan's test.

Some traditional cowpea cultivars responde to drought through extreme stomatal closure and restriction of water loss (Shackel and Hall, 1979). In a comparison of mungbean, soybean, cowpea and peanuts (Pandy, *et al.*, 1984), the first three species showed patterns of response similar to beans,

including reaching minimum F_p of -1.2 to -1.4 MPa, but peanuts were much less affected, reaching only -0.4 MPa.

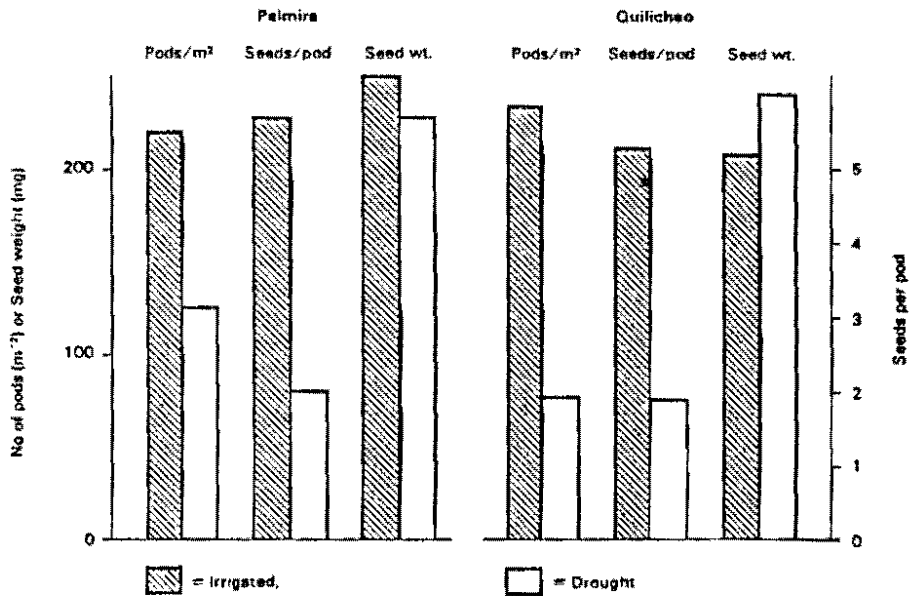


Fig. 22 Effect of drought from preflowering to end of pod fill at Palmira and Quilichao, Colombia on yield components of susceptible line A 70. Source: Sponchiado, 1985.

2. Drought Tolerance Mechanisms:

A great many drought tolerance mechanisms have been proposed, and demonstrated to function in very specific contexts. However, the warning from the previous section that drought effects vary greatly depending on specific drought conditions is equally valid for consideration of tolerance mechanisms.

We define "drought tolerance" in an agronomic sense. For a group of materials which give similar yields under non-stress conditions, a material is tolerant if it yields well compared to the others under conditions involving water deficits. Among mechanisms which may confer tolerance are those which ecologists usually classify as drought escape and drought avoidance. An outline of possible mechanisms is provided in Table 25. It follows classifications used by Turner (1984) and others, with the notable addition that for conditions where beans are grown, tolerance to factors related to drought such as high temperatures or saline soils may be essential. The discussion that follows emphasize the physiology of the basic mechanisms.

Drought escape

Bean crops may "escape" or at least reduce drought stress either by maturing early or delaying maturity until drought stresses have abated, this latter strategy termed recuperation. The usefulness of the two strategies varies with timing and intensity of the stress. Severe stresses occurring later in the growth cycle favor earliness, while mild stresses relatively early will favor later maturing lines with capability for recuperative growth.

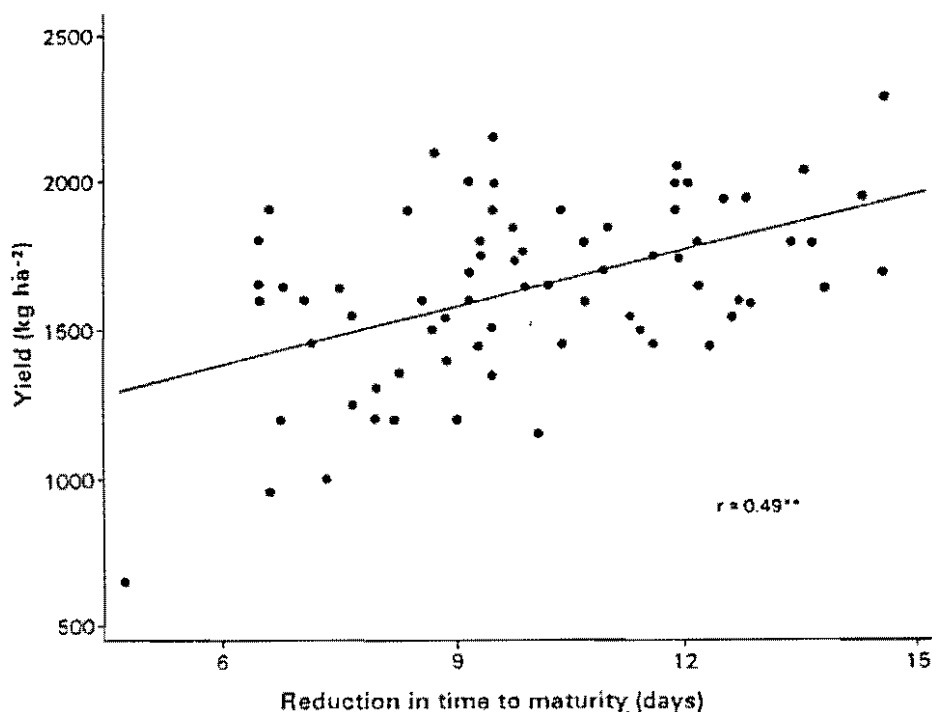


Fig. 23 Acceleration of maturation under drought stress as indicated by reduction in days to maturity of stress vs irrigated plots for 72 lines. CIAT-Palmira, 1984.

Table 25. Classification of possible drought tolerance mechanisms in beans.

