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SUMMARY

Common beans (*Phaseolus vulgaris* L.) are an important world crop with a relatively low productivity in most cropping systems. Physiological factors influencing yield are discussed in this paper with respect to field research in the tropics. The comparative earliness of the majority of the germplasm is closely associated with suboptimal canopy development which leads to lower yield potentials. Leaf area development is dependant on the basic nodal structure as is the potential sink. Increases in nodal structure led to increases in both source and sink and consequently yield. The species is comparable to soybeans in terms of various efficiency parameters (yield per unit leaf area duration, harvest index and yield per day of growth cycle) and differences in crop growth rate are proportional to differences in leaf area. Water stress tolerance, and specific adaptation to temperature extremes have been identified in the species while the results of photoperiod response evaluations appear to have future application in predicting phenological responses.

INTRODUCTION

The common bean (*Phaseolus vulgaris* L.) is the most widely grown of the four cultivated species of *Phaseolus* all of which have their centers of origin and domestication in the American tropics. This species is the most important grain legume in the world for direct human consumption. Of the estimated mean annual world production of 8.3 million mt (1976–78), 47% were produced in Latin America and the Caribbean, 16% in Africa, 15% in China, 11% in North America and 8% in Europe (Sanders, unpublished data, 1980).

The dry edible bean is an important protein and calorie source in human diets in developing countries particularly in eastern Africa and throughout most of the Americas. The green pod is also one of the most widely eaten vegetables in the world. Weighted mean per capita dry bean consumption (1975–77) was 15 kg/annum (range 2–24) and 12 kg (range 3–50) for the main producing countries in Latin America and Africa respectively.

The common bean is not recognised as a high yielding species with reported national average yields usually less than 1t/ha in most developing countries and below 1.4 t/ha in most developed countries. Research at the international level is conducted by CIAT in Colombia in collaboration with national institutions throughout the world. In this paper some aspects of the physiology of yield and adaptation under field conditions in the tropics will be discussed, with particular reference to work at CIAT.

GERMPLASM

Phaseolus vulgaris is a highly polymorphic legume species showing considerable variation in growth habit, vegetative characters, flower color and in size shape and color of seeds and pods. The current world germplasm bank, assembled at CIAT, consists of 26×10^3 individual collections of which 9.5×10^3 have so far been evaluated (CIAT, 1979). The collection is classified into four main growth habits, viz. determinant bush (I), indeterminant erect bush (II), indeterminant prostrate and semiclimbing (III), and indeterminant climbing (IV) types. Data in Table 1 demonstrates this wide variability for key parameters when evaluated at CIAT-Palmira. The relative degree of determinacy for the growth habits can be compared by noting the change in mean main stem node number between flowering and maturity. Mean seed weight is higher in I and IV materials. The main difference between Type II and III lies in the heavier degree of prostrate branching in Type III compared to the more erect canopies in Type II.

The most common growth habit in the collection is the prostrate heavily branched Type III materials. This probably reflects human selection pressure among the genetic diversity for land races which are appropriate for low density seedings in rustic production systems usually involving maize-bean intercropping. The majority of Type I collections are derived materials from temperate latitudes. The majority of Type IV land races occur in cropping systems at altitudes

Table 1. Mean data[a] for selected morphological and phenological characters for the four growth habits of P. vulgaris: data in body of table show mean and standard deviation in brackets.

Parameter	Growth habit I Determinant bush	Growth habit II Indeterminant bush	Growth habit III Indeterminant semi-climbing	Growth habit IV Indeterminant climbing
% of total evaluated	23.7	23.2	33.3	19.8
Plant height, cm	44(18)	92(44)	103(28)	160(50)
Nodes[b] at flowering	8.3(1.5)	13.3(1.9)	14.3(2.1)	14.8(4.0)
Nodes[b] at maturity	8.6(1.4)	17.0(2.0)	18.9(2.6)	22.7(4.0)
Seed weight, mg/seed	336(100)	236(80)	257(89)	294(107)
Days to flowering	34(3)	39(4)	38(5)	40(6)
Duration of flowering	22(6)	25(5)	28(6)	29(7)

[a] Data derived from evaluation of 9.5×10^3 germplasm collections at CIAT-Palmira (3°N, 1000m altitude, mean temperature 23.8°C) at density 20-25 plants/m^2. [b]Number of main stem nodes.

>1800m in the tropics, while Type II and III are most common at lower altitudes (500-1800m). The climbing Type IV materials are mostly grown in direct association with maize at these higher altitudes while the bush types are grown in monoculture and in relay and direct associations, chiefly with maize.

ECOLOGY

Agroecological surveys (CIAT, 1979) of the production areas in Latin America have defined a preliminary set of 110 microregions to which mean monthly temperature, rainfall and estimated evaporation parameters have been assigned. Based on the bean production statistics for these microregions a relative weighting can be given to the relative importance of climatic limitations in traditional production areas. A remarkable concentration of production (76%) occurs in microregions with mean flowering period temperatures in the range of 19-23°C (Table 2). Although these microregions are located over an extremely wide range of latitudes and altitudes, annual cropping systems have evolved which reflect the general temperature adaptation characteristics of the species.

The other important feature of the data is the ∿70% of production in microregions which are affected by mean growing season water deficits of more than 0.1 mm per day under rainfed conditions. In the majority of these latter microregions increasing late season stress towards the end of the tropical and subtropical wet season appears to be

Table 2. Distribution of production of common beans (*P. vulgaris*) in Latin America according to cluster analysis of crop climate for 110 microregions of production: data in body of table shows percent of Latin American production occurring in mean climates within each two way cluster group.

Mean cropping season water balance regime (mm/day)	Mean temperature regime at flowering °C				Total
	>23°	19°–23°	14°–19°	<14°	
Excess water (>0.1)	1	3[a]	n	n[c]	4
Adequate water (0.1 to –0.1)	n	17	n	1	18
Water stress (–0.1 to –3)	6	42	11	n	59
Severe drought (<–3)	n	14	n	n	14
Total	7	76	11	1	95[b]

[a] Highest rainfed municipio yields in Latin America occur in this grouping e.g. western El Salvador. [b] 5% of total annual production not allocated. [c] n= negligible production indicated in preliminary data survey.

the main type of deficit experienced. This probably reflects the common practice of growing maize and beans in sequential relay systems with beans placed in the latter phase of lower mean temperatures (in the subtropics) and declining mean rainfall and increasing variability.

The production distribution of the species reflects the moderate temperature conditions in the centers of diversity in the highlands of Meso-America and northern South America. Areas of diversity and of domestication (Evans, 1976) occur in the 500-1800m altitude range with a high frequency of wild types recorded at ca. 1200m in Meso-America (Miranda, 1974). Smartt (1969) and Evans (1973) discuss the evolution and domestication of the species from wild climbing ancestral materials of which P. aborigineus is probably a modern survivor.

PHOTOSYNTHESIS

Photosynthesis of Single Leaves

Phaseolus vulgaris is a C_3 plant. Maximum reported values of net photosynthetic rate (Pn) during the ontogeny of individual leaves range from 25-40 mg CO_2 dm^{-2} h^{-1} (Tanaka and Fujita, 1979; Izhar and Wallace, 1967; Louwerse and Zweerde, 1975) which is comparable with C_3 cereal crops such as rice (Tanaka, 1966). In an extensive series of experiments in Hokkaido, Tanaka and Fujita have shown a normal increase in Pn during leaf expansion and a decline with leaf age with large differences in the shape of the Pn curves versus time, depending on leaf position, nitrogen content of the media and other factors. A very high correlation of Pn with leaf N content was recorded with the highest Pn values at ∿16 mgN dm^{-2} of leaf. Saturating light intensities for individual leaves also vary considerably with leaf age and on such factors as the irradiance conditions experienced during leaf growth. (Louwerse and Zweerde, loc.cit.). Saturation values of 150–250 J m^{-2} sec^{-1} are commonly reported by most workers. Tanaka and Fujita found no significant differences in Pn of different bean cultivars under comparable conditions of leaf age. On the other hand, Izhar and Wallace report cultivar differences of the order of 9–35%. Pn rates in the Hokkaido studies were initially reduced by adjacent sink removal (pods) but recovered above the controls due to higher subsequent nitrogen availability. Stem carbohydrate accumulation was shown to be very sensitive to source sink manipulation through leaf and pod removal.

