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EFFECTS OF WATER STRESS IMPOSED AT MID-POD FILLING
UPON YIELD AND DRY MATTER PARTITIONING IN DRY BEANS
(Phaseolus vulgaris L.)

By

CATALINA SAMPER

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ABSTRACT

EFFECTS OF WATER STRESS IMPOSED AT MID POD FILLING UPON YIELD AND DRY MATTER PARTITIONING IN DRY BEANS (Phaseolus vulgaris L.)

By

CATALINA SAMPER

Two experiments were conducted to study the genetic potential for differential storage and remobilization of non-structural carbohydrates and its relation to yield performance of cultivars grown under conditions of drought imposed in the mid-pod filling stage, and low soil nitrogen. A close relationship between grain yield and the change in stem and leaf dry weights from anthesis to maturity implicates assimilate remobilization as an important contributor to seed yield under late season water stress. The daily assimilate partitioning to the fruit was found to be determined by genotype and influenced by water treatment. The top yielding cultivars were those which had a long vegetative phase and a high fruit growth rate accompanied by a seed filling period that did not differ in length between the water treatments. The geometric mean as opposed to other criteria for selecting drought tolerant cultivars proved to be very advantageous. It is suggested that an understanding of the type of water limitation and a quantification of the drought environment are necessary for designing an ideotype to be used in developing drought tolerant cultivars intended for a particular production system.

To Dad, Mom and Ivan

for their love, generosity and
encouragement of my growth

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INTRODUCTION

Varietal differences in the amount of starch present at flowering time, grain filling and physiological maturity in the dry bean (Phaseolus vulgaris L.) have been previously reported (4,30). The capacity of certain genotypes to store and remobilize starch to the grain may be an advantage when the plants are subjected to stress and their photosynthetic activity is reduced.

The general objective of the project of which this thesis is part of, was to study the relationship between photosynthate partitioning, remobilization, and the seed filling processes in several genotypes of P. vulgaris grown under different stress conditions. Initial objectives were: 1) to determine the effect of drought stress imposed during the latter part of the seed filling period on the yield performance of 22 different bean cultivars and to relate their performance under stress to their ability to accumulate and remobilize non-structural carbohydrates; 2) to compare the effect of nitrogen fertilizer versus biologically fixed nitrogen (BNF) under stress conditions, and subsequently to determine the relationship between total amount of non-structural carbohydrates and their remobilization with the plant's ability to buffer the adverse environmental conditions; 3) to identify bean genotypes having tolerance to drought and high BNF

potentials and to relate their performance under stress conditions with the patterns of accumulation and remobilization of starch and soluble sugars; 4) to identify specific traits or physiological characteristics that could be associated with better cultivar performance under drought conditions, 5) to use the information and genetic materials obtained during the course of this research as sources of new improved germplasm in the development of varieties with resistance to drought and with the capacity to fix nitrogen under water stressed conditions.

For these purposes an experiment was conducted in Iguala, Mexico, from December of 1982 to April of 1983. This experiment was intended to study and exploit the genetic potential for differential storage and remobilization of non-structural carbohydrates and the genetic capacity for higher levels of BNF, and to relate this to the yield performance of cultivars under conditions of drought and low soil nitrogen.

A second experiment was conducted in the summer of 1983 in Durango, Mexico to provide further data on varietal performance under stress.

LITERATURE REVIEW

Yield constraints

Over forty five percent of the world production of dry edible beans (Phaseolus vulgaris) is consumed in Latin America. Nevertheless, low yields of this crop are limiting the traditional role beans play as a staple food in the diets of poor and middle income consumers of this region. Although bean yields of over 4000 kg./ha. have been reported from experimental plots at the Centro Internacional de Agricultura Tropical(CIAT) in Colombia, the average bean yield in Latin America remains near 600 kg./ha. (52). In the dryland production region of Mexico the long-term yields are reported to average less than 300 kg./ha. (1). A significant closing of the gap between current yields and potential yields must be achieved if this crop is to fulfill its role in meeting the nutritional needs of the population.

In large areas of Latin America and Africa, where beans constitute a major source of dietary protein, production is limited mainly because beans are a crop of the small farmer and the conditions under which the crop is usually grown are typified by low soil fertility, and minimal technical inputs, such as irrigation, fungicides and insecticides .

Approximately 20% of all potentially arable land in the world is in arid and semiarid zones, and about 16% of the world's population lives on these lands (41). Research and development in arid and semi-arid agriculture has,

therefore, global significance. Arid and semi-arid lands have been defined in a number of different ways. Their main characteristic is a low and variable seasonal rainfall, a condition which is often directly exacerbated by other variable elements of the climate, such as temperature, sunshine, wind and humidity conditions. Beans, among a few other crops, are dryland staples in many developing countries, providing a major source of affordable protein and carbohydrate. Bean breeding over the years has focused on improving agronomic adaptation along with disease resistance, with less direct emphasis upon yield itself. It is acknowledged by bean plant breeders that there have been no decisive breakthroughs in yield, excepting increases originating from disease resistance or favorable maturity adjustments (2). Increasing yield is imperative, but this objective must be integrated with the genetic improvement of adaptation and resistance to stresses brought about by diseases, insects and physical causes. The improvement of both agronomic characters and yield could maximize the responses of the bean plant to available resources characteristic of the site and local production system. This is especially important for the Latin American small farmers, because the conditions under which the crop is usually grown are typified by the lack of irrigation systems, little or no use of fungicides and insecticides, and small amounts of fertilizers. In Mexico, where 1.7 million hectares are planted annually with beans, 24 out of the 30 states that produce beans raise them under rainfed

conditions. During 1970 to 1975 approximately 1.2 million hectares were planted annually with beans, and the average yield was around 545 kg./ha (35). This was enough for the internal demand, but from there on only during 1978 and 1980 was production considered to be at its normal level. As a consequence, during 1980 Mexico had to import more than 250,000 tons of beans to satisfy the internal demand.

This production shortfall originated basically because of adverse climatic effects such as drought and early frost. In Mexico, beans are planted twice a year, during the Spring-Summer and the Autumn-Winter cycles. During the Spring-Summer cycle when the majority of the total production is obtained, about 1.4 million ha. are planted and 530,000 tons are harvested. In this cycle typical low yields of 387 kg/ha are caused by adverse environmental factors such as drought -scarce or irregular rainfall- and early frost in the northern part of the country. During the Autumn-Winter cycle about 260,000 ha. are planted and 246,000 tons are harvested; this corresponds to 31% of the total national production and 16% of the total planted area. It is interesting to note that with only 16% of the total planted area almost one third of the total national production is obtained, with average yields being 933 kg./ha. In states such as Nayarit, Sinaloa and Baja California where irrigation is widely practiced, average yields are over 1100 kg./ha., while for the country as a whole 88% of the area that produces beans is rainfed only

and the average yields are about 350 kg./ha. Of this, 88% or approximately 1 million ha. are in the states of Aguascalientes, San Luis Potosí, Zacatecas and Chihuahua. These areas are frequently affected by either scarce or badly distributed rain throughout the growing season. In the state of Durango, nearly 30% of the planted beans are lost annually due to insufficient water, and in bad years such as 1979 the losses can reach up to 60% of the total planted area¹ (1).