-
- I. Drought escape
 - A. Earliness
 - B. Recuperation
 - II. Drought tolerance with high plant water potential
 - A. Maintenance of water uptake
 1. Greater root growth
 2. Increased hydraulic conductance
 - B. Reduction of water loss
 1. Reduced area of evaporation
 2. Greater resistance along pathway of water loss
 3. Reduced gradient from leaf to atmosphere
 - III. Drought tolerance with low water potential
 - A. Maintenance of turgor
 1. Osmotic adjustment
 2. Increased cell elasticity
 - B. Desiccation tolerance
 1. Membrane stability
 2. Protein function
 - IV. Integrated mechanism: assimilate partitioning and remobilization
 - V. Drought tolerance through adaptation to factors related to drought
 - A. Heat tolerance
 - B. Low soil fertility
 - C. Salt tolerance
 - D. Soil diseases and pests

Drought tolerance with high plant water potential

Various tolerance mechanisms thought to function in bean crops result in maintenance of relatively high plant water potentials. These include those which permit greater water uptake, and those which reduce water loss.

Maintenance of water uptake:

As in many other crops, drought tolerance in beans has been associated with greater root growth. Comparing tolerant and susceptible materials in a fertile soil permitting deep root penetration, Sponchiado (1985) showed that roots of tolerant materials penetrated about 50 cm deeper than susceptible ones (Fig. 24). Differences in root growth and yield were also associated with greater exploitation of available soil moisture by the tolerant lines. However, this mechanism was not effective in a shallower soil where a pH of 5 at depths below 30 cm prevented extensive root growth (Fig. 25), and in this environment, yield differences reflecting supposed tolerance were not found (Table 26).

Increased efficiency of roots in extracting soil moisture must also result in greater water uptake. One alternative is for a crop to be able to tolerate lower root water potentials and thus extract soil water held at lower potentials. However, since this is basically a mechanism of tolerating desiccation, it is discussed later. Another alternative is for roots to have greater hydraulic conductance, either axially (for transport along the xylem) or radially (for uptake from soil to the xylem). Taylor (1980) concluded that axial resistance in soybean roots may be important at root depths over 1 m, but Passioura (1983) suggested that because of capacity for secondary growth of xylem, axial resistance would not be limiting in dicotyledonous plants.

Reduction of water loss:

Besides increasing water uptake, a crop may have adaptations which reduce water loss. Unfortunately, reduced flow of water vapor usually implies reduced diffusion of CO₂ into the leaf, and thus limitations in photosynthesis.

As mentioned previously, drought causes marked reductions in LAI, but there is no evidence that tolerant bean lines have greater reduction than susceptible materials. Tolerant materials show similar LAD as susceptibles (see Table 24).

Reduced leaf area may be compensated for through a greater mesophyll surface area per unit leaf area (Nobel, 1980), this occurring with increased leaf thickness and/or reduced cell size, which in turn affects SLA. Changes in leaf thickness was considered in an experiment with two bean lines differing in their response to water stress (Fig. 26). Line A 211 was able to maintain higher LAI without increasing leaf thickness as much as the line XAN-40 did. Drought yield of 25 genotypes have been correlated with the leaf thickness index ($r = .7011$), but the correlation under irrigation was even larger ($r = .9111$, Fig. 27). This index may be related to photosynthetic efficiency in terms of carboxylating area, and in absence of water stress, may be used for assessing genotypic photoassimilation ability.

Mechanisms involving increased resistance primarily involve barriers to water loss at the leaf-atmosphere interface. The greatest amount of water loss is usually via stomata, so considerable attention has been given to studying differences in stomatal resistance among bean lines. Simple relations among stomatal resistance and level of tolerance are not expected because of the relation between transpiration and CO₂ uptake. Rather, stomatal response to environmental conditions is probably critical in determining water use efficiency. Ideally a plant should regulate transpiration so that it occurs when moisture gradients are low (low vapor pressure deficit in atmosphere) but

radiation levels are above the compensation point. The main mechanism which would provide this response in C_3 plants is stomatal sensitivity to humidity.

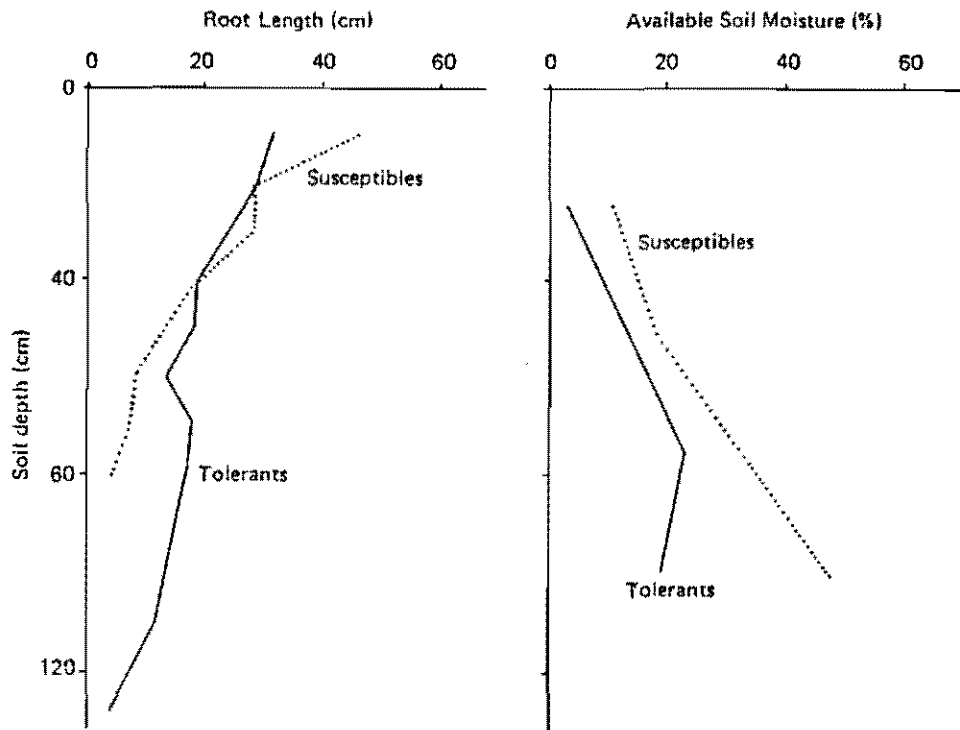


Fig. 24 Comparison of mean root growth and available soil moisture in drought tolerant (BAT 85 and BAT 477) and susceptible (BAT 1224 and A 70) line - Palmira.