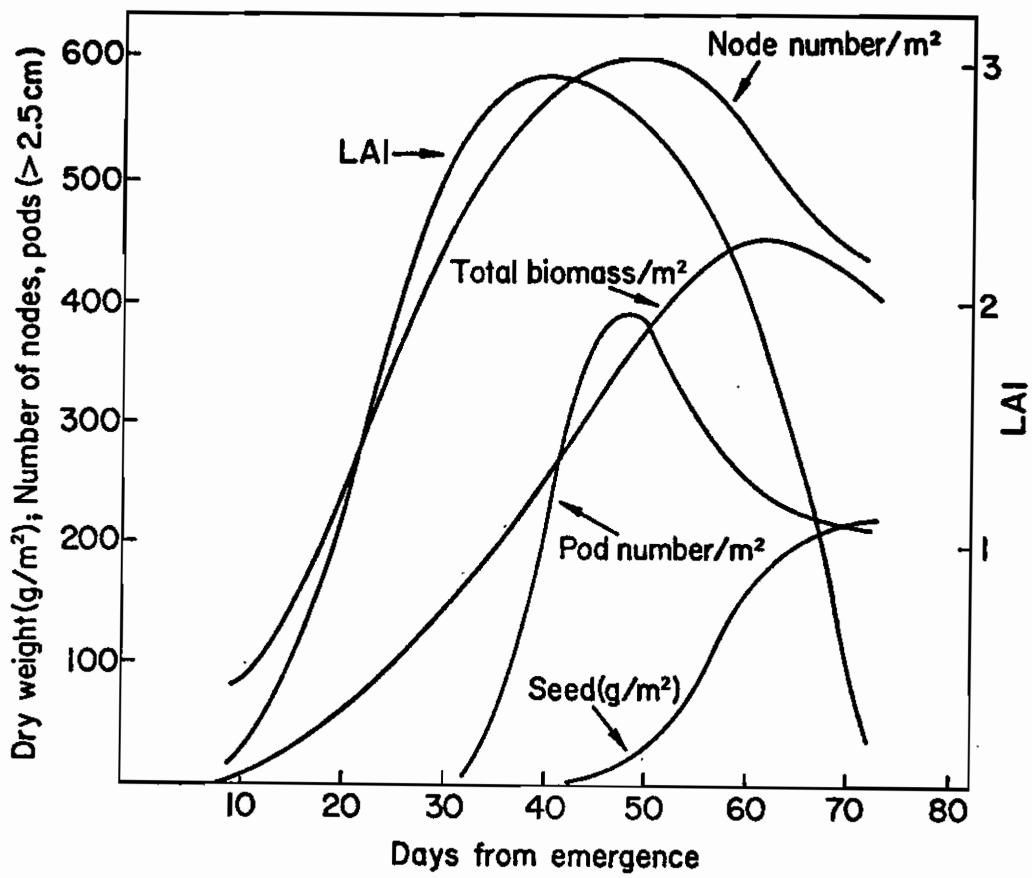
Photosynthesis of the Crop Canopy

Sale (1975) reports one of the few studies available on field canopy photosynthesis in the species. In a high radiation environment (20 MJ m^{-2} day^{-1}) in southern Australia, bean canopies had maximum canopy net photosynthesis ($P'n$) values of from 35–40 mg dm^{-2} h^{-1} at saturating irradiance values of 600–650 W m^{-2} and LAI of >4.5. No change in $P'n$ was recorded over a range of LAI values from 4.5–7.3. These data are very similar to those recorded for soybeans (Jeffers and Shibles, 1969) and wheat (Puckridge and Ratkowsky, 1971; Walcott and Laing, 1976) except that soybeans showed some $P'n$ response to increasing LAI above 4.5. As in many other species 95% of incoming radiation is intercepted by bean canopies at a LAI of ∿ 4 (Aguilar et al 1977).

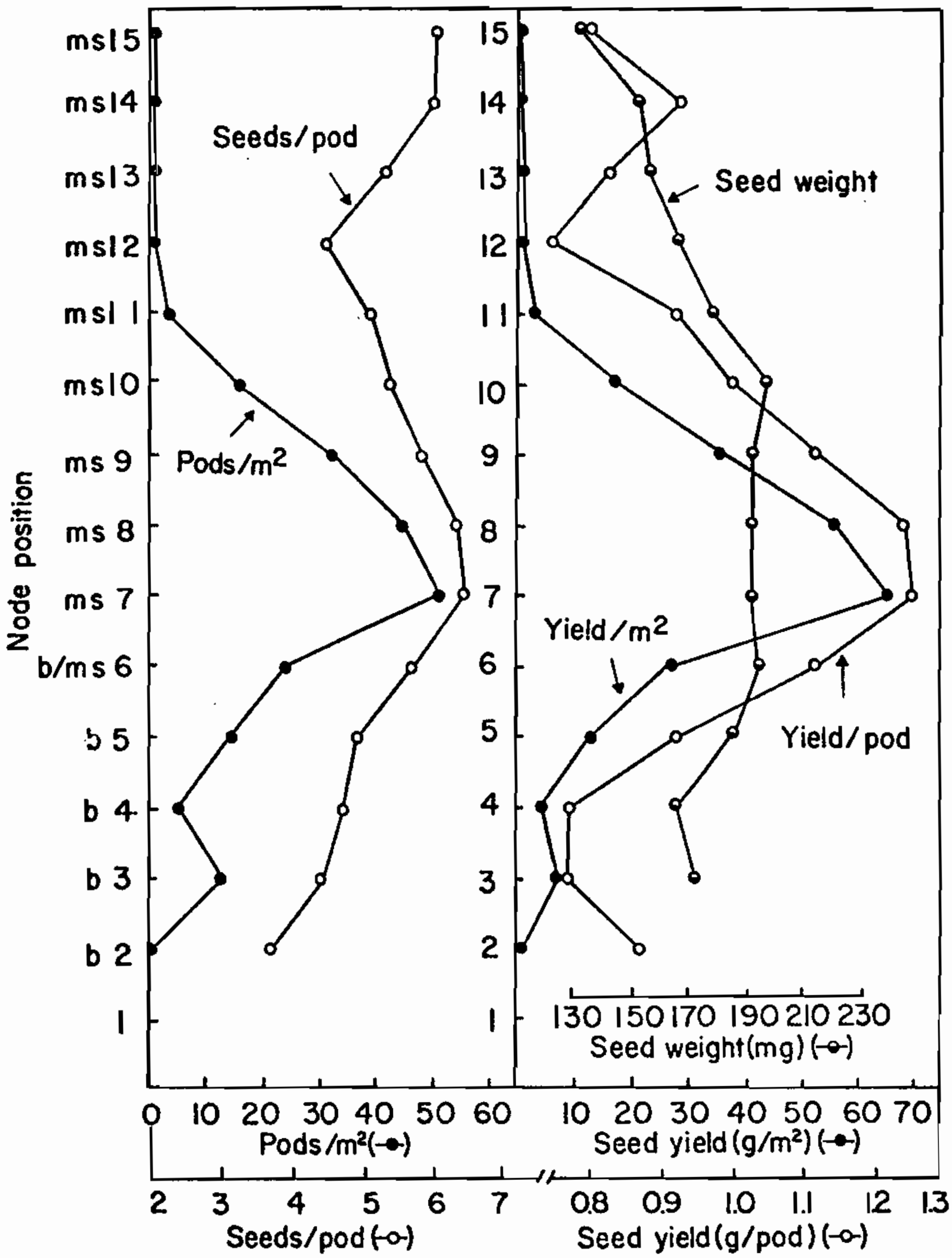
CROP GROWTH AND YIELD

Studies on a Single Cultivar

Key growth parameters are presented in Fig. 1 for a typical indeterminant bush cultivar (Porrillo Sintetico, growth habit II) grown at CIAT under irrigated and protected conditions at a density of 25 plants/m^2. The crop yielded 2.4 t/ha (14% basis) in 76 days from emergence to physiological maturity (DAE). The maximum LAI values at 40 DAE were less than 3 with a maximum biomass accumulation of 4.5 t/ha at 62 DAE. Pod number (counted when greater than 2.5 cm in length) increased to a maximum at 46 DAE and declined with small pod abscission. The flowers which ultimately abscissed where those opening late in the flowering phase particularly on the upper nodes and branches (CIAT, 1976). The rapid decline in LAI and pod number coincided with the rapid grain growth phase (50-65 DAE). Rapid senescence of the crop was thus closely associated with grain growth as photosynthate and other metabolites where translocated to the developing grain. Leaf senescence occurred first at the lower nodes and proceeded sequentially up the main stem and later on the branches. The profile structure of yield in a similar crop of the same cultivar (Fig. 2) shows peak yield/node/m^2 at node 7 and a close association of yield per node with pod number per node. Seeds per pod and particularly seed