In Colombia, in the states of Huila, Nariño and Antioquia where the average farm sizes are 29.5 , 9.2 and 4.4 hectares, respectively, the percentage of farms that use irrigation is 2, 0, and 0 and the average yields are 680, 467 and 533 kg./ha. (45). On the other hand, in the state of Valle del Cauca, where the average farm size is 48.0 ha., 45% of the farms use irrigation and the average yield is 906 kg./ha.

Among factors other than drought tolerance that could contribute to improved crop yields , the availability of fixed nitrogen to crops is probably one of the greatest importance. In 1974 , 40×10^6 tons of fertilizer nitrogen with an approximate value of 8 billion dollars were used , as opposed to the 3.5×10^6 tons that were used annually twenty five years ago (28). The scarcity of nitrogen fertilizers and their increased selling price has produced a tremendous interest in the search for alternative technologies. Inoculation of legumes with Rhizobium at the farm level appears to offer promise as a possible substitute

for nitrogen fertilizers. Recent reports from farm trials performed in Colombia by CIAT show that in the absence of any nitrogen amendments, inoculation of a local variety with a mixture of Rhizobium strains gave yields that were not significantly different from a farmers' technology treatment, in which 20 kg./ha. of chemical nitrogen in the form of urea and 2 tons/ha. of chicken manure were applied. Substitution for nitrogen fertilizers by a Rhizobium inoculant would reduce total costs of production by 34%, while the net return per peso invested would rise from 5.5 to 7.7 pesos.

A bean breeder who wants to develop a variety for the small farmers of Latin America should be aware that increased yields must be obtained with very limited cash inputs.

Allocation of Assimilates

In recent years breeders have been considering the development of plant ideotypes (14). In dry beans an ideotype for production under monoculture has been proposed by Adams (2), who suggested that productivity increases in dry beans could be obtained if a more efficient allocation of assimilates into the economic sink is developed by breeding.

Two of the principal physiological processes that can be considered for improvement of crop yields are photosynthate production and photosynthate partitioning to the economically important organs. However, the importance of transpiration as a central factor in explaining the

influence of water limitation on productivity, as pointed out by Fischer and Turner (20) cannot be overlooked. It depends on the inevitable association between water loss and CO₂ assimilation. Dry matter production over a given period of time is a function of the total transpiration for the given period and the water use efficiency. The importance of respiration rates in determining the net accumulation of dry matter is commonly overlooked. As Gifford et. al. (22) pointed out, in leaves the fixed carbon is partitioned between its retention in the plant and its photorespiratory release. Over long periods, a full understanding of productivity requires consideration of how each increment of dry weight is allocated to both vegetative and reproductive sinks.

The potential for increasing crop productivity by optimizing canopy structure has been documented by experimental research, modeling, and computer simulation (51). Assimilate partitioning is a dynamic process and varies with the stage of plant development. In the vegetative stage of the dry bean plant, the distribution of assimilates is dominated by the proximity between the source and the sink. After flowering, when the developing pods become major sinks, there is a more complex pattern, although the relationship between leaves and pods in their own axils still predominates (3).

Use of ¹⁴C as a tracer, and changes in dry weight of specific organs have been important techniques in helping to

understand assimilate distribution. However, many important aspects of this process, like the mechanisms of regulation, accumulation and remobilization of storage assimilates under different conditions, still remain to be studied in order to provide guidelines for the increase of yields by manipulation of photosynthate partitioning.

Large varietal differences in the ability to translocate ^{14}C - assimilates and a clear trend for varieties with the higher translocation rates to have higher photosynthetic rates, were reported by Adams and Reicosky (3). From data obtained on carbohydrate translocation patterns in beans, they suggested that the two facets upon which breeding studies might be focused were rate of translocation and direction of partition to sinks of the assimilate. They also suggested that these characters may be under genetic control and might be used in a plant breeding program.

In recent years, attention has been given to carbohydrate production and partitioning in plants as factors related to crop yield; carbohydrate mobilization may be especially important under stress conditions (6). Varietal differences in carbohydrate accumulation or partitioning may be related to maintenance of a high rate of seed filling during periods of temporary environmental stress when photosynthesis is adversely affected.

Evans (18) considers that whereas photosynthesis during the storage phase can be an important determinant of yield,

photosynthesis prior to that contributes to the determination of storage capacity and generates reserves that may be mobilized during the storage phase.

Gifford et al. (22), reviewing the partition of photoassimilates and crop productivity, examined the photosynthetic basis for increasing yield of major field crops in terms of improving the partitioning of photoassimilates to organs of economic interest. Although little is known about the regulation of carbohydrate partitioning between starch storage (for later utilization) and sucrose synthesis (for immediate export), they affirm that sink demand plays a very important role. The partitioning of photosynthetically fixed carbon is important for plant growth not only because the formation of sucrose partially determines the carbon export from photosynthesizing leaves, but also because leaf starch is mobilized to sucrose when current photosynthesis is low relative to sink demand for assimilates. In their discussion, they suggest that photosynthesis and the mechanism of phloem loading determines the amount of photosynthetic assimilate available for translocation, while the mechanism and kinetics of unloading into competing sinks determines the partition of loaded materials.

Carbohydrates reach a maximum concentration in the plant's vegetative parts around flowering time, after which they start to decrease. Yoshida (59) found that stored carbohydrate could be translocated into the rice grain, thus contributing to grain filling, or it could be consumed as a

substrate for respiration. The carbohydrate loss from the vegetative parts during grain filling provides only a maximum estimate of the contribution of the stored carbohydrates to the grain.

Evidence that stored carbohydrate can be translocated into the grain has been obtained for rice and wheat by labeling the stored carbohydrate with ^{14}C . Cock and Yoshida (11) showed that under normal field conditions 60% of the stored carbohydrate was translocated into the grain. When photosynthesis during the ripening period is restricted by shading or defoliation, the stored carbohydrate appears able to support the grain growth of rice and corn at almost the normal rate for some time. Perhaps the stored carbohydrate can serve as a buffer to support normal grain growth despite weather fluctuations (59). Whether the yield capacity or assimilate supply limits the grain yield is not clear. However, defoliation and shading experiments in rice at or after heading clearly demonstrate that impaired photosynthesis during the ripening period can severely limit the grain yield (49). Assimilate supply may limit grain yield under stress conditions: if photosynthetic activity is limited by shading, or if translocation of assimilates into the grain decreases, a certain portion of the grains may remain unfilled (59).

Biological Nitrogen Fixation

Beans are a crop of small farmers in much of the third

world, and are often produced on marginal soils deficient in nitrogen. In a world of rising fertilizer prices, the need for cultivars with improved ability to fix nitrogen is especially important. The identification of genetic variability for biological nitrogen fixation (BNF) in beans has made selection for enhanced BNF possible (5).