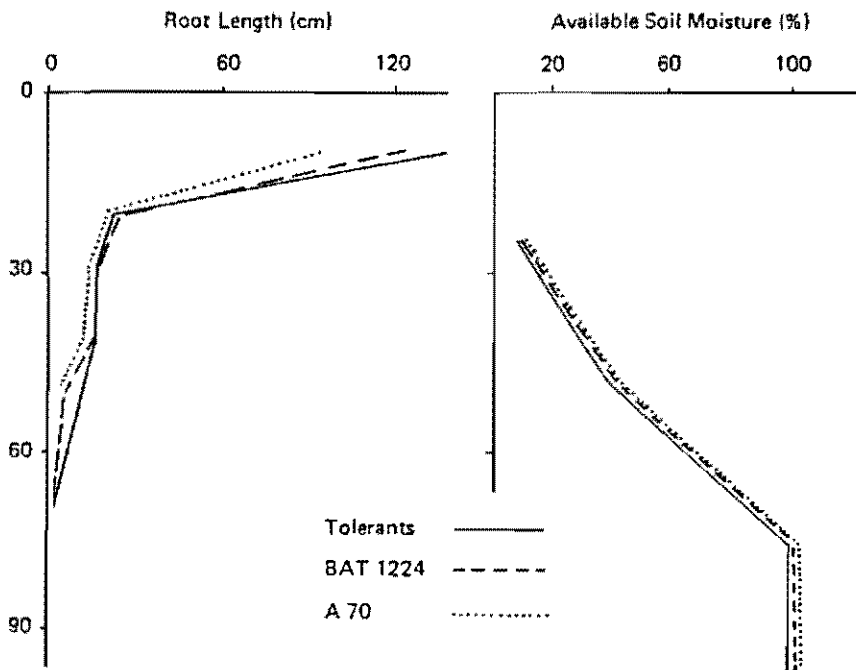


Fig. 25 Comparison of mean root growth and available soil moisture in drought tolerant (BAT 85 and BAT 477) and susceptible (BAT 1224 and A 70) lines - Quilichao.

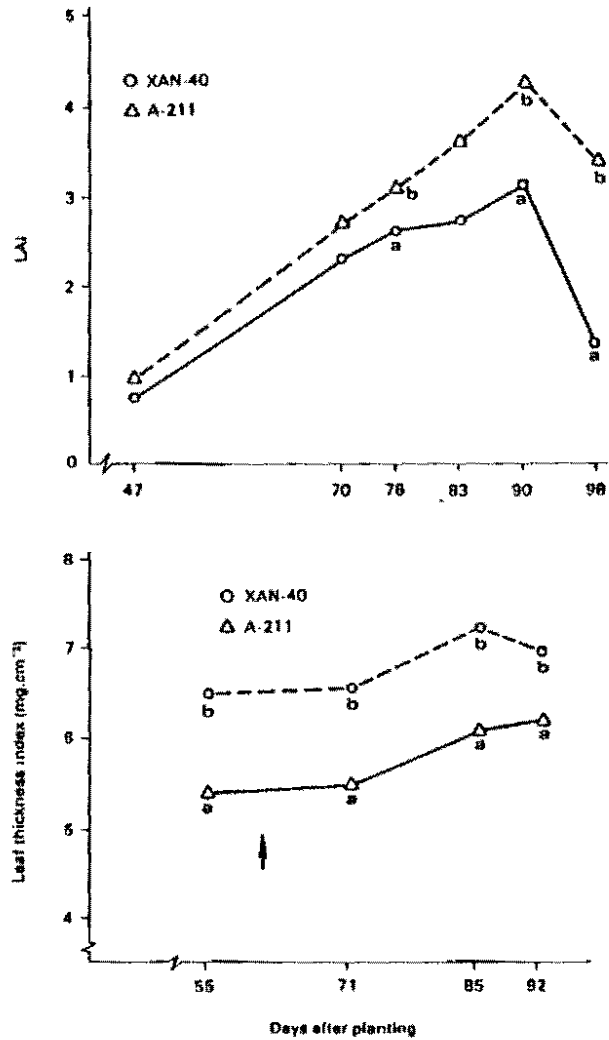


Fig.26 Mean leaf area index and leaf thickness index of two bean genotypes (XAN-40: susceptible and A 211: tolerant) with differing response to water stress under four stress conditions. Arrow shows 50% flowering. Mean separation by MRT Duncan 5%. Chillan, 1985. Source: Jara, Izquierdo and Matta, 1988.

Amount of cuticular wax was related to rate of water loss in sorghum (Ebercon, et al., 1977), and large varietal differences in cuticular resistance of rice leaves were found (Yoshida and de los Reyes, 1976). Woodfin (personal communication) reported considerable variation in cuticular wax formation among bean cultivars.

Boundary layer resistance will increase with greater leaf pubescence, (Ehleringer, 1980) although this mechanisms has not been studied in beans.

Assuming resistance along pathways of water loss are equal, cultivars may differ in water use through effects on the water vapor pressure gradient from leaf tissue to the atmosphere. The external pressure will be equal, but internal vapor pressure will vary with leaf temperature. Thus factor affecting leaf temperature will reduce water loss. Leaf orientation can reduce radiation interception, but at the cost of some light energy intercepted for photosynthesis. Leaf pubescence and cuticular waxes sometimes appear to reflect infrared light with relatively little effect of FAR. Variation in leaf color both among varieties and between dorsal and ventral sides of the same leaf area considerable in beans, but do not have not been examined in relation to leaf temperature effects.

Reduced leaf size will can also reduce temperature since for a given total leaf area convective cooling is greater for a surface divided into smaller sections (Gates, 1968). This effect has lead breeders in other crops to breed for smaller leaf sizes. Hiebsch et al. (1976) did not detect improvements with iso-lines of soybeans differing in leaf size. Leaflet size was significantly reduced by an intense post-flowering water stress, but the relationship between drought leaflet area and stress degree-day measured by infrared thermometry was not consistent among 25 bean genotypes (Izquierdo, 1985, unpublished).

Drought tolerance with low plant water potential

Although the preceding mechanisms will reduce water loss, most stress conditions are sufficiently severe that water potentials drop to levels which affect plant function. This leads to the possibility of adaptations permitting the plant to function at low water potentials.