1. Key growth parameters for cv. Porrillo Sintetico versus days from emergence: CIAT-Palmira.



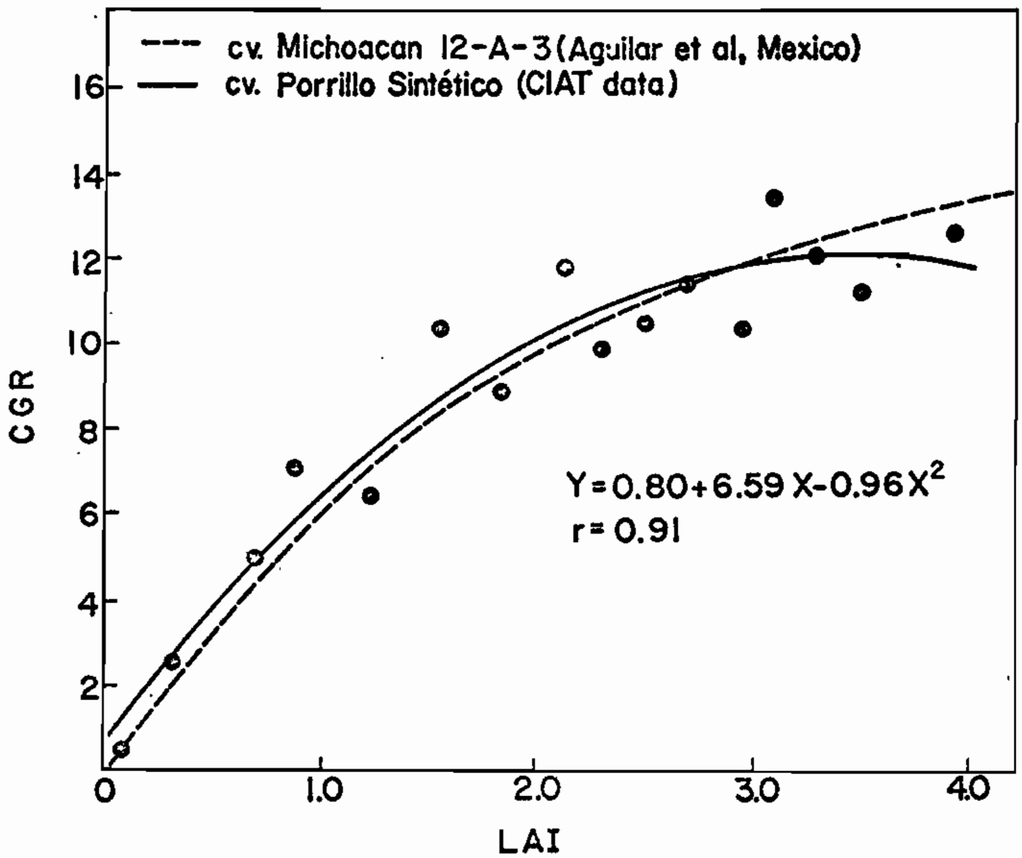
2. Yield and yield component profile by main stem node number for cv. Porrillo Sintetico in a typical experiment, (b refers to nodes at which branches were subtended).

weight were more conservative but it is clear that the highest seed yield per pod was also recorded at node 7. The first flowers to open in this cultivar normally occur on racemes borne at node 7. In most crops of Porrillo Sintetico ∿ 10% of the yield was normally borne on branches subtended at nodes 3-5. Branch yield as a proportion of total, normally increases with the degree of lodging.

From the trends in the above parameters a clear picture of a typical growth pattern for a bush bean cultivar can be drawn. The crop was of relatively short duration and thus did not have sufficient time to develop a higher LAI prior to the onset of grain growth. Considerable supporting evidence suggests that earlier formed reproductive tissue has a strong advantage with respect to the partitioning of current photosynthate in this species. Maximum main stem carbohydrate (sugar plus starch) content of approximately 12-15% of stem dry weight occurred just prior to the onset of grain growth with a very rapid decline to 2-3% as grain growth proceeded. The actual maximum level of stored carbohydrate in the stem varied considerably from one crop to another and appeared to be related to crop vigor and leaf area availability. In many experiments under CIAT conditions there has been no indication of an increase in stem carbohydrate storage during the grain growth phase. Tanaka and Fujita (loc.cit.) found increasing carbohydrate storage during grain filling which they suggest is evidence of a sink limitation to yield during the filling phase. No such conclusion can be drawn from available CIAT data.

Crop growth rate (CGR) in the same cultivar when meaned over a number of experiments shows a curvilinear response to increased LAI (Fig. 3). An approximate curve for a similar Type II cultivar in the studies of Aguilar et al (loc.cit.) in Mexico under similar solar radiation conditions (16-18 MJ m^{-2} day^{-1}) are in close agreement with the CIAT study at least up to a LAI of $\sim$ 4. The Mexican crop was grown at a higher plant density of 28/m^2 and had a longer growth cycle ($\sim$ 95 DAE). The crop developed a higher maximum LAI and CGR of 5.3 and 16.5 g/m^2/day respectively with a final seed yield of 4210 kg/ha. In normal crops of Porrillo Sintetico at CIAT values of maximum LAI are normally < 3.5.

The values of LAI ≥ 3 in Fig. 3 were generated artificially by photoperiodically inducing an extension of the growth cycle. In this experiment the moderately photoperiod sensitive cv. Porrillo Sintetico was grown in normal field plots at distances of 0-25m from a linear light source (300W incandescent lamps) giving an effective day length of 16h30 near the source compared to the natural 12h20 prevailing at a distance >12m. The long day sensitive cultivar flowered 15 days later near the lights. Physiological maturity occurred 26 days later than the control plot. Yield and other key parameters for plots harvested at different distances from the lights are presented in Table 3. Yield increased by 48% to 4123 kg/ha at a maximum LAI of 4.0. Vegetative node no./m^2 increased by 45% due to the longer preflowering period. The greatly increased proportion of yield on branches was clearly a product of the extra nodes formed on the branches. The only yield



3. Crop growth rate in cv. Porrillo Sintetico meaned over a series of experiments for the same time periods versus the main LAI (data for a hand drawn curve from Aguilar et al 1977 for comparison).

Table 3. Effect of photoperiodically extending the growth cycle of P. vulgaris (cv. Porrillo Sintetico) on selected growth and yield parameters under field conditions. CIAT-Palmira, 1976.

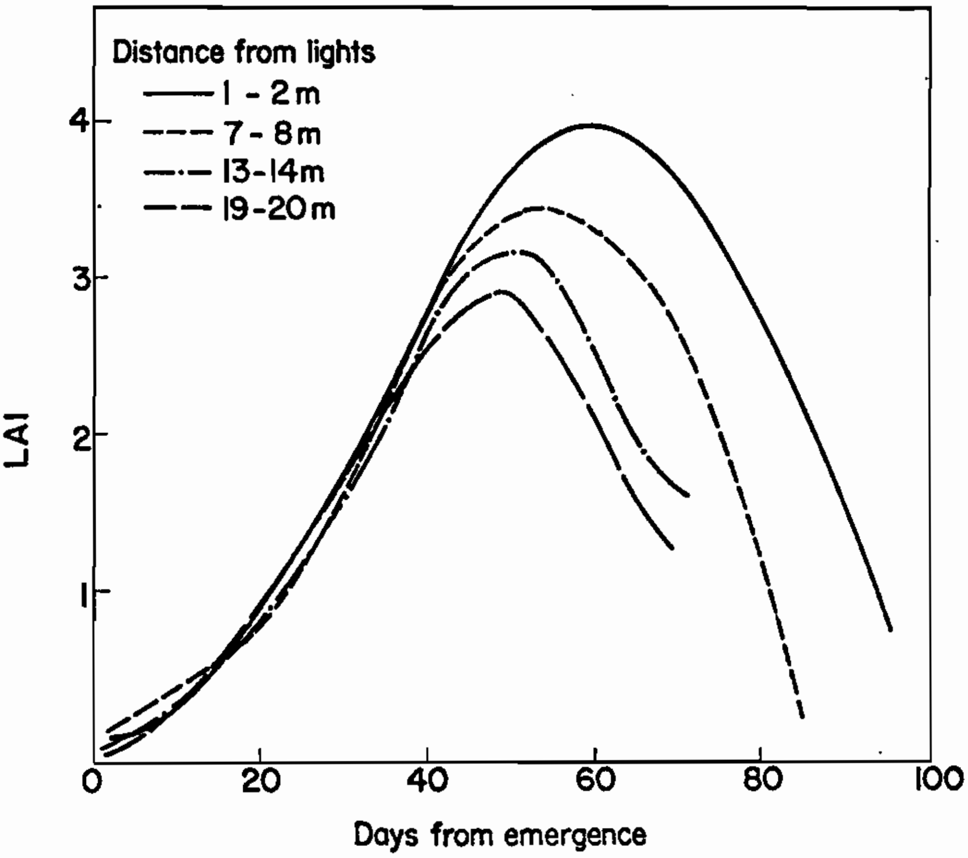
Parameter	Plot distance from linear light source, m				r[e]
	1-2[a]	7-8	13-14	19-20[b]	
Seed yield (kg/ha)[c]	4123	3474	2983	2772	
Harvest index (%)	49	50	51	54	- 0.87
Days to flowering	51	43	36	36	0.98
Days to physiological maturity	95	84	71	69	0.99
Seed yield/day (kg/ha/day)	43	41	42	40	0.77
No. pods/m^2	314	255	214	208	0.99
No. seeds/pod	5.7	5.8	5.6	5.5	0.69
Seed weight (mg/seed)	197	201	210	207	- 0.92
No. nodes main stem/m^2	520	460	407	370	0.99
No. nodes branches/m^2	268	272	147	179	0.82
% yield on branches	82	39	18	14	0.99
Percent flower abscission[d]	59	-	-	68	-
Maximum LAI	4.0	3.8	3.0	2.7	0.95
LAD (days)	187	150	110	99	0.99
Yield/LAD	2.2	2.3	2.7	2.8	- 0.95

[a] Effective day length 16h30. [b] Represents normal control crop since photoperiodic effect of 300W incandescent lamps diminished to zero at ~12m; effective daylength 12h20. [c] 14% moisture basis; plant density 25/m^2. [d] Percent of opened flowers which finally abscissed. [e] Correlation with yield, r= 0.91 required for significance at 1%.