Graham (25) suggested that at least three factors could contribute to the variability in N-fixation observed in P.vulgaris : a) supply of carbohydrates to the nodules, b) relative rates of nitrogen uptake from soil, and c) time to flowering. Hardy and Havelka (29) indicated that the amount of photosynthate available to the nodules may be the most significant factor limiting N-fixation. They examined factors that affect photosynthate availability to the nodule such as light intensity, size of photosynthetic source, competitive sinks, CO₂ enrichment and photosynthate translocation. With respect to the effect of variation of each of these parameters on N-fixation in soybeans, N-fixation correlates directly with the amount of photosynthate available to the nodule. Nodules in general maintain low reserves of readily utilisable carbohydrates relative to their requirements for fixation, so they probably rely for their growth and functioning on photosynthetic products currently translocated from the leaves, or on carbohydrate reserves mobilized from other regions of the plant (42). Experimental evidence is consistent with this view, since a very close relationship

has been observed between photosynthesis, amount of photosynthate , and N-fixation. Reducing light or defoliation decreases fixation, while supplemental light increases it (7,26,27,29,42,47,48,50) ; pod removal increases N-fixation (7,27,28) presumably by leaving more photosynthate available for the nodules. Lawn and Brun (33) indicated that the decline in soybean nodule activity was associated with the development of the pods as a competing assimilate sink. The fact that the decline in nodule activity coincided with the time when pod growth rate first exceeded total top growth rate is an indication of mobilization of previously assimilated material into the pods.

Factors, both genotypic and environmental, which tend to lessen competitive effects by enhancing the photosynthetic source-sink ratio, may be expected to minimize a decline in N- fixation and should be considered in the future development of higher yielding varieties with high BNF potential.

In order to understand how varietal differences in N-fixation might relate to carbohydrate supply and availability in the bean nodule, Graham and Halliday (23) planted fourteen commercial varieties, inoculated and sampled at initiation of fixation and at the beginning of decline in fixation rates. Marked varietal differences were found, and a highly active N- fixing variety (P590) showed a higher soluble carbohydrate percentage in all organs and also partitioned more of its total carbohydrate to the

nodule as compared to an inactive N-fixing line (P635). In this study, climbing varieties which had been previously reported to be good N-fixers (24) were found to hold more of their carbohydrate in the soluble form.

The ontogenetic development of four dry bean cultivars with reference to the relationships that may exist between symbiotic nitrogen fixation and the energy supply (in the form of carbohydrates) to the nodules was studied by Martinez (39). His data are consistent with the hypothesis that carbohydrate supply to the nodules limits fixation. He showed that an increase of total photosynthate available to the symbiotic system, achieved through CO₂ enrichment, resulted in higher rates of nitrogen fixation. The nitrogen in the bean plant is stored temporarily in the leaves, and it is suggested that mobilization of this nitrogen to the seeds results primarily from leaf aging. Martinez (39) showed a similar phenomenon of mobilization of carbohydrates temporarily stored in the stems and leaves.

Wilson et al. (57) performed experiments to study the nonstructural carbohydrates, the nitrogen content of plant tissues and the nitrogenase activity throughout the development of male sterile and male fertile soybean plants. Male sterile plants set approximately 85% fewer pods than the male fertile plants, and reduced pod set was found to increase carbohydrate accumulation in the leaf and root systems. Although roots of male sterile plants contained

greater quantities of carbohydrate, a decline in nitrogenase activity occurred after flowering. The low percentage of soluble carbohydrates in roots of either type (male sterile and male fertile) during the pod filling stage might be one of the many possible explanations for the similar trends observed in male sterile and male fertile nodule activity.

In efforts to increase N-fixation it is not necessary to restrict selection only to genetic factors that affect nodulation, increase nitrogenase activity or generate larger amounts of accumulated nitrogen. Certain genotypes may be superior to others in their allocation of assimilatory resources to the various plant parts (27,29,42) . The functional economy of whole plants and the interactions of their organs during growth should be considered in order to determine the plant factors that are responsible for the variation in nodulation and nitrogen fixation (58).

Effective photosynthate partitioning

The selection of cultivars with more effective partitioning of nitrogen and carbon assimilates to the reproductive organs than older cultivars was thought to be the key factor for the improvement of yield in other crops, namely rice (59), peanuts (16) and cotton (56).

Genotypic variation in carbohydrate and nitrogen remobilization during periods of environmental stress, when

photosynthesis is adversely affected, may enable maintenance of a high rate of seed filling and may buffer and stabilize yields. Photosynthate partitioning has been shown to be under genetic control in cereals (15), soybeans (32) and sugar beets (46). In beans, Adams et. al. (4) showed genetic variation for accumulation of starch during reproductive development. Izquierdo (31) also showed that differences in sugars and starch (total nonstructural carbohydrates) and nitrogen were associated with cultivars and physiological stages over the entire reproductive growth period. Izquierdo (31) showed genetic variation of seed filling parameters (rate and duration) in this crop and the relationship of these parameters to patterns of assimilate partitioning among genotypes. He concluded that yield differences among cultivars are more associated with the length of the seed filling period than with the rate of seed growth.

Constable and Hearn (12) performed a series of experiments with sorghum and two soybean varieties (Ruse and Bragg) under two different water treatments. Sorghum and Ruse soybean showed a significant (17-25%) loss in stem dry weight during grain filling under both treatments. In Bragg soybeans, only the stressed plants had a loss in stem dry weight during grain filling. One can infer that in sorghum and in Ruse, the significant loss in stem dry weight during grain filling could have been a consequence of relocation of dry matter from the stem to the developing grain. This

agrees with Yoshida's conclusion (59) that the weight loss from vegetative parts during grain filling sets an upper limit to the possible contribution of stored carbohydrates to the grain. An apparently large difference between soybean cultivars in the effect of water treatment on the contribution of stem storage to yield was reported by Constable and Hearn (12); in cultivar Ruse an estimated 25% of grain dry weight could have come from the stem, while in Bragg only the stressed plants appeared to use stem reserves. This suggests that Bragg was sink limited and had little requirement for storage carbohydrates, except during stress. Rawson et al. (43) substantiate Constable and Hearn's conclusion that when water deficits restrict current photosynthesis during grain development, the plant may buffer yield by drawing heavily on reserves. Also, Egli and Leggett (17) have suggested that soybean seed growth rates are not closely related to rates of photosynthate production because storage carbohydrate acts as a buffer between seed growth and photosynthesis.

Evidence supporting the idea that plant growth rate and seed yield are not directly affected by total photosynthesis was reported recently by Ford et al. (21). They used soybean lines divergently selected for rates of $^{14}\text{CO}_2$ uptake per unit leaf area and tested the effect of this divergent selection for leaf total photosynthesis on crop growth rate and seed yield. Their data showed that selection for improved photosynthesis per unit area did not necessarily enhance seed yield.

The effects of drought on nodulation and nitrogen fixation in field grown cowpeas were studied by Zablotowicz et al. (60). The nodulation process was inhibited by drought, and maximum nodulation was observed at mid-pod fill in the drought regime while plants from the well watered regime showed maximum nodulation at early flowering. As the plants matured beyond mid-pod fill, there was no significant difference in nodule mass between water treatments. Droughted plants failed to form nodules of high nitrogenase activity during the early stages of development, and at the reproductive stages the N-fixation capacity of the crop decreased, probably because there was insufficient carbohydrate to support high activity at this stage.