Maintenance of turgor

Since water enters roots through flow along a gradient, lower root water potentials (P_r) will result in greater exploitation of soil volume. Thus a crop which has a greater reduction in P_p or P_r for a given amount of water loss, should show more drought tolerance. However, with loss of turgor, evidenced by wilting, the plant loses the ability to continue tissue expansion or to utilize mechanisms such as leaf orientation which utilize differences in turgor pressure. This indicates the need for mechanisms which permit low P_p or P_r without loss of turgor.

When water deficit is severe, plant cells accumulate solutes, which lowers their internal osmotic potential, in order to at least partially maintain turgor pressure, and thus permit continued cell expansion and growth. Osmotic potential may be regulated through shifts in concentrations of potassium, sugars, amino acids, and organic acids (Turner and Jones, 1980; Morgan, 1984). Markhart (1985) compared osmotic adjustment of Phaseolus vulgaris and Phaseolus acutifolius grown in containers, and did not detect differences. Jara (1985) found significant differences of about 0.05 MPa at time of flowering among two bean cultivars under field conditions, but not at other growth stages.

Assuming mechanisms of osmotic adjustment are the same in different growth stages, growth of seedling roots in media with low potentials might provide a simple index of capacity for turgor maintenance through osmotic adjustment. In a comparison of 25 cultivars, percent inhibition of

radical elongation was highly correlated ($r = 0.72$) with drought susceptibility measured with Fisher index (Fig. 28).

The mechanical characteristics of tissues also affect turgor maintenance. Reduced tissue elasticity, indicated by a high bulk tissue elastic modulus (E_m), will result in a small decrease in water content per unit reduction in water potential. The protoplasm will retain more water under stress, but at the cost of loss of turgor. Kim and Lee-Stadelmann (1984) could not detect differences in E_m of beans in stress and control conditions, and while Jara (1985) did find such differences for four water regimes under field conditions, varietal differences were not significant.

Table 26. Yield, root growth and other parameters of two drought tolerant lines (BAT 85 and 477) and two susceptibles (BAT 1224 and A 70) for plantings at CIAT-Palmira and CIAT-Quilichao. D = Drought treatment; C = Irrigated control.

Variable	Treat- ment	BAT 85	BAT 477	BAT 1224	A 70
Palmira					
Yield (kg ha ⁻¹)	D	1458a*	1457a	548 b	570 b
	C	2517a	2538ab	2344a	2768 b
90% root depth (cm)	D	100	100	60	60
	C	50	50	50	50
Root dry weight (mg)	D	541	599	534	494
	C	660	715	725	598
Canopy temperature (°C)*	D	34.0	34.3	36.8	37.5
	C	29.2	29.6	29.6	29.9
Leaf water potential (kPa)*	D	810	840	1100	1100
	C	450	460	480	470
Quilichao					
Yield (kg ha ⁻¹)	D	589a	724a	723a	192 b
	C	2896a	2952ab	2663 b	2124
90% root depth (cm)	D	30	40	30	30
	C	30	20	20	20
Root dry weight (mg)	D	924	899	792	668
	C	476	611	688	492
Canopy temperature (°C)*	D	38.4	39.8	38.8	41.4
	C	28.6	28.0	28.5	28.5
Leaf water potential (kPa)*	D	840	860	950	1030
	C	400	450	450	500

* Yields followed by the same letter do not differ according to Duncan's $p = .05$.

* Measured during periods of maximum stress.

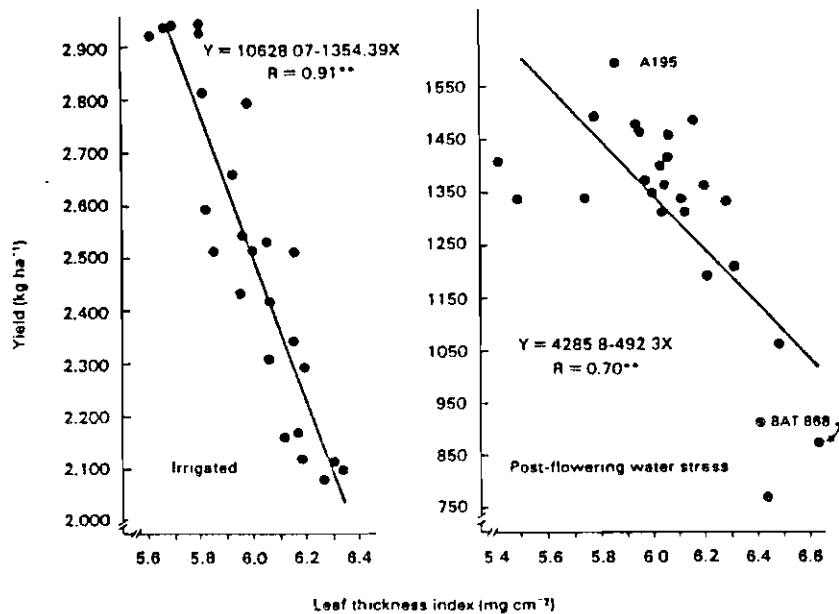


Fig. 27 Linear regression of leaf thickness index on yield of 25 bean genotypes (CIAT-BIDYT, 1985) under irrigated and post-flowering water stress. The index measured during pod filling. Source: Huepe, 1986.

Dessication tolerance:

At very low plant water potential physiological processes may be disrupted. This subject is poorly understood, but it appears that effects of dessication may be divided among those on cell membrane function and those on protein function. Under dessication cell membranes appear to lose integrity, and the efficiency of processes requiring membranes are reduced (Leopold, et al., 1981). Similarly, although it is easy to hypothesize effects of dessication on enzymatic proteins, such effects, much less varietal differences, are apparently unresearched in beans.

Integrated mechanism: assimilate partitioning and remobilization.

The previous mechanisms have been discussed as results of independent physiological processes, but it should be realized that they interact and may share common basis. For example remobilization of N and stored carbohydrates (starch) may be enhanced under drought stress, and this would permit greater root growth or capacity for osmotic adjustment.

Studies of carbohydrate remobilization under drought conditions (Samper, 1984) suggest that tolerant cultivars are more efficient at remobilizing carbohydrate during podfilling. Induced or accelerated remobilization of stored dry matter due to water stress has been observed in barley by Gallaher et al., 1975. Remobilization could be triggered by the stress and then support the seed filling instead of the impaired photosynthetic leaf area. Figure 29 shows a yield reduction due to a post flowering water stress affecting 16 bean genotypes. A tendency of genotypes that accumulated stem dry matter either under stress or check conditions to produce significantly reduced yields was observed. On the other hand, genotypes which remobilized stem reserves produced superior yield, but there are exceptions, and the response is not clear under the post flowering stress.