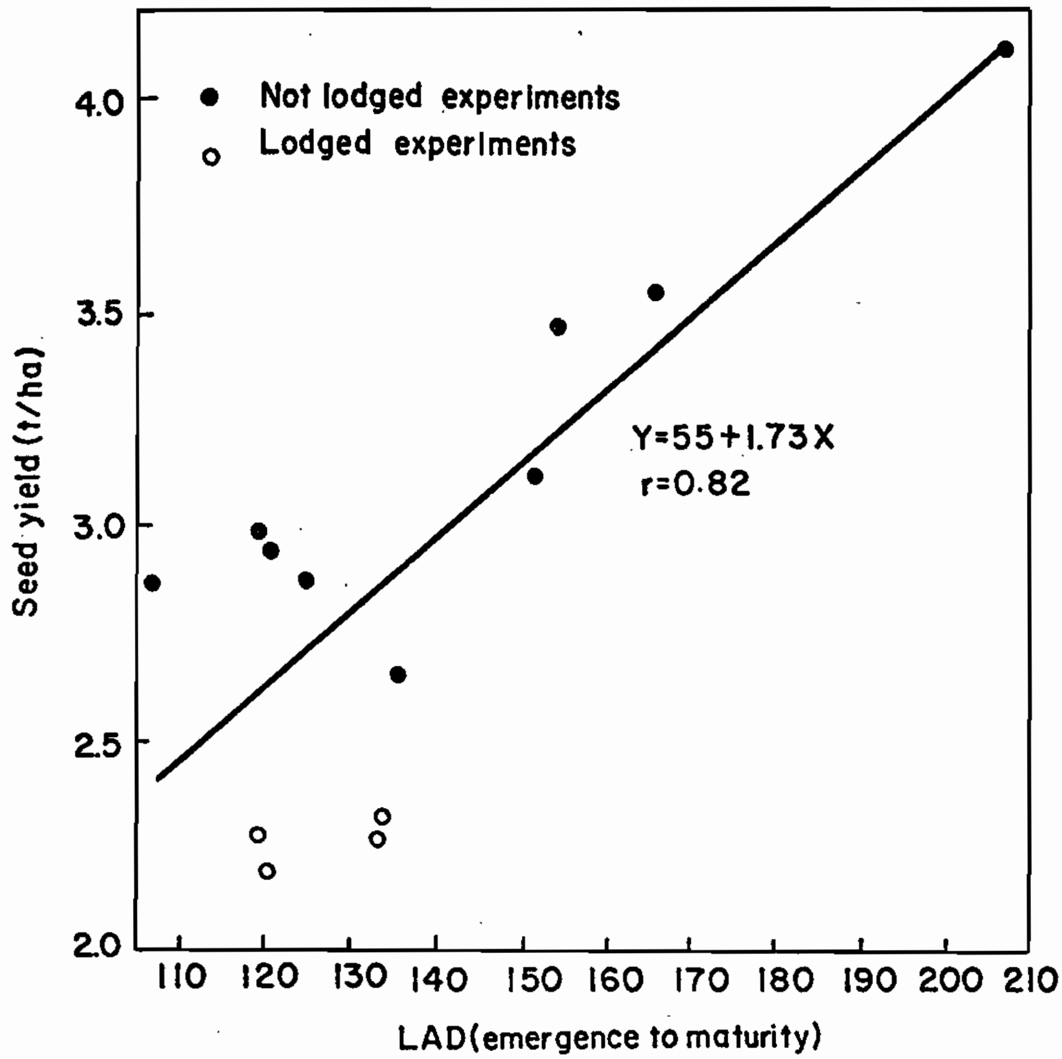
component significantly affected by the treatment was pods/m^2. Fitted leaf area index curves in Fig. 4 show the effects of the increased length of the growth cycle on development. In this case the basic form of the curves were not altered by the treatment.

Physiological and phenological constraints on yield of normal crops are clearly demonstrated in this data. By increasing the length of the growth cycle, an increase in both the basic nodal structure and of leaf area duration allowed a concurrent increase in both source and potential sink i.e. racemes subtended in the extra vegetative nodes. The percentage of flower abscission decreased significatively as yield increased. This suggests that the extra leaf area available produced a more favorable photosynthate status in the plant thus allowing a higher proportion of flowers to set pods. The yield per unit of leaf area duration from emergence to physiological maturity and harvest index declined as yield increased suggesting lower canopy yielding efficiency at the high yield levels.

A series of experiments with cv. Porrillo Sintetico grown in different semesters gave yields ranging from 2.19 - 4.12 t/ha. The variation in control yield was associated with a range of soil (alkalinity, poor drainage), and some uncontrolled disease and insect constraints (CIAT, 1977). The combined data for these trials and those of the extension experiment show a high positive correlation of yield for parameters such as LAD (Fig. 5), pods/m^2 ($r = 0.94$) and total dry matter (0.81) and a negative correlation with harvest index (-0.28). These data support the



4. Leaf area index for cv. Porrillo Sintetico versus days from emergence for four treatments at different distances from a linear light source (curves fitted by trigonometric functions).



5. Seed yield versus LAD for 13 crops of Porrillo Sintetico grown in different semeters and fields, including four data points from the photoperiod extension experiment (Table 3).

conclusion that yield variation in this cultivar was associated with an increase in both source and potential sink. Data from the experiments of Aguilar et al (loc.cit.) also show a strong relationship between post flowering LAD and yield for a single cultivar where the different treatments were generated by sowing at a range of densities. The authors suggest that these data do not necessarily indicate a cause and effect relationship since pod number was also highly correlated with yield.

Experiments using Porrillo Sintetico were conducted to evaluate the effects of increasing (through canopy CO_2 fertilization) and decreasing (through shading) photosynthate supply during the post-flowering period. CO_2 fertilization at 1200 ppm increased yield by 40% when applied from -5 to 15 days from first flowering in open topped field chambers (CIAT, 1977). This increase was mainly through improved pod set at secondary positions on existing racemes. A small increase in seeds/pod and seed size was also recorded.

Shading treatments (66% interception) when applied for eight individual weekly periods from -13 to 43 days from flowering reduced yields by a maximum of 18.5% in the period immediately following first flowering with much lower reductions after 22 days. The yield components were affected sequentially with the largest yield reductions associated with reduced pod set during the critical phase when final pod number/plant was being determined. Seeds per pod and seed weight were less affected but reduction in yield was associated with effects on these components when shading was applied during the critical period for each component.

In summarising the work on Porrillo Sintetico it is clear that yield was increased either by increasing source and sink concurrently through an extension of the growth phase or by increasing photosynthate supply by CO_2 fertilization for a given leaf area. The critical importance of pod set in yield is also clear as is the association between increased source and pod set. Since lodging considerably lowered yields at a particular LAD value (Fig. 5) an improvement in this character is one means by which canopy efficiency could be improved particularly in potentially high yielding crops where lodging is more serious. Other means of improving canopy efficiency through improved leaf display and/or leaf shape are yet to be explored in this species. Considerable research on beans at Cornell (Wallace et al 1972) has not been able to show a clear relationship between yield and genotypic differences in photosynthesis efficiency of individual leaves.

Comparative studies among growth habits

Key parameters (Table 4) for a typical experiment at CIAT comparing selected cultivars from the four growth habits show similar conclusions to those obtained for single genotype. Over a wider range of maximum LAI values (3.4 - 6.0) yield was positively correlated with both structural parameters such as node number and with the amount of available leaf area. A decline in the canopy efficiency parameters (yield/LAD and harvest index) was associated with increased yield particularly in the Type IV cultivar. In the latter case the artificial support

Table 4. Mean yield and other key growth parameters for selected and representative cultivars of *Phaseolus vulgaris* L. from four growth habits in growth analysis experiments. CIAT-Palmira, 1977.