Field canopies of two semi-dwarf wheat genotypes were subjected to water stress that caused visible wilting during the grain filling stage, and the distribution of photosynthesis within canopies and the patterns of translocation of labeled assimilates following $^{14}\text{CO}_2$ uptake were determined (32). In stressed plants 24 hours after labeling, 46% of the ^{14}C was found in the grain compared to 35% in the control plants. Of the total ^{14}C recovered from the shoots at maturity, 83% was found in the grain of stressed plants and 69% in control plants. The lower percentage of ^{14}C in grain of control plants at maturity was due to its accumulation in stem segments, primarily in the form of structural carbohydrates. Fischer and Turner (20) stated that water stress during seed filling has its

major effect upon current assimilation through reductions in assimilatory activity and assimilatory surface. They concluded that water stress not only increases the proportion of current assimilate translocated to the seed, but also may increase the contribution from assimilate stored prior to seed filling.

In the broad bean , Vicia faba , N-fixation has been found to be severely suppressed once flagging of the lower leaves has commenced (47). If flagging of the lower leaves takes place, photosynthesis is likely to be arrested and since these leaves are likely to be the main providers of C to the nodules, it is possible that the first reduction of N-fixation during drought will be caused by reduction in assimilate supply (42) .

Drought tolerance mechanisms

Plant responses to water stress can be classified broadly into escape, avoidance or tolerance mechanisms (36,54). Escape can be achieved through more rapid development and through developmental plasticity, whereby the coincidence of critical developmental stages with periods of drought is avoided (34). Water stress avoidance involves mechanisms either to reduce water loss or increase water uptake. Water stress tolerance implies the ability to survive large water deficits and may involve mechanisms such as osmotic adjustment.

Lawn (34) evaluated the response of four different

grain legumes, soybean (Glycine max), black gram (Vigna mungo), green gram (Vigna radiata) and cowpea (Vigna unguiculata) to water stress under field conditions. These four legume species responded to the stress in several ways, but the degree of expression varied substantially between species. Each cultivar exhibited some tendency to escape through faster development in response to stress; the effect was small in soybean and large in the Vigna cultivars, particularly in the flowering to maturity period. Each cultivar also exhibited to some degree two mechanisms which served to avoid dehydration by reducing plant water loss. The most important of these was stomatal control of water loss in response to declining leaf water potentials, for which there appeared to be substantial differences in response between cultivars. Finally, under stress, each cultivar showed some paraheliotropic leaf movement; in these studies there was some suggestion that paraheliotropy helps to lower leaf temperatures under stress and presumably further restrict water loss.

Developmental plasticity can be seen as a mechanism that facilitates the matching of crop growth and development to the constraints of the environment, especially in terms of minimizing the occurrence of the critical reproductive phase during drought periods. Faster development may allow the successful completion of the plant's life cycle before the existing water supply is exhausted. Turk et al. (53), growing cowpeas under water stress, observed that drought

resulted in earliness when present at moderate levels, but severe drought delayed reproductive activity. This provides the plant with two possible adaptive responses. Under moderate drought the plant produces early pods which may mature before the soil water is depleted. If there is severe drought at early flowering, the plant remains in a vegetative stage but has the ability to continue reproductive activity if water is supplied. Determinate types flower, whether water levels are optimum or not, while indeterminate types remain in a vegetative stage under adverse conditions. Once rains start, the latter enter into the reproductive phase while the former can start a whole new cycle. It can be speculated that more determinate cultivars may have less capacity for recovery after mid-season drought.

Leaf movements which orient the leaf parallel to the sun's rays, leaf flagging, and rolling are common features of response in dry situations especially once leaf water potential begins to fall (20). It is unknown whether these leaf movements are beneficial to the plant. Shackel and Hall (44) considered that leaf movements in cowpeas could substantially reduce heat load and water deficits in cowpeas by minimizing transpiration. On the other hand, Lawn (34) states that paraheliotropic leaf movements act to reduce total light interception by the canopy, implying a reduction in photosynthesis. Recently, Ludlow and Bjorkman (37) reported that the paraheliotropic movement of water stressed

Macroptilium atropurpureum cv. Siratro protected the primary photosynthetic reactions from damage by excess light (photoinhibition), heat, and the interactive effects of excess light and high leaf temperatures. They concluded that even though heat damage is more severe when it occurs, photoinhibition may be a more common phenomenon during drought, unless paraheliotropic leaf movements reduce the amount of solar radiation incident on water stressed Siratro leaves.

The importance of root morphology for maintaining a supply of water to the plant should not be overlooked. Under drought conditions, an extensive root system is a characteristic that enables the plant to exploit a higher proportion of the available soil water without incurring severe plant water deficits (8). Deeper root penetration of soybean was particularly evident in the drought periods (Lawn, 34). He suggested that perhaps this root system is related to the tendency of soybeans to keep stomata open longer into the drought periods, thus maintaining a supply of photosynthate for continued root growth.

No definite conclusions can be reached about the "best" strategy to overcome drought stress. However, one can conclude that there is no absolute character to "drought resistance". Rather, there are several alternative and perhaps inter-related mechanisms, and their relative success depends on the seasonal pattern of water availability, on soil type and depth, and on other factors.

The most appropriate strategy for a particular environment presumably will be the one that simultaneously maximizes production and minimizes risk in that environment. Identifying the appropriate strategy requires assessment of the probability of particular seasonal patterns of water availability for that particular environment.

One effective approach to breeding for higher yield under stress would be to identify physiological and morphological components causing varietal differences in economic yield in the presence and absence of stress, and to gain an understanding of their genetic control. Evidence indicates that genetic variability exists for all such components (55). If physiological genetic data are used in selecting parents, it should be possible to select directly for yield, using standard selection and breeding procedures. Knowledge of the physiological genetics of yield will improve the plant breeder's understanding of desirable plant types and habit, and appropriate selection and breeding methods can then be used. As world food demand increases, production of drought tolerant beans may become increasingly important to make optimal use of water-limited lands.

MATERIALS AND METHODS

An experiment was conducted at the Campo Agrícola Experimental de Iguala-CAEIGUA-, Iguala, Mexico. The station is located in the state of Guerrero, at the meridian $99^{\circ} 45'$ longitude West and the parallel $18^{\circ} 30'$ latitude North. The altitude at the station is 739 meters above sea level. The average minimum temperature is 7°C and the average maximum is 42°C , with an annual average of 24.5 . The average annual precipitation is 1155 millimeters, and the rainy season starts during the last part of June. Eighty percent of the total annual precipitation occurs between the months of May and October. The experiment was planted in the second week of December, and the final harvest was taken in the last week of March. Precipitation and temperatures were recorded during the course of the experiment, and are shown in Figure 1.