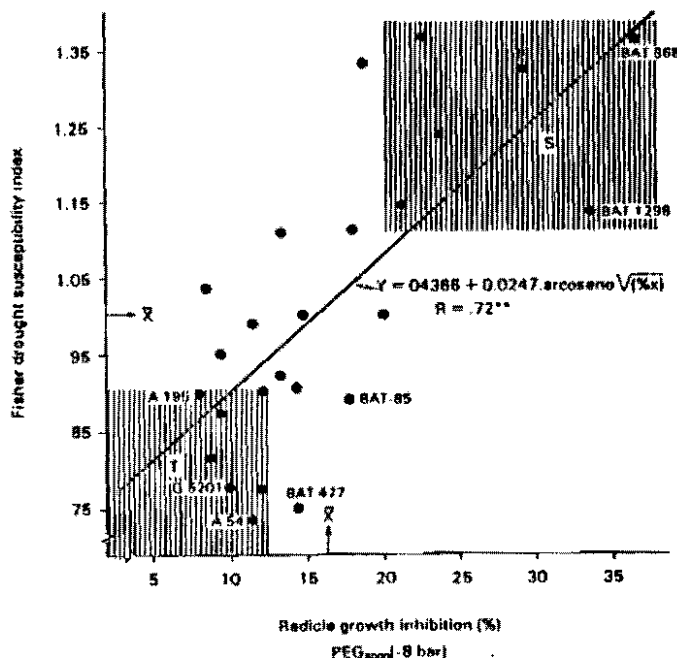


Fig. 28 Linear regression of the radicle growth inhibition caused by PEG (-8 bar) on the Fisher drought susceptibility index of 25 bean genotypes, Chillan. Source: Izquierdo and Huepe, 1986, unpublished.

3. Drought Tolerance Through Adaptation to Conditions Associated with Drought:

Most discussions of drought tolerance do not consider the importance of characteristics which, while perhaps not directly related to drought, are potentially essential components of drought tolerant bean varieties. Drought in bean growing areas is often associated with higher temperature conditions, and because of limitations on transpiration, plants under stress may experience unusually high leaf temperatures (Figure 30). Thus high temperature tolerance mechanisms may be needed in drought areas.

Many regions in tropical areas combine poor soil fertility with drought, and limitations on movement of water will also reduce nutrient availability. Genotypes which are especially efficient under poor fertility may be advantageous. It has often been speculated that materials tolerant to poor soil fertility should have greater root growth, and thus one might expect materials tolerant to infertile soils to perform well under drought conditions in similar sites. However, in a comparison of 2 drought tolerant lines and 8 materials selected for tolerance to acid soils, the drought tolerant materials were superior (Table 27).

Nitrogen fixation is reduced under drought stress (Laing *et al.*, 1984). In soybeans, fixation appeared to be more sensitive to drought stress than was photosynthesis (Weisz *et al.*, 1985), suggesting that some drought yield reductions may reflect nitrogen effects.

Drought environments where limited irrigations are practiced may cause problems of soil salinity. Although salinity causes what is physiologically a drought situation (see section on salt tolerance), additional problems are caused by toxic or deficiency effects of certain ions. Thus drought tolerance under saline conditions may require other adaptations.

Finally, certain diseases and pests are particularly problematic in drought situations. Perhaps the most notable is *Macrophomina solani* which only becomes problematic under drought conditions (Schwartz, et al., 1978). Screening for drought tolerance and *Macrophomina* tolerance at CIAT have produced remarkably similar results (Abawi and Pastor-Corrales, personal communication), and it is speculated that this reflects common tolerance mechanisms for the two problems.

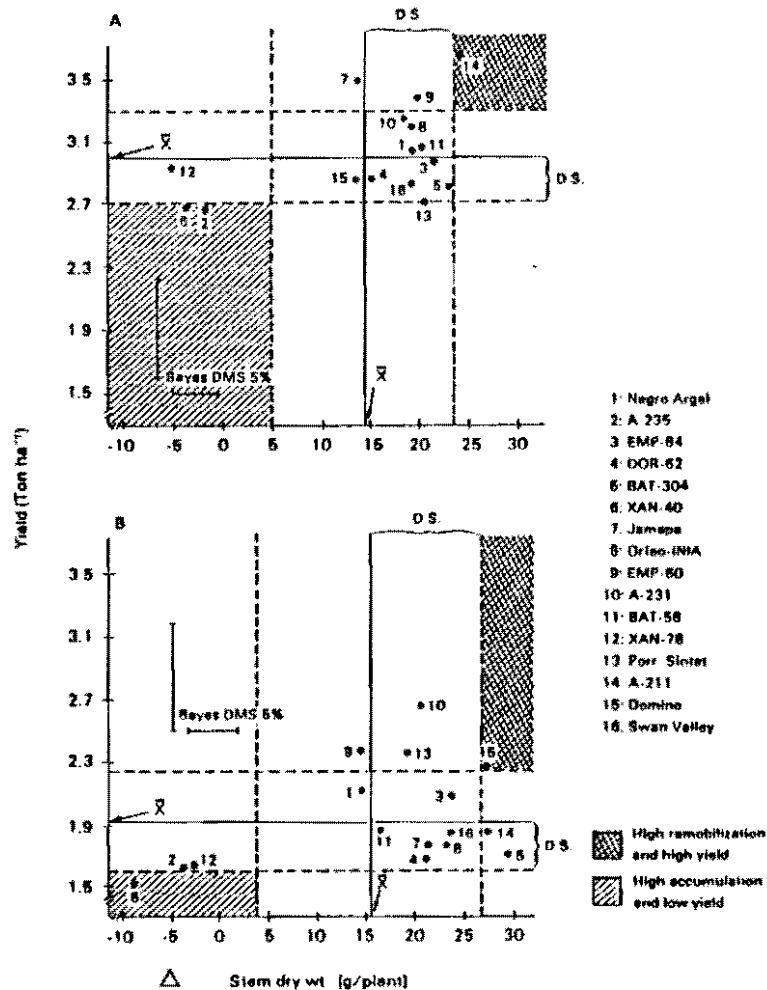


Fig. 29 Quadrant analysis of yield and stem dry weight changes during the reproductive growth period of 16 bean genotypes under: A) irrigated and B) postflowering water stress. Chillan, 1984. Source: Hernandez, 1984.