Parameter	Cultivar[a] and Growth Habit				
	G1540	G4495	G3353	G2525[d]	r^e
	I	II	III	IV	
Yield (kg/ha)[b]	2423	2730	3221	3653	
Yield/day kg/ha/day	34	35	37	39	0.83
No. nodes/m^2 at harvest	413	587	923	864	0.94
Maximum leaf area index	3.4	3.6	4.1	6.4	0.94
Leaf area duration (LAD days)[c]	114	130	164	261	0.93
Yield/LAD	2.1	2.1	2.0	1.4	–

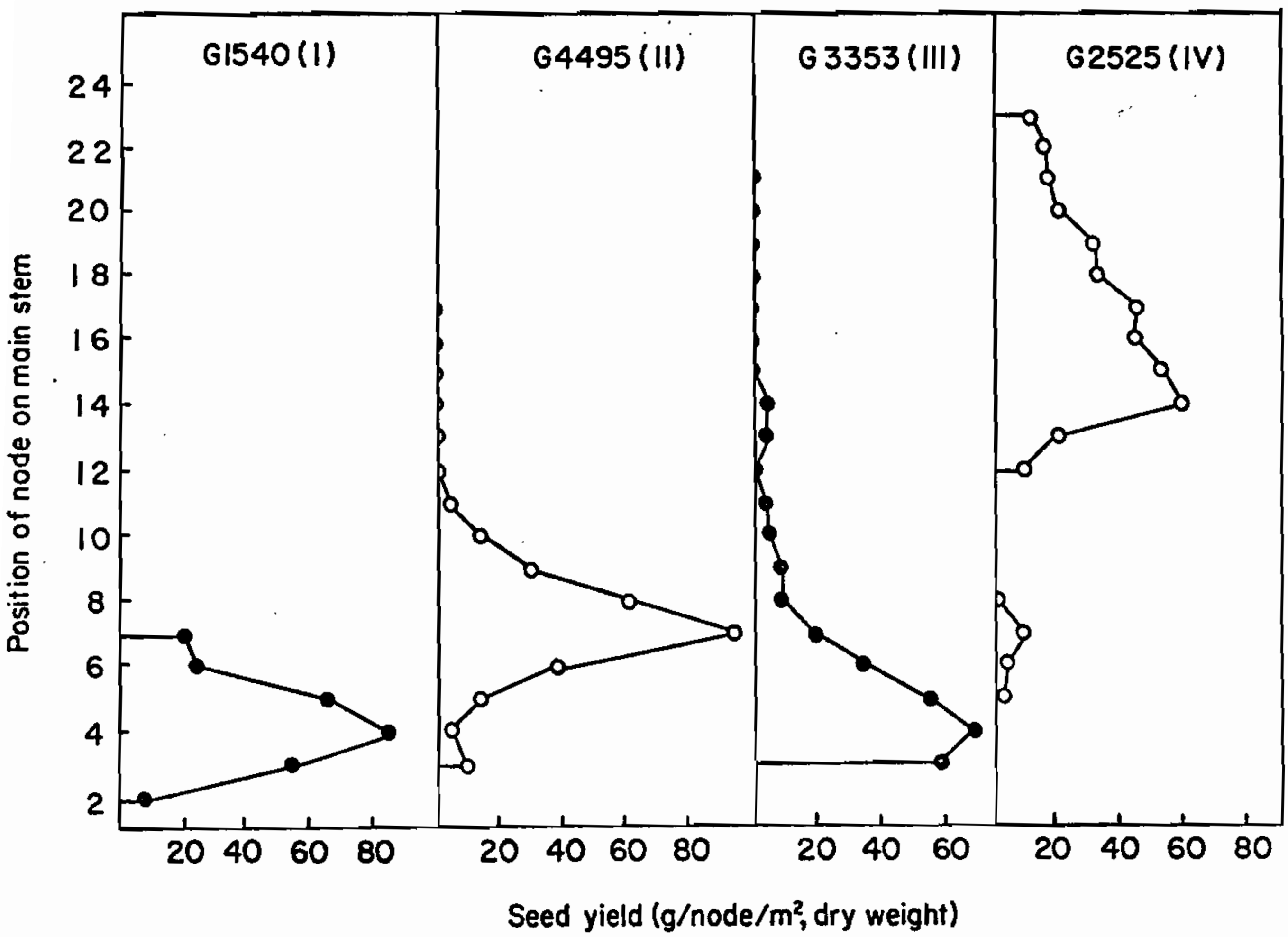
[a]CIAT collection number. [b]14% moisture basis. [c]Integrated from emergence to maturity. [d]Type IV cultivar supported on 2m high trellis. [e] Correlation with yield.

necessary for these climbing cultivars and the longer growth cycle allowed more leaf development. The profile structure of yield by node number in the four cultivars (Fig. 6) indicates that the lower nodes of the Type IV cultivar suffered almost complete flower abscission probably due to excessive leaf area development and self shading which decreased the levels of photosynthate availability to lower nodes during the pod number determination phase.

Under optimum conditions at CIAT yield differences among high yielding cultivars for each growth habit are more or less in proportion to the yield differences in Table 4. In each growth habit higher yields than those shown in Table 4 have been obtained in both germplasm bank and improved materials. Consistent yields across experiments of 2.5 - 3.0; 3.0 - 3.5; 3.0-3.8 and 4.0-4.5 t/ha for each growth habit respectively have been measured in well bordered and irrigated plots. In general later cultivars are normally higher yielding.

Comparative studies among grain legume species

Grain legume species are morphologically similar in that the basic building block of the plant is a nodal unit with leaf and pod attached. A comparative experiment was conducted at CIAT to evaluate the importance of the factors already outlined for *P. vulgaris* across a wide range of species. The best adapted genotypes for most of the species were selected from previously conducted yield trials. The trials included improved materials available from international and national programs. The climatic conditions at CIAT-Palmira are considered sufficiently moderate



6. Yield profiles by main stem node number for representative cultivars from the four growth habits (see Table 4).

(mean temperature 23.8°C) that no particular species was disadvantaged. *P. coccineus* could not be included in the trial since the species is relatively unadapted at prevailing temperatures. Mean species seed yield ranged from 2.2 to 4.5 t/ha. Harvest index was negatively related to yield while biomass, LAD and days to maturity were all highly and positively correlated (Table 5).

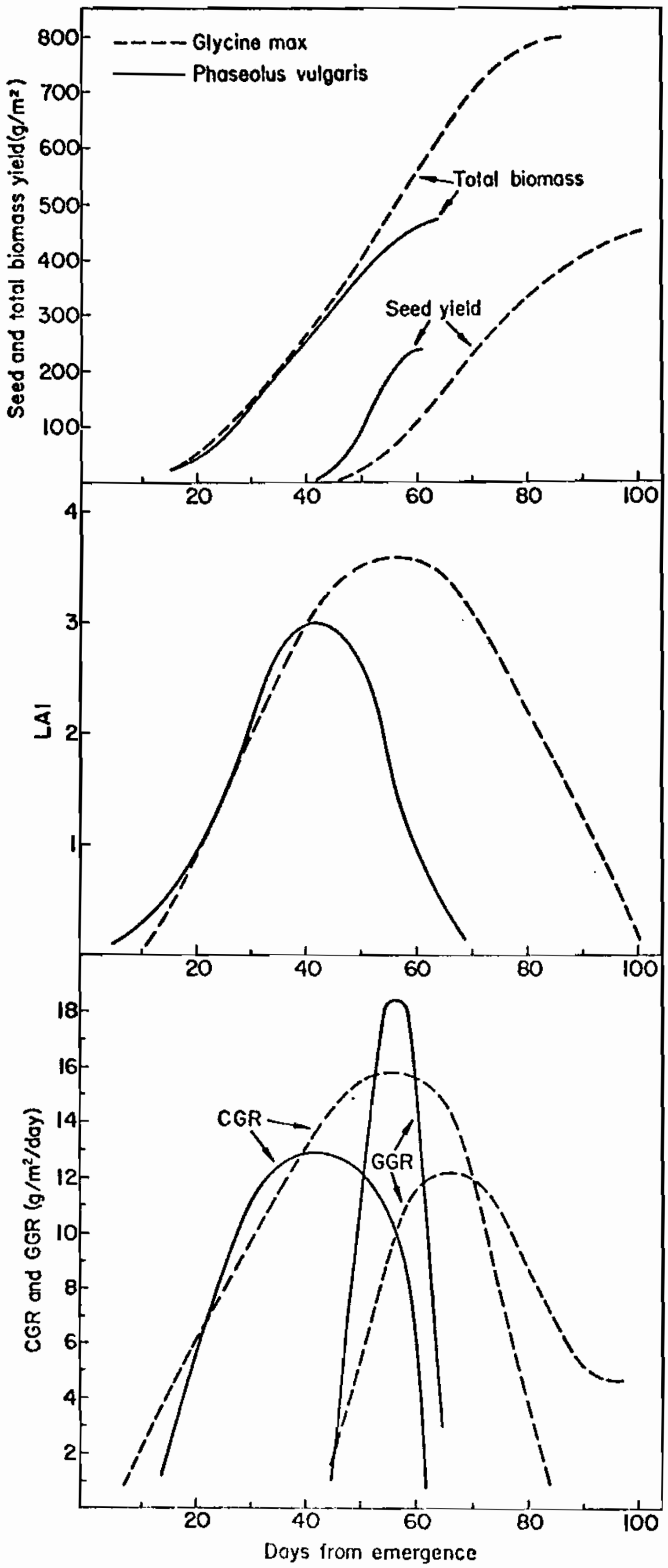
Common beans were intermediate in yield and unlike some other species e.g. *Vigna spp.*, were highly synchronized with respect to pod maturity. Harvest index, yield/LAD and yield per day were comparable with soybeans and higher than for other species. The difference in CGR between soybeans and common beans was consistent with the difference in maximum LAI. Detailed comparison of trends in growth parameters with time for one cultivar in common beans (Porrillo Sintetico) and soybeans (Fig. 7) indicate that the growth patterns for the two species are of similar form except that common beans are much earlier in maturity and thus have lower values of LAI and CGR. Peak grain growth rate is much higher in beans and the grain growth phase is proportionally much more rapid.