The experimental plots were on a silty clay soil, with a high alkaline pH that varied between 8.25 and 8.75. The organic matter content as well as total nitrogen were low , the percentage of organic matter being 1.05 and the total nitrogen 0.112 ppm. The levels of potassium, calcium and magnesium were high, but the phosphorus content was relatively low (10.22 ppm). Before planting, 40 kg. of phosphorus per hectare were applied to all plots and 40 kgs. of nitrogen per ha. (in the form of Urea) were applied to half of the plots. At planting time all plots were

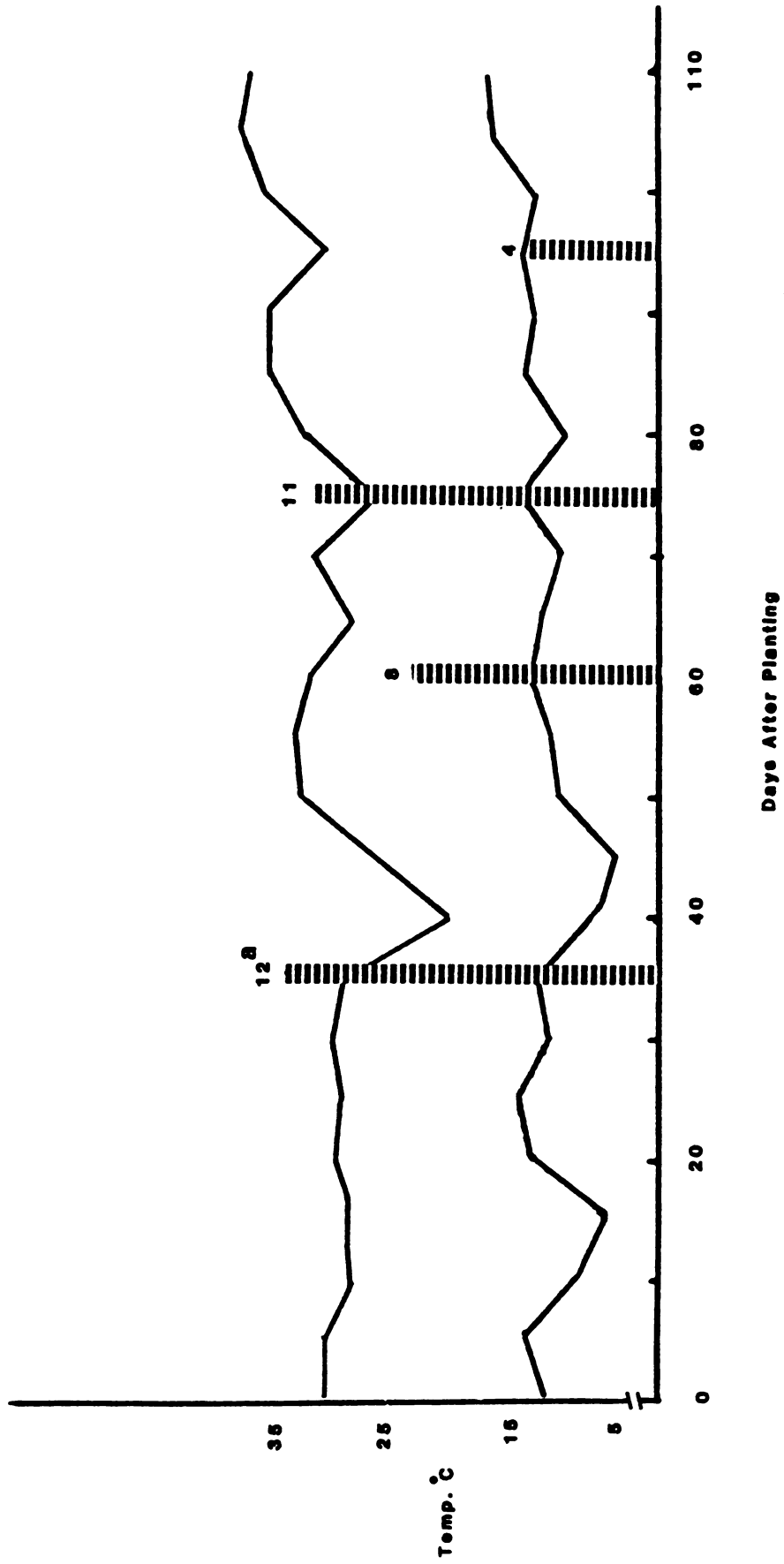


Figure 1. Maximum and Minimum Daily Temperatures. Iguala, 1982-3.

a=Millimeters of rain

inoculated with a commercial granular Rhizobium inoculant, NITRAGIN L x 441 for dry beans, obtained from the Nitragin Company in Wisconsin ; 1.5 gms. of inoculant per meter of row were applied. Twenty one dry bean genotypes were selected on the basis of their performance under drought as well as on their nitrogen fixation capabilities. They included:

a) three good nitrogen fixing lines from the University of Wisconsin: 23-61, 21-58, and 21-54.

b) five CIAT lines reported to have some tolerance to drought: BAT 332, BAT 85, BAT 47, A-162, and BAT 798.

c) seven Mexican lines with some tolerance to drought: Pinto Nacional 1, Durango 222, Ojo de Cabra, Bayo Madero, C-5, 1213-2, and LEF-2-RB.

d) two Michigan State varieties with good architecture and high yielding potential: Neptune and 61065.

e) two Michigan State lines that showed leaf flagging under severely dry conditions and were high yielders: 81017 and 800122.

f) two Michigan State lines that showed leaf flagging under severe dry conditions and were poor yielders: 790131 and 800205.

A Tepary bean, Phaseolus acutifolius was also planted.

Each plot consisted of 6 rows 4 meters long; the distance between rows was 75 cms. and the distance between plants within a row was 10 cms. Two empty rows were always left between adjacent plots in order to facilitate water

management. The experimental units were arranged in a split plot design with three replications. The combination of nitrogen source and water level was the whole plot factor and cultivars were the split plot factor.

All plots were flood-irrigated every two weeks starting before the planting day, until flowering time. Individual plots of each cultivar were treated as separate units for water management. After flowering, only the so-called "plus" water plots continued to receive water.

A commercial micronutrient foliar spray was applied 42 and 50 days after planting. Insects were controlled by spraying once a week with available commercial insecticides. Two center rows of each plot were used for periodic sample collection, two were used for final harvest, and the two outer rows were discarded. Flowering notes were recorded and when 50% flowering was reached, the first sample was taken. Ten of the twenty two planted cultivars were selected for detailed sampling. This selection was based on previous information regarding differences in N-fixation potential and drought tolerance. The 10 cultivars chosen for more detailed study included 8 drought tolerant lines (4 from Mexico, 2 from CIAT and 2 from MSU), one good N-fixing line from Wisconsin and one drought susceptible line from MSU.

Each sample consisted of five plants that had uniform competition, they were dug up trying to get as much of the roots as possible. Each sample was separated into stems, roots and leaves; this material was placed in an oven at 80° C for one hour and then was left out in the sun for

completion of drying. After dry weights were recorded, the tissue from each sample was ground in a Wiley mill and saved for starch and soluble sugars determinations. At the same time a 2-plant sample was taken (plants were kept entire); after drying they were ground and saved for total Kjeldahl nitrogen determinations. The second sample was taken 15 days after flowering, the time when the stress was expected to become effective. The third and last sample was taken at physiological maturity. The sampling procedures for the second and third samples were the same as for the first sample, except that in the last two samples pods were also separated.