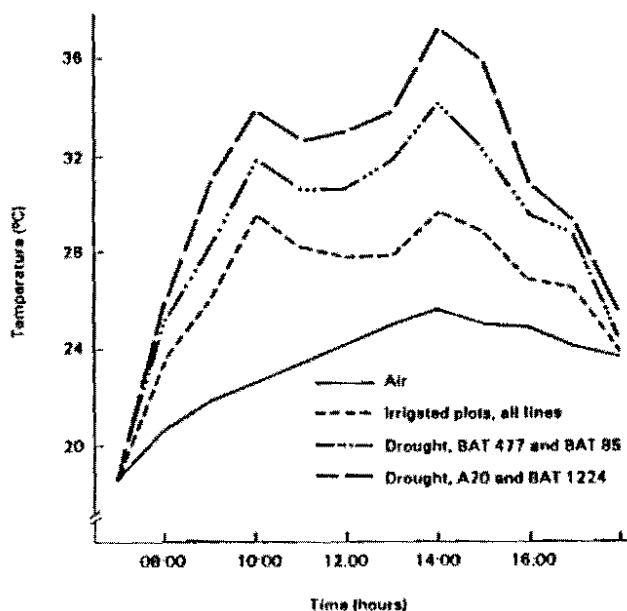


Fig. 30 Air and foliage temperatures for four bean lines grown under drought and irrigated conditions. Source: Sponchiado, 1985.

Table 27. Comparison of yields under drought stress in acid soils for 8 lines tolerant to acid soils, and 2 lines tolerant to drought. Santander de Quilichao, Colombia.

Line	Yield
	kg ha ⁻¹
Tolerant to acid soils:	
A 257	862
A 254	843
Carioca	825
VA 67	815
NAG 60	815
G 4830	812
BAT 1297	810
A 440	713
Drought tolerant:	
BAT 477	1096
G 5059	870
Mean	846
S.E.	71

4. Conclusions:

The reader may conclude from this review that drought tolerance is too complicated to merit study. We would argue that while the complexity of effects of drought has eliminated simple solutions, the prospects for improving yield under drought are good. Improvements in bean crop productivity can be made only through two basic approaches: 1) by modifying plant genotypes to fit their environment better ; and 2) by changing the environment to ameliorate the effects of environmental stresses. To overcome the constraints in both approaches, agronomists, breeder, physiologists and genetic engineers require a clear understanding of the physiological basis underlying yield and stress tolerance.

Studies on individual mechanisms may be integrated by simulation models which can predict effects of changes in climate and soil type. For example, Jones and Zur (1984) used dynamic simulations of soybean growth to test the relative importance of three mechanisms, osmotic adjustment, increased root growth, and increased stomatal resistance at full turgor, under clay and sandy soils concluded that greater root growth was the most effective mechanism, while increased stomatal resistance always resulted in reduced photosynthesis.

B. Excess Soil Water

Heavy rains often lead to soil flooding (water in excess of field capacity), especially in poorly drained soils. Beans are sensitive to such conditions, and yield reductions are frequently greater than one might expect. This can be attributed to the nearly immediate adverse effects on plant growth. Wadman-van Schravendijk and van Andel (1985) found that leaf and root growth halted within 2 days of flooding, this being associated with a severe drop in transpiration, but a rise in leaf ABA concentration.

The cause of damage from inundation is directly related to reduced gas diffusion in flooded soils, resulting in depletion of available O₂ and accumulation of CO₂ and ethylene in the root zone. Accompanying this is an inhibition of respiration, partial loss of root function, and possibly, accumulation of toxins due to blockage of respiration or activation of alternate, anaerobic processes. Higher soil temperatures, frequently found in tropical regions, can exacerbate problems of gas diffusion due to reduced solubility of gases and greater respiratory activity (Forsythe et al., 1979). Problems with root rots are often associated with flooding.

True tolerance mechanisms have not been identified in beans, but as in other crops, recovery from inundations is related to ability to produce new adventitious roots (Kahn et al., 1985). In trials at CIAT, flooding by maintenance of the water table to within 7 cm of the top of beds resulted in an average of approximately 50% yield reduction, but considerable varietal differences were found (Figure 31).

C. Saline Soils

Beans are considered salt sensitive, although Phaseolus coccineus has been classified as intermediate between moderately tolerant and moderately sensitive legume species (Lauchli, 1984). Problems in this crop associated with salinity are generally greatest in arid regions under irrigation, but localized areas of saline soils are found in many mesic environments.

Immediate effects of excess salinity include reduced plant growth, especially leaf area, and burning of leaf margins. These may reflect three underlying processes:

1. Physiological drought due to low osmotic potentials (high solute concentrations).

2. Nutrient imbalances due to relatively high concentrations of specific elements, especially sodium, inhibiting uptake of others.
3. Toxic effects of specific ions, particularly chloride and sodium.

Evidence for an osmotic effect comes from demonstrations that high relative humidity reduces stress effects, and that leaf relative water content is reduced markedly under stress (Ayoub and Ishag, 1974). Ayoub and Ishag (1974) also detected reductions of calcium and potassium cations under conditions of high sodium, but noted that the reductions did not reach levels thought to produce deficiency symptoms. High levels of chloride in bean leaves were associated with reduced photosynthesis, stomatal conductance, and RuBP carboxylase efficiency (Seeman and Critchley, 1985). These and similar findings suggest that effects of salinity are probably multiple, and it would be a mistake to emphasize a single mechanism.