While soybeans commenced flowering at the same time as beans the post flowering phase was proportionally much longer. The in-determinant soybean cultivar had a longer flowering period due to the extra nodes on the main stem which must go through the flowering process. The grain filling process in soybeans proceeds at a lower maximum rate and is spread over a longer period. The rate of decline in LAI during senesence is slower in soybeans. In general pod number per plant is

Table 5. Key parameters of growth and yield for nine 'grain' legume species: CIAT–Palmira[a], 1979.

Species	No. Genotypes per species	Yield[b] kg/ha	Yield[b] % at first harvest	Yield per day kg/ha/day	Days Flower	Days Mature	Maximum LAI	CGR at max. LAI	LAD[c] days	Yield/LAD	Total biomass kg/ha	Harvest index[d] %
Cajanus cajan	1	4479	68	26	67	174	5.2	10.1	298	1.5	9400	41
Glycine max	2	3899	100	38	34	102	4.2	14.9	195	2.0	5440	62
Phaseolus lunatus	2	3682	68	26	35	139	3.6	8.5	179	2.1	5990	53
Vigna ungiculata	2	3292	82	30	43	109	4.0	8.7	147	2.2	6145	46
Arachis hypogea	1	3080	100	27	28	114	6.0	13.8	323	1.0	5570	48
Phaseolus vulgaris	3	2637	100	34	35	78	2.8	10.0	108	2.4	3733	61
Vigna radiata	2	2533	83	26	38	99	3.0	10.8	99	2.6	4295	51
Vigna angularis	1	2748	100	31	35	88	4.0	14.3	158	1.7	3930	60
Phaseolus acutifolius	2	2170	100	29	39	76	3.6	12.4	105	2.1	3125	60
L.S.D. (0.05)		277	-	3	4.9	23.7	2.9	6.9	25	1.0	1428	3.8
C.V.%		9.4	9.4	9.9	1.4	3.1	14.3	11.9	16.0	2.4	16.7	5.8
r (versus yield)[f]		-	-	0.04	0.56	0.86	0.50	−0.16	0.92[e]	−0.59[e]	0.91	−0.50

[a] Latitude 3° N, Altitude 1000m, Mean temperature 23.8° C. [b] 14% moisture basis. [c] Integrated area under LAI curve emergence to final physiological maturity. [d] Dry seed yield/total biomass minus leaves and petioles, at maturity. [e] Correlation does not include data for *A. hypogea*.
[f] r= 0.73 for significance at 1%.



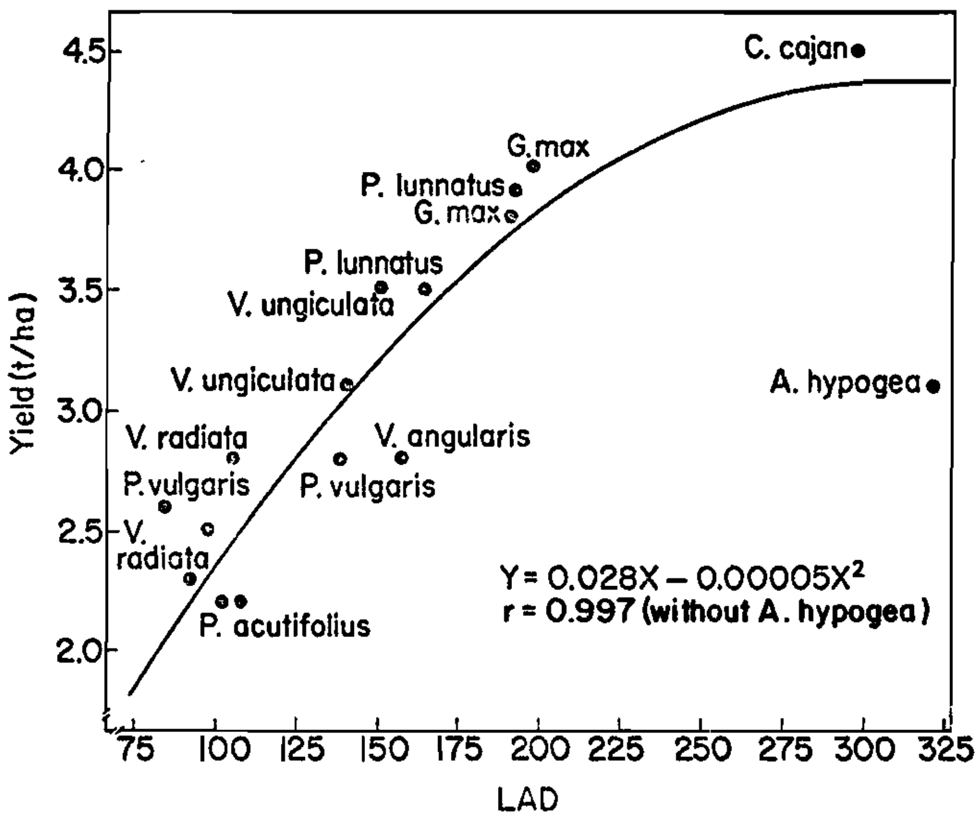
7. Growth parameters for P. vulgaris (cv. Porrillo Sintetico) and Glycine max (v. ICA-Tunia): curves derived from trigonometric curve fitting procedures.

usually the dominant yield component in beans while seeds per pod and particularly seed weight show only comparatively small changes across environments and treatments. These data suggest that common beans are more conservative in an evolutionary sense. Bean plants apparently adjust potential sink size (pod number) to the available source and then proceed to fill that sink as rapidly as possible. This in turn influences the rapid rate of senescence of the leaf canopy.

Seed yield versus LAD for each of the 16 genotypes in the nine species is plotted in Fig. 8. Arachis hypogea (peanuts) is the only species in the list which has a drastically different morphology. It is also the obvious outlier in this relationship. The quadratic curve fitted to the data does not include A. hypogea. For the remainder of the species the data is remarkable in that one variable (LAD) can be used to explain a large proportion of the variation in yield of 15 genotypes from four genera and eight species. Since all of the species are constructed with similar building blocks it seems logical to conclude that yield among grain legumes is simply related to the number of building blocks present, which is in turn chiefly a function of time.

COMPONENTS OF ADAPTATION

Regression analyses of the 1976 IBYAN (International Bean Yield and Adaptation Nursery; CIAT, 1977) data showed for the first time that some photoperiodically insensitive II black seeded cultivars e.g. Jamapa (Mexico) and ICA Pijao (Colombia) are very widely adapted



8. Seed yield (14% moisture basis) versus LAD integrated from emergence to final physiological maturity for 16 genotypes from 8 legume species. CIAT- Palmira, 1979.

to both tropical and temperate latitudes in growing seasons with mean temperatures within the range from 17-25°C. In the IBYAN program the highest experimental yields have been obtained in irrigated experiments in countries such as Chile and Israel with long days, low relative humidity, relatively high solar radiation and lower fungal disease pressure. The lowest yields have consistently been produced in high rainfall humid tropical lowland situations (mean temperature > 25°C) where fungal disease and insect pressure can be extremely limiting. Research on the physiological components of adaptation at CIAT has mainly concentrated on responses to water stress, temperature and photoperiod.