Additional observations and notes such as occurrence of leaf flagging, leaf dropping and leaf yellowness were recorded. A leaf dropping scale from 1 to 5 was adapted, where 1 was no defoliation and 5 was complete defoliation. Scores for each plot were taken 85 days after flowering (before physiological maturity was reached). At harvest time both economic and biological yield were recorded and the Harvest Index was calculated.

A random sample of 10 plants was taken at harvest time to observe if there were any differences for seed weight and seed number between the plant's upper and lower pods. For this purpose the two lowest pods as well as the two highest pods of each sampled plant were taken and their seed number and weight recorded.

Starch contents were determined with a colorimetric method with perchloric acid, described in Appendix B.

RESULTS

I. Water Effects

The objective of this experiment was to determine the effect of drought stress imposed during the latter part of the seed filling period on the yield performance of 22 different cultivars and to relate their performance under stress with the ability to translocate non-structural carbohydrates. To accomplish this objective, the different genotypes were irrigated every two weeks from planting until anthesis. Working under the assumption that with high temperatures and high solar radiation the potential evaporation was high, we expected the irrigation water to be depleted at about two weeks after it was added. Based on these assumptions, withholding the water at anthesis presumably would cause an effective stress in the middle of the seed filling period, defined as 2 weeks after flowering. The control plots were continuously irrigated every two weeks throughout the entire growing season. Different cultivars were treated independently, meaning that each plot was considered as a separate unit for irrigation purposes.

The first evident symptom of water deficit was premature defoliation; it started to occur two weeks after the plants were expected to be under stress. A two-week lapse between the time that we had intended to have the

stress and the first visible signs of stress might indicate that we did not actually impose the stress at the physiological stage that we had originally intended. However, we can not assure that the plants were not under stress before this time because measurements that would have indicated that, such as stomatal closure, osmotic adjustment and photosynthesis reduction, were not taken. Another indication of the presence of the water stress in the crop consisted in the reduction of the length of the seed filling period (days from flowering to physiological maturity), in the water stressed plots as compared to the irrigated plots. Perhaps a faster development allows the completion of the reproductive stage before soil water is completely exhausted.

It is evident that we did have a water stress, but what we can not assure is the degree of the stress or its precise timing.

The degree of correlation between control and stress yields has been considered to be an indication of the severity of the stress (9,10). A mild drought stress reduces yield, but the grain yield of the stressed plots is highly correlated with the yield potential in the absence of the stress. Severe stress provokes very different responses among genotypes with similar yield potential, and the correlation between grain yield under stress and yield potential is weaker. Since in this case the correlation of control yield vs. stress yield was found to be positive and highly significant (calculated $r = 0.895$), we can infer that the

stress was moderate rather than severe.

Since there were not significant effects of N-treatment, the water effects described herein are based on both the plus and minus N treatments.

A. Biological Yield

A significant cultivar effect as well as a significant water effect were indicated by the Analysis of Variance. Twelve of the twenty two cultivars had a significant reduction of Biological Yield under water stress, while only two cultivars, MSU 800122 and Mexico LEF-2-RB, showed a significant increase for this trait under stress (Table 1). The other eight cultivars didn't show any significant differences between treatments, but except for cultivars MSU 61065 and CIAT BAT 332 , Biological Yield was reduced under water stress. In the case of 800122 and LEF-2-RB we have no evidence that will allow a reasonable explanation. The size of the biological yield reduction in some cultivars was unexpectedly high, considering that the stress was not effective until late in the season. In fact, in cultivar Bayo Madero this reduction was more than 50%.

Differences in magnitude for Biological Yield were observed; the high values of 81017, Ojo de Cabra, and Bayo Madero contrast with the relatively low values of Durango 222 and Pinto Nacional. It is interesting to note that entry

Table 1. Biological yield (kg/ha) under two water treatments. Iguala, 1982-3.

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	4945	3443 **
2	Wisc 21-58	4674	3761 **
3	Wisc 21-54	4464	3536 **
4	Neptune	5088	4254 **
5	61065	3908	4012 **
6	800122	4305	5280 **
7	81017	6050	4308 **
8	800205	4233	3728
9	790131	4021	3457
10	LEF-2-RB	4360	5298 **
11	1213-2	3853	2951 **
12	C-5	3277	2515 *
13	Bayo Madero	7592	3371 **
14	BAT 332	3862	4044
15	BAT 85	4049	3482
16	BAT 47	4263	3980
17	A-162	4551	3761 *
18	BAT 798	3973	3019 **
19	Pinto Nacional 1	3187	2316 **
20	Durango 222	3642	3288
21	Ojo de Cabra	5819	3827 **
22	Tepary	3888	3875

* = LSD at .10 (672)

** = LSD at .05 (802)

22, the Tepary bean, P. acutifolius , known to be a drought tolerant line, showed no difference in Biological Yield between the plus and minus water treatments.

B. Economic Yield

The Analysis of Variance revealed a significant cultivar effect and also a significant water effect at the 5% level. Only six of the twenty two entries showed a significant yield decrease under the water stress conditions, as compared to the non - stressed plots (Table 2). Of these six cultivars, four were Mexican lines (1213-2, C-5, Bayo Madero and Pinto Nacional 1) and two were MSU lines (800122 and 800205). Among the other sixteen entries, ten showed a non-significant decrease in Economic Yield under stress conditions and six had a non-significant yield increase.

Water stress, when imposed during the seed filling period, seemed to have a greater effect on the economic yield of the cultivars that retained more assimilates in the stems at maturity. A significant negative correlation of 0.448 between economic yield and stem % of dry weight at Physiological Maturity under water stress supports this assertion. Inherently low yielding genotypes such as 790131 and Durango 222 displayed a decrease in stem weight only under stress at P.M.; under non-stress stem weight was not reduced. The correlation between stem % of total dry weight

Table 2. Economic yield (kg/ha) under two water treatments. Iguala, 1982-3.

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	1536	1500
2	Wisc 21-58	1887	1743
3	Wisc 21-54	1330	1440
4	Neptune	1554	1673
5	61065	1815	1938
6	800122	1571	1178 **
7	81017	2086	2001
8	800205	1822	1487 **
9	790131	1225	1064
10	LEF-2-RB	1964	1775
11	1213-2	1514	1200 **
12	C-5	1502	1181 **
13	Bayo Madero	1183	742 **
14	BAT 332	1779	1919
15	BAT 85	1966	1751
16	BAT 47	1843	1780
17	A-162	1833	1744
18	BAT 798	1081	1044
19	Pinto Nacional 1	1262	889 **
20	Durango 222	1102	985
21	Ojo de Cabra	628	693
22	Tepary	1521	1484

* = LSD at 0.10 (217)

** = LSD at 0.05 (259)

and economic yield for both cultivars was non-significant under the plus water treatment, while under water stress for both 790131 and Durango 222 there was a significant negative correlation, with values of 0.850 and 0.975 respectively. Even though these are low yielding genotypes, their economic yield was not significantly reduced under stress. This is consistent with the hypothesis that remobilization is enhanced under stress conditions.