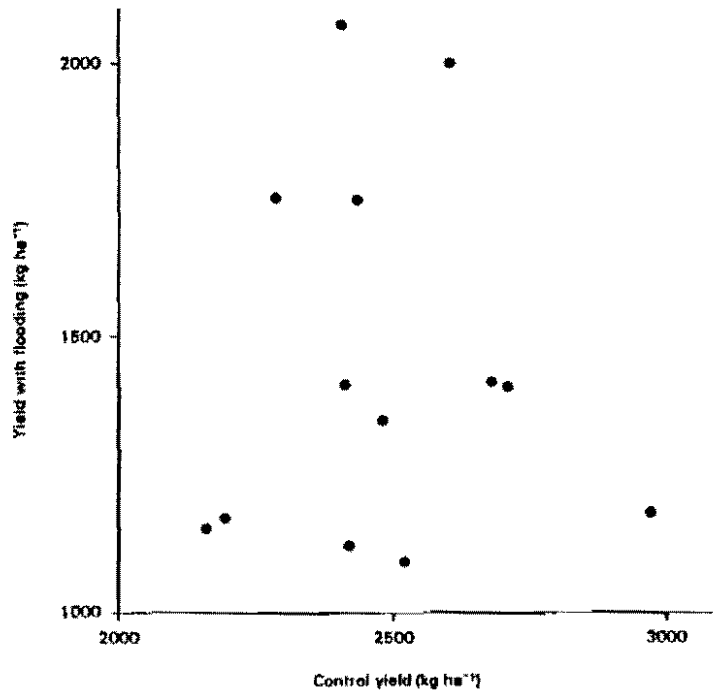


Fig. 31 Yields of 13 bean cultivars grown under flooded control field conditions. CIAT-Palmira, 1976.

At moderate levels of salt tolerance beans do show have been ascribed to their ability to accumulate sodium ions in root parenchyma vacuoles. Some soybeans appear to combine this mechanism with an ability to exclude excess chloride from shoots, and this might be a promising avenue for increasing salt tolerance in *Phaseolus vulgaris* (Lauchli, 1984). General recommendations for screening for salt tolerance in all crops were given by Greenway and Munns (1980). Smillie and Nott (1982) have described a chlorophyll fluorescence as a rapid test for salt tolerance, they using bean as a susceptible check.

Studies of genetic variation for salt tolerance among *Phaseolus vulgaris* cultivars are rare. Howler (personal communication) detected varietal differences under field conditions, but noted that variability in salinity under field conditions makes large scale screening difficult. Debouck (personal communication) collected land races of beans from apparently saline soils in Mexico.

Several investigators have reported the selection of salt-tolerant cell lines in sweet pepper, sugar cane, coffee, rice and taro. However, regeneration of plants from salt tolerant cells have been limited in these crops, and has apparently never been attempted with beans.

D. Generalized Stress Tolerance: "Rusticity"

It is frequently commented that while traditional bean cultivars may lack specific disease or other stress resistances, they often outperform supposedly "improved" materials under farm conditions.

Alfaro (1981) concluded from 124 bean cultivar trials at 80 locations and 20 countries that the yields of "Jamapa" and "Porrillo Sintetico", used as standard checks of known adaptability, were not frequently surpassed by diverse materials. However, the low values of the stability index (b) for cv. Porrillo Sintetico in the analyses of Voysest and Garcia (1984), suggest that this cultivar performs relatively better in poor sites as compared to similarly yielding cvs. Jamapa and ICA Pijao (Table 28). Low b values are indicative of relatively good yield in poor environments and lack of response in rich sites. Cv. Porrillo Sintetico stands out consistently for lower b values for similar mean yields in a given IBYAN. Since stresses varied greatly among sites in the IBYAN's, the better performance of cv. Porrillo Sintetico in poor sites presumably reflected some generalized stress tolerance or "rusticity" rather than resistance to a few specific stresses and/or diseases.

Other examples of rusticity comes from studies of cultivar response to artificial defoliation. In a comparison of 17 cultivars receiving a 60% defoliation at 30 days from planting cv. Carioca actually increased yield under the defoliation stress while line EMP 84 showed a marked yield reduction (Fig. 32). This would suggest that cv. Carioca would maintain its yield under a wide range of stresses affecting leaf growth, a conclusion consistent with cv. Carioca's popularity in Brazil.

Table 28. Comparison of regression response (b) and mean yields across sites of three cultivars used as checks in International Bean Yield and Adaptation Nurseries from 1976 to 1981. Data from Voysest and Garcia (1984).

Year	No. of trials	Porrillo Sintetico		Jamapa		ICA Pijao	
		b	Yield	b	Yield	b	Yield
		kg ha ⁻¹		kg ha ⁻¹		kg ha ⁻¹	
1976	54	0.77	1539	1.02	1572	0.79	1566
1977	31	0.88	1623	1.09	1627	-	
1978	33	0.84	1486	1.06	1498	1.17	1529
1979	32	0.80	1501	1.06	1579	1.06	1554
1980	48	0.95	1584	1.06	1656	1.06	1637
1981	26	0.89	1565	1.01	1723	-	
Mean	37	0.86	1550	1.05	1610	1.02	1570

Calculating a generalized stress yield as the geometric mean of yields under 33% defoliation and under post flowering drought, data from Hernandez (1984) show a low correlation between stress and control yields (Fig. 33). The contrast between A 231 and Orfeo INIA is particularly striking with both lines yielding about the same in control plots, but differing by 800 kg ha⁻¹ under stress. The comparison of cvs. Porrillo Sintetico and Jamapa is also instructive, with Jamapa outyielding Porrillo Sintetico by 800 kg ha⁻¹ in the control, but being slightly inferior under stress.

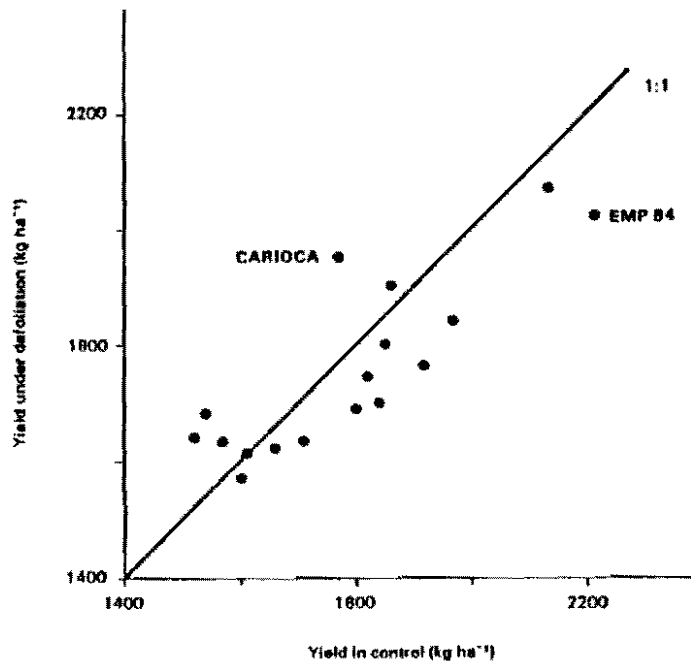


Fig. 32 Relative yield performance of 17 bean lines under 60% defoliation at 30 days after planting. CIAT-Palmira, 1983.