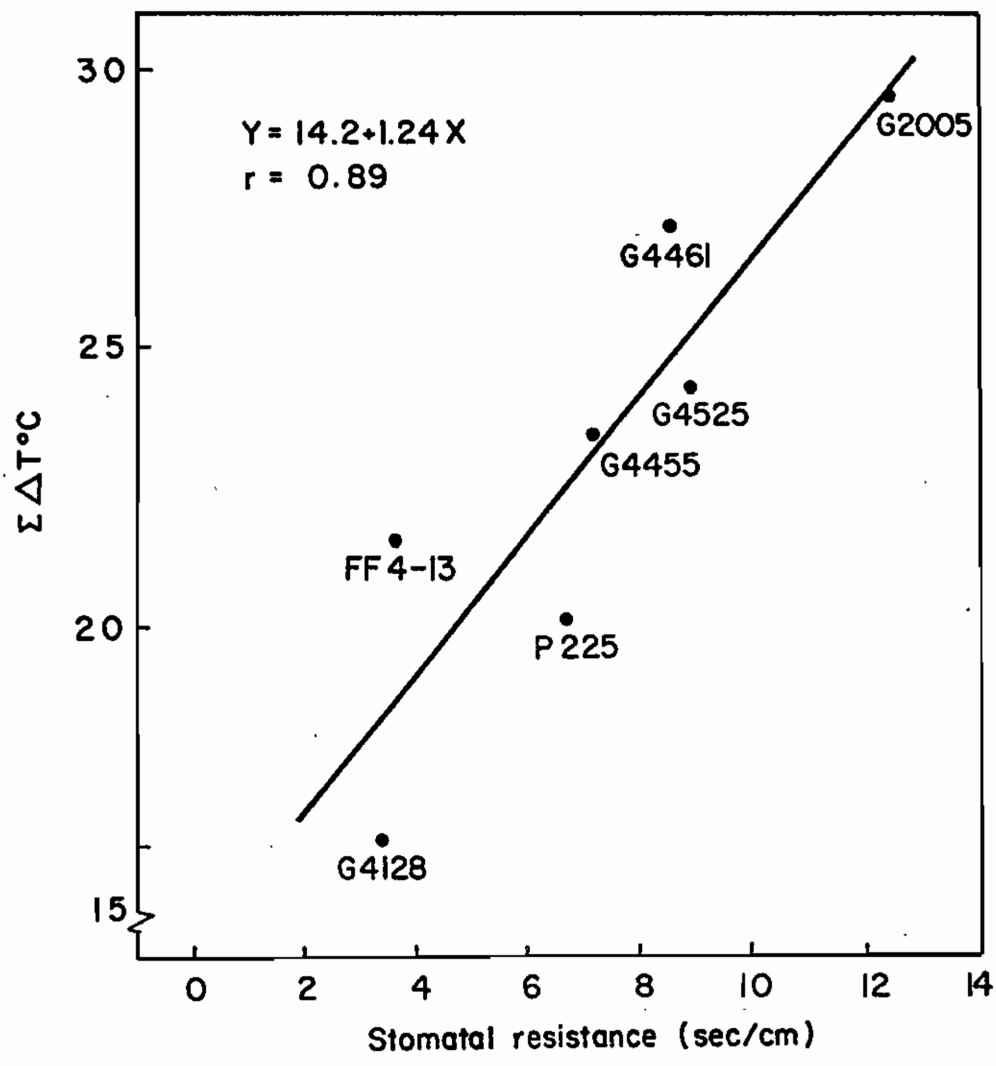
Water stress tolerance

Water stress is a common feature of production conditions in Latin America (Table 2) and most probably in other tropical and subtropical regions of the world where irrigation is limited.

Common beans with a very short growth cycle are particularly susceptible to short periods of stress during the flowering and early pod determination phase (Stoker, 1974). Cultivar differences in yield response (% yield reduction from well watered controls) to periods of stress for up to 23 days after flowering have been demonstrated (CIAT, 1979). Diurnal curves of pressure bomb measurements of plant water potential (Ψ_s determined on stem tissue), stomatal resistance (r_s sec cm^{-1}, upper exposed leaves) and canopy temperature (T°C infrared thermometry) were determined on a tolerant and a susceptible cultivar.

The stress tolerant cultivar (G 4128) had a higher level of Ψ_s during the day than the susceptible cultivar (G2005). Stomatal resistance was extremely high through the warmer period of the day in the susceptible cultivar. Mean canopy temperature in the irrigated plot rose to a maximum of 25.5°C which was about $\sim$ 2°C less than ambient air temperature. The temperature differential ($\Delta T°C$) between the irrigated and stress plot rose to 6.5°C and 2.5°C for the susceptible and tolerant cultivar respectively.

Infrared thermometry is a rapid means of characterizing the stress experienced in field plots of homogeneous genotypes (Blum et al 1978). Measurements were made on each day of the stress cycle on adjacent stressed and nonstressed plots. The accumulated daily values of $\Delta T°C$ for the whole stress period provide an index of the stress experienced. A high correlation across genotypes (Fig. 9) between $\Sigma\Delta T$ and the mean of repeated determinations of r_s from 11.00h to 13.00h on each cultivar was obtained. A high correlation for individual cultivars was also evident between the yield reduction % of stress plots compared to immediately adjacent nonstressed plots and $\Sigma\Delta T$. In this experiment paired plots of a range of cultivars where grown at random positions in a large field (150m x 150m) to evaluate the degree of field variability in severity of water stress. The data suggests that not only do cultivars differ in the degree of internal stress experienced over a stress cycle but also differ in the slope of yield response to the stress experienced. In other words the same degree of stress in different cultivars can



9. Relationship of canopy temperature differential (ΔT°C) accumulated over six days during the drying cycle and the mean of repeated measurements of stomatal resistance (r_s) from 11h00 to 13h00 on one day in the cycle.

reduce yields by differing degrees. Water stress has its greatest impact on pod number in these experiments while seeds per pod and seed size are again more conservative.

Further research on the tolerance mechanisms involved is in progress. The data so far suggests that the tolerant materials were able to maintain a higher leaf water potential under conditions where soil water supply is limited and/or under high evaporative demand. This suggests that tolerant materials probably have a stronger root system which is better able to exploit available water reserves during stress periods. While other physiological factors could be entertained in explaining these differences it seems clear that the first priority for research should be with respect to root systems.

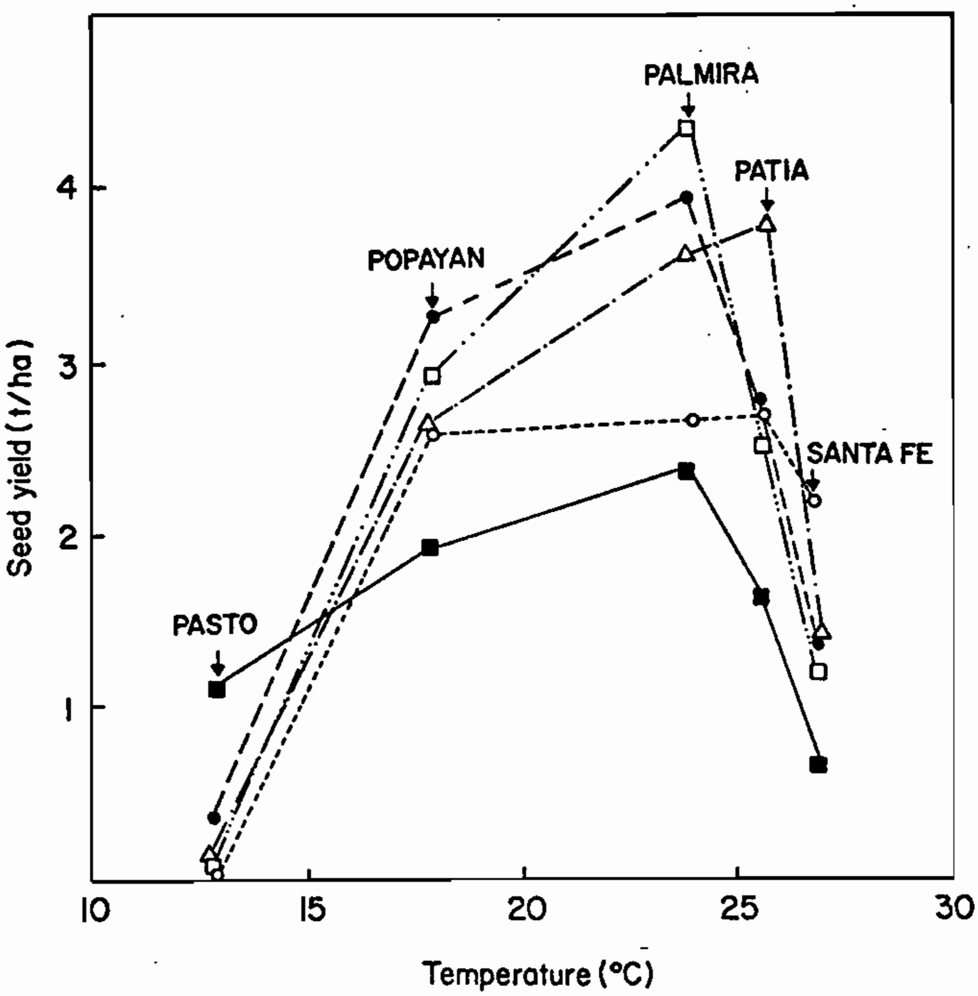
Temperature Response

The comparatively narrow range of mean temperature conditions under which most common beans are produced (Table 2) suggests that temperature may not be as critical as water stress in influencing adaptation in traditional areas of production. Increasingly, demands for material with adaptation to more extreme conditions are being received from collaborators particularly material with high temperature tolerance for production in irrigated areas where high atmospheric humidity is not a factor.