Bayo Madero and 800122 incurred significant reductions in economic yield under stress as well as a significant increase in stem dry weight , suggesting either a poor remobilization and a low capacity to buffer adverse environmental effects, or a weak sink that does not have the ability to utilize the stored assimilates. 800122, a late maturity cultivar, did not flower until late in the season; for this reason , as shown in Figure 2, during the reproductive stage it was subjected to high temperatures. I believe that the high temperatures during this stage of development kept this particular variety from remobilizing and senescing normally, and as a consequence yield was significantly affected.

The three Wisconsin cultivars 23-61, 21-58 and 21-54, as well as Neptune, A-162 , BAT 85 and Ojo de Cabra, had a significant reduction in biological yield under stress, however, their economic yield was not significantly reduced.

This is supportive of the hypothesis that in those genotypes that have the ability to remobilize assimilates from stems ,storage photosynthates act as a buffer between

seed growth and photosynthesis. However, we can not determine if the contribution to seed yield is coming mainly from assimilates that were produced before the plants were subjected to the water stress, or if the seeds were filled with photosynthates produced after the onset of stress.

C. Harvest Index

The AOV revealed a significant cultivar and water effect on Harvest Index (H.I.) at the 1% level. Seven entries showed a significant increase in H.I. under water stress as compared to the non-stressed plots (Table 3). They include the Wisconsin lines 23-61 and 21-54, the MSU lines Neptune and 81017, the Mexican lines Ojo de Cabra and Bayo Madero and the CIAT line BAT 798. Significant reductions of biological yield under stress account for differences in Harvest Index for these cultivars. In the case of Bayo Madero, reductions in both economic and biological yield occurred.

Two lines, MSU 800122 and Mexico LEF-2-RB, had a significant reduction in H.I. under the minus water treatment. Nine out of the thirteen remaining lines had a non-significant H.I. increase under stress, while the other four had a non-significant decrease. It is interesting to note that the Tepary bean (entry 22) had almost the same value for H.I. under both stress and non stress conditions.

Table 3. Harvest Index under two water treatments. Iguala, 1982-3.

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	0.33	0.43 **
2	Wisc 21-58	0.41	0.46 **
3	Wisc 21-54	0.31	0.41 **
4	Neptune	0.32	0.40 **
5	61065	0.47	0.48 **
6	800122	0.39	0.22 **
7	81017	0.36	0.46 **
8	800205	0.42	0.42
9	790131	0.30	0.32
10	LEF-2-RB	0.44	0.37 **
11	1213-2	0.40	0.41
12	C-5	0.43	0.47
13	Bayo Madero	0.15	0.22
14	BAT 332	0.45	0.46
15	BAT 85	0.49	0.51
16	BAT 47	0.39	0.44
17	A-162	0.41	0.46
18	BAT 798	0.27	0.34 **
19	Pinto Nacional 1	0.39	0.38
20	Durango 222	0.30	0.30
21	Ojo de Cabra	0.15	0.24 **
22	Tepary	0.39	0.38

* = LSD at 0.10 (0.60)

** = LSD at 0.05 (0.70)

D. Seed Size

The AOV for this trait, measured as weight of 100 seeds, reveals a significant effect for cultivars and water treatment. All entries incurred a reduction in single seed weight of about one centigram due to stress (Table 4). However, only three out of the twenty two entries had a statistically significant reduction in the weight of 100 seeds under the water stress treatment. These three entries were all Mexican lines (Bayo Madero, Pinto Nacional and Durango 222).

Variations in economic yield due to water stress in the cultivars Bayo Madero and Pinto Nacional were due to reduction of seed size as well as seed number. Smaller seeds under a low water regime are the consequence of incomplete filling, indicating lower photosynthesis and/or an inadequate reallocation of carbohydrates during the seed filling process.

E. Seed Number

The AOV for the number of seeds per square meter indicated a significant cultivar effect as well as a significant cultivar - water interaction, but the water effect itself was not statistically significant. Since the water stress did not become effective until the late part of the growing season, when the number of seeds had already

Table 4. Weight of 100 seeds (grs) under two water treatments. Iguala, 1982-3.

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	18.25	17.41
2	Wisc 21-58	20.93	20.08
3	Wisc 21-54	20.05	19.16
4	Neptune	16.42	15.93
5	61065	18.28	17.71
6	800122	16.36	15.68
7	81017	20.60	19.07
8	800205	16.68	15.76
9	790131	23.11	22.01
10	LEF-2-RB	25.10	24.05
11	1213-2	35.96	34.71
12	C-5	34.65	33.51
13	Bayo Madero	43.60	41.48 **
14	BAT 332	16.88	16.20
15	BAT 85	20.78	19.58
16	BAT 47	26.78	26.10
17	A-162	19.51	19.23
18	BAT 798	20.38	19.16
19	Pinto Nacional 1	35.63	33.10 **
20	Durango 222	50.58	45.07 **
21	Ojo de Cabra	39.55	39.45
22	Tepary	11.96	11.48

* = LSD at 0.10 (1.55)

** = LSD at 0.05 (1.85)

been determined, no water treatment effect is to be expected for this trait. Only two of the twenty two entries had a significant reduction in the number of seeds under the water stress treatment, while three had a significantly larger number of seeds under stress (Table 5) . The three cultivars that had a significant increment in the number of seeds (Neptune, 61065 and BAT 332) had a reduction of seed weight under stress. This might be an indication of component compensation, in which the reduction of seed weight is caused by the increment in seed number. Although the reductions in seed number for Bayo Madero and Pinto Nacional were not statistically significant, they can be considered large enough to explain the economic yield loss observed under water stress.

F. Length of Vegetative and Reproductive Stages

The AOV for the length of the seed filling period, measured as the number of days between 50% Flowering and Physiological Maturity, showed a significant cultivar effect as well as a significant water effect. All cultivars, without exceptions, incurred a reduction in the length of the seed filling period under the water stress treatment (Table 6). However, these reductions turned out to be significant only for 15 of the 22 entries.

Variability in seed filling duration between cultivars and between treatments within cultivars is shown in the

Table 5. Seed number (seeds/mt²) under two water treatments. Iguala, 1982-3.

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	842	862
2	Wisc 21-58	902	868
3	Wisc 21-54	663	752
4	Neptune	946	1051 *
5	61065	994	1108 *
6	800122	957	787 **
7	81017	1013	1049
8	800205	1093	944 **
9	790131	534	474
10	LEF-2-RB	732	735
11	1213-2	421	347
12	C-5	434	353
13	Bayo Madero	269	178
14	BAT 332	1052	1181 **
15	BAT 85	949	894
16	BAT 47	688	682
17	A-162	940	907
18	BAT 798	531	545
19	Pinto Nacional 1	354	269
20	Durango 222	221	216
21	Ojo de Cabra	159	176
22	Tepary	1272	1293

* = LSD at 0.10 (101)

** = LSD at 0.05 (121)

data. Since seeds compete for available assimilates, if the sink capacity at the initiation of the seed filling stage is higher than the source supply, extending the duration of seed filling under non-stress conditions theoretically should provide more available photosynthate to the seed which in turn will produce heavier seeds and higher yields.