Possible characteristics which might confer rusticity include:

1. Ability to produce recuperative growth, presumably resulting from remobilization of carbohydrate or nitrogen reserves and an indeterminate growth habit.
2. Good competitive ability.
3. High tissue concentrations of compounds such as phenolics with inhibitory effects on a broad range of pathogens or pests organisms.
4. Greater partitioning to root growth.
5. Buffer ability for adequate pod retention and seed filling.

Earliness also might be considered a mechanism since it permits escape of many stresses. Data from the 1976 IBYAN supported this. For sites within 30° of the Equator (thus eliminating trials with severe photoperiod effects), early maturing cultivars had significantly lower regression response on site mean yield (b parameter), indicating that they yielded relatively better as compared to late cultivars at the poorer sites (Fig. 34). That the regression response was not significantly correlated with yield ($r = 0.22$) demonstrated that low values of b in early cultivars did not simply reflect poor yields across sites (White, 1984).

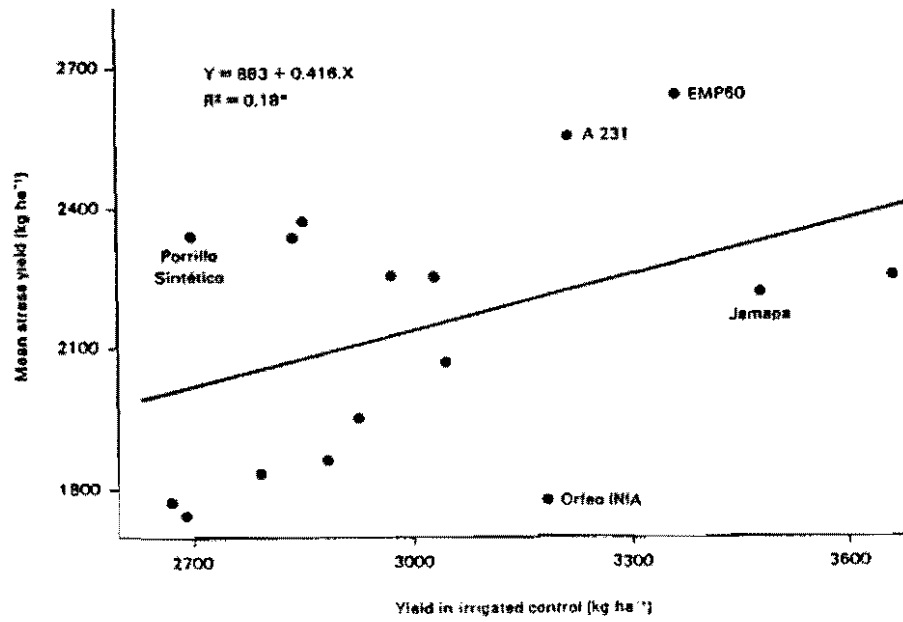


Fig. 33 Comparison of stress and irrigated control yield on 16 bean lines. Stress yield is geometric mean of defoliation and drought treatments. Based on data from Hernandez, 1984.

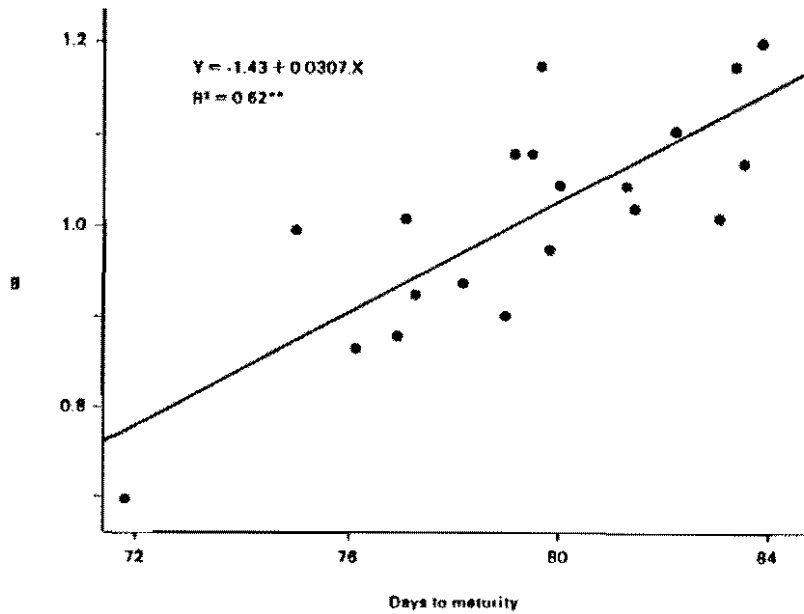


Fig. 34 Relationship between mean days to maturity and regression response of yield (b) for 20 cultivars of the 1976 IBYAN. Source: White, 1984.

While there is evidence suggestive of differences in "rusticity" of bean cultivars, it is difficult to decide whether such a characteristic is best sought by selecting under a moderate level of various stresses, or identifying specific characteristics related to rusticity. Effects of local adaptation could confound results unless such work is restricted to specific sites.

V. CONCLUSION

Crop physiology is often criticized for the lack of tangible benefits it has provided to farmers, this criticism certainly extending to research on the common bean. While in some cases criticism was invited by over enthusiastic promises about the utility of certain lines of work, we would argue that the complexity of interactions of physiological processes precludes rapid solutions. It is seldom possible to reach firm conclusions about a given set of physiological processes, because each process interacts with others. The evolution of our knowledge of physiological processes is perhaps best likened to the manufacture of a complex machine. Although great strides may have been made in constructing our physiology machine, and it may even have sub-units which seem to function well, only as the machine nears completion will it approach its intended level of productivity. Even then, if some parts were poorly manufactured, it may not meet expectations until the flaws are identified and corrected. We would argue that patience and care are needed to assure that the physiology machine is well built. As in any construction project, priorities can and should be set. Nitrogen remobilization in relation to leaf senescence and seed growth is among the area where our understanding is most deficient. In comparison to photosynthesis, respiration is almost untouched, yet the few studies in other crops indicate great potential for increasing yields. And in all research, greater pains should be taken to assure that conditions used are relevant to what may occur in bean fields, not laboratory benches or greenhouses.

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