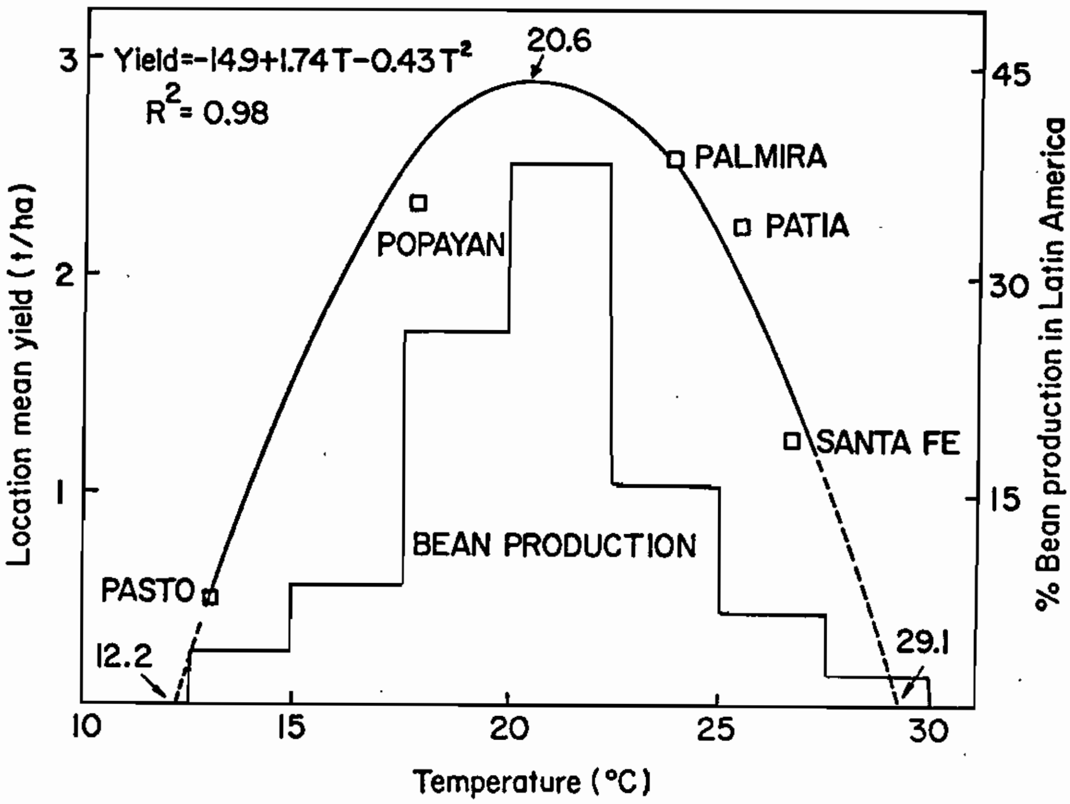
A series of replicated experiments were conducted with 250 promising parental materials and some advanced lines at five different altitudes in Colombia under irrigated and protected conditions. Yield results (Fig. 10) for the five highest yielding lines at each location, when plotted against the full range of temperatures, suggest that at the temperature extremes quite specific cultivar adaptation is involved. At the lowest temperature location the large seeded Type I and IV materials were the best adapted but these particular lines performed poorly at the other locations.

At the high temperature location small black seeded materials from Type II and III where the best adapted in terms of yield and these performed comparatively poorly at the intermediate temperature locations. Complete reproductive failure at various stages was the main symptom of poor adaptation at the low temperature where only 68 of the 250 entries actually set viable seed. At the highest temperature flower abscission was high in unadapted materials even though vegetative growth was relatively unaffected. The vast majority of the entries did, however, produce viable seed. Material well adapted at each of the three intermediate temperature locations performed reasonable well at the other two locations. The latter evidence supports the observation that genotypes are available with wide adaptability to the temperature conditions prevailing in the major portion of production areas. Specific selection for the temperature extremes appears necessary.

A close correspondence (Fig. 11) exists between a quadratic function fitted to the mean experimental yield (including only material with more than zero yield) at each location and the estimated distribution of bean production in Latin America in relation to temperature (from Table 2)



10. Mean yield of the five highest yielding lines at each of five locations/altitudes in Colombia plotted against the mean growing season temperature at each location/altitude. The place names refer to the curve for the mean for the 5 best lines at that location plotted at all other locations. Altitude range 350m to 2700m.



11. Quadratic function fitted to mean yield of 250 genotypes at each of five locations/altitudes in Colombia versus mean growing season temperature at each location: yield mean includes only entries which actually set seed at each location. Data for the distribution of bean production in Latin America by growing season temperature is presented for comparison (see Table 2).

The minimum, optimum and maximum mean temperatures suggested by this curve are 12.2, 20.6 and 29.1°C respectively. These rather rough extrapolations are intended only as practical guide to the temperature limits on growth in the field. Jones (1971) measured the effects of temperature on photosynthesis of leaf discs in P. vulgaris. The optimum temperature for Pn was 21°C.

Photoperiod Response

Photoperiod response and photoperiod by temperature interactions responses have been extensively studied by various authors (Padda and Munger, 1969; Coyne, 1967, 1960; Hartmann, 1969; Ojehomon et al, 1968). Genotypes of P. vulgaris have been identified which are either day length neutral or respond to long days by delayed flowering. Temperature interactions particularly night temperature modify the flowering response in individual genotypes. The degree of flowering delay in a particular long day environment depends on the genotype. This quantitative response has been evaluated in the field at CIAT-Palmira at an effective day length of 18h compared to the normal control of 12h20. Flowering delay responses have been classified into five basic groups with increasing sensitivity (Table 6). A total of 800 germplasm collections have been screened. The distribution of these materials according to growth habit over the five response groups indicates that the percentage of materials in the highly photoperiod sensitive classification (>30 days delay) is higher with increasing indeterminacy while Types I and II contain the

Table 6. Summary of photoperiod response screening results in *Phaseolus vulgaris* L. germplasm bank materials: data from field screening at CIAT-Palmira, mean temperature 23.8°C, altitude 1000m.

Growth habit	Photoperiod response group and days flowering delay					Total
	1 < 4[a]	2 4-10	3 11-20	4 21-30	5 >30	
I	97 (43)	22 (10)	59 (26)	30 (13)	18 (8)	226 (100)
II	163 (55)	40 (14)	67 (23)	17 (6)	7 (2)	294 (100)
III	61 (30)	26 (13)	41 (20)	38 (18)	40 (19)	206 (100)
IV	15 (18)	7 (9)	18 (22)	10 (12)	32 (39)	82 (100)
Total	336 (41)	95 (12)	185 (23)	95 (12)	97 (12)	808 (100)

[a] Days of flowering delay at 18h days compared to natural day length of 12h 20 min.

highest proportion of photoperiodically insensitive materials. Speculation as to the evolutionary reasons for these trends are somewhat hampered until fuller information can be obtained as to the exact origin of the materials. The wide adaptability of certain genotypes is undoubtedly due inpart, to photoperiod insensitivity.

As a first step in developing a generalized phenology model the IBYAN data for 1976 was utilized to study the response of cultivars from the different photoperiod response classifications. Cluster analysis was performed on the days to flowering data for the 20 IBYAN entries common to all locations. The data (Fig. 12) indicate that cultivars from the same growth habit and photoperiod classification had a similar phenological response across locations in both tropical and temperate latitudes. The few exceptions appear related to photoperiod by temperature interaction in these particular genotypes. The data suggest that a simple photoperiod classification could be used as a basic input into a phenology model (Jones and Laing, 1977) in order to predict phenological responses of particular genotypes in particular locations. This type of model could help considerably in international germplasm programs which at the present time must be conducted with a large number of materials in the hope of finding adapted materials.

sowing is feasible.

- Increasing the water stress tolerance characteristics of materials generally would probably make the largest contribution to commercial production of any of the available physiological options.

- Improvement in the temperature adaptation characteristics for hotter climates particularly where irrigation is available should lead to expansion of production into non traditional areas of production.

- For most rainfed stress environments early materials with a higher yield potential can be developed mainly through improvement in general vigor but quantum increases in yield cannot be expected given the temporal and environmental constraints.

- Improvement in the adaptation of P. vulgaris to problem soils in the tropics particularly acid soils with high levels of aluminium toxicity also appears to be highly necessary for many regions.

- Improvement in the nitrogen fixation characteristics of the species is vital particularly for the rustic low input conditions under which production commonly takes place.

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