Earliness has been associated with improved adaptation in crops subjected to drought, probably as a mean of escaping the stress through faster development. If this reduction in the length of the reproductive stage under adverse conditions induces an earlier partition of carbohydrates to the seeds, early genotypes should be able to buffer adverse environmental effects in a more efficient manner. This is supported by the data shown here where the cultivars Ojo de Cabra, Bayo Madero, Durango 222 and C-5 were among the lowest yielding lines and had the longest seed filling period under stress. All the top yielding cultivars 81017, 61065, LEF-2-RB, BAT 85 and BAT 332 had a relatively short reproductive phase under water stress. High temperatures during the reproductive stage as occurred in Iguala (Figure 2), probably reduced the length of the period from Flowering to P.Maturity by inducing an earlier partition of carbohydrates that, in turn, hastened leaf senescence.

Developmental plasticity helps plants cope with an adverse environment, especially in terms of delaying or accelerating the onset of the reproductive phase so as to escape the more

Table 6. Days between flowering and physiological maturity
under two water treatments. Iguala, 1982-3.

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	37	33 **
2	Wisc 21-58	38	34 **
3	Wisc 21-54	37	34 **
4	Neptune	37	34 **
5	61065	35	34
6	800122	34	34
7	81017	41	38 **
8	800205	37	36
9	790131	30	28 *
10	LEF-2-RB	39	36 **
11	1213-2	42	40 *
12	C-5	45	45
13	Bayo Madero	52	48 **
14	BAT 332	30	29
15	BAT 85	33	33
16	BAT 47	41	40
17	A-162	41	38 **
18	BAT 798	45	33 **
19	Pinto Nacional 1	41	39 *
20	Durango 222	50	47 **
21	Ojo de Cabra	52	49 **
22	Tepary	44	41 **

* = LSD at 0.10 (2)

** = LSD at 0.05 (3)

Figure 2. Flowering dates and maximum daily temperatures.
Iguala, 1982-3.

1=Wisc 23-61, 2=Wisc 21-58, 3=Wisc 21-54, 4=Neptune, 5=61065,
6=800122, 7=81017, 8=800205, 9=790131, 10=LEF-2-RB, 11=1213-2,
12 = C-5, 13 = Bayo Madero, 14=BAT 332, 15=BAT 85, 16=BAT 47,
17= A-162, 18=BAT 798, 19=Pinto Nacional, 20=Durango 222,
21=Ojo de Cabra, 22=Tepary.

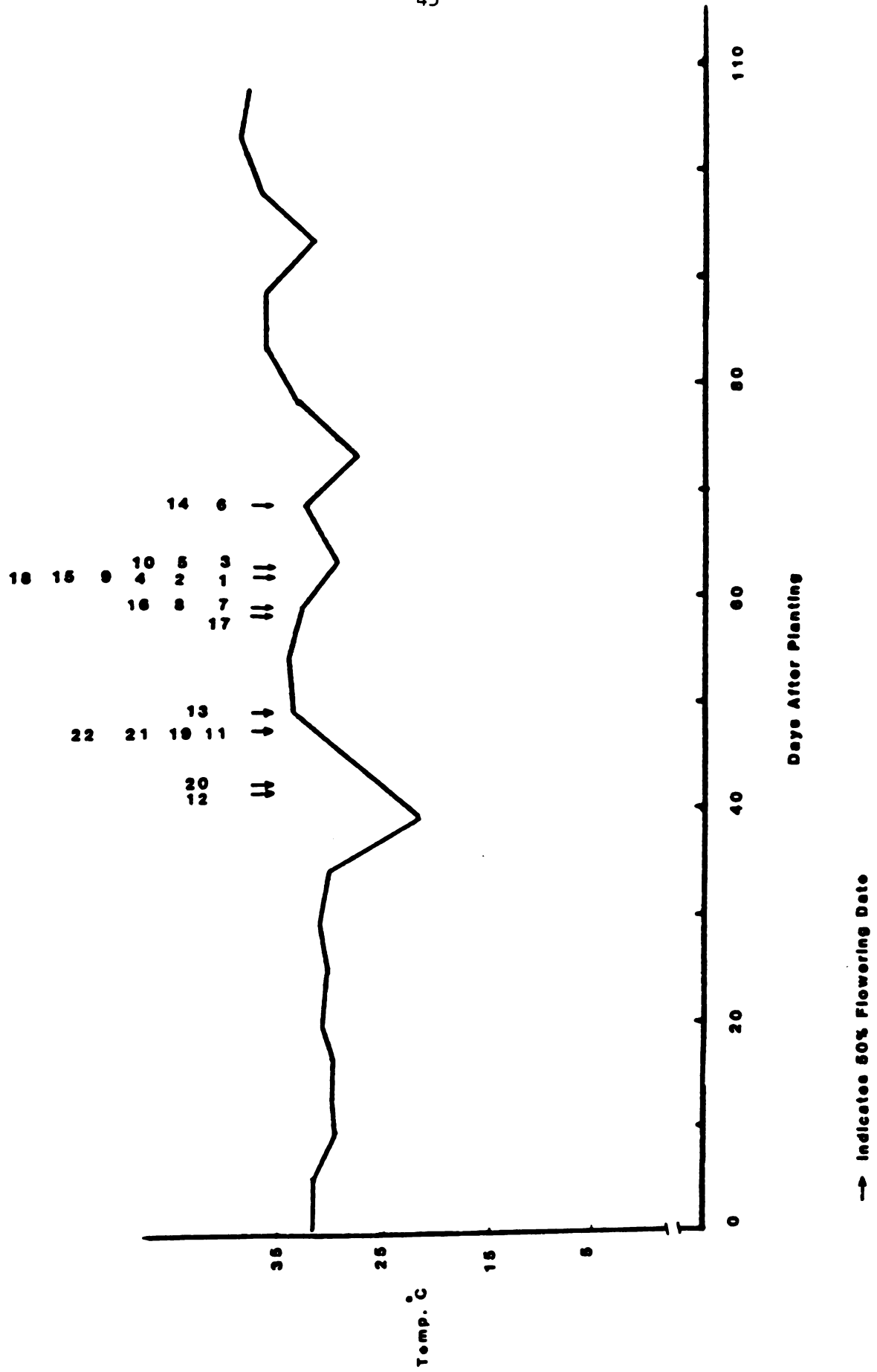


Figure 3. Biological Yield Under Irrigation and Flowering dates. Iguala, 1982-3.

1=Wisc 23-61, 2=Wisc 21-58, 3=Wisc 21-54, 4=Neptune, 5=61065,
6=800122, 7=81017, 8=800205, 9=790131, 10=LEF-2-RB, 11=1213-2,
12 = C-5, 13 = Bayo Madero, 14=BAT 332, 15=BAT 85, 16=BAT 47,
17= A-162, 18=BAT 798, 19=Pinto Nacional, 20=Durango 222,
21=Ojo de Cabra, 22=Tepary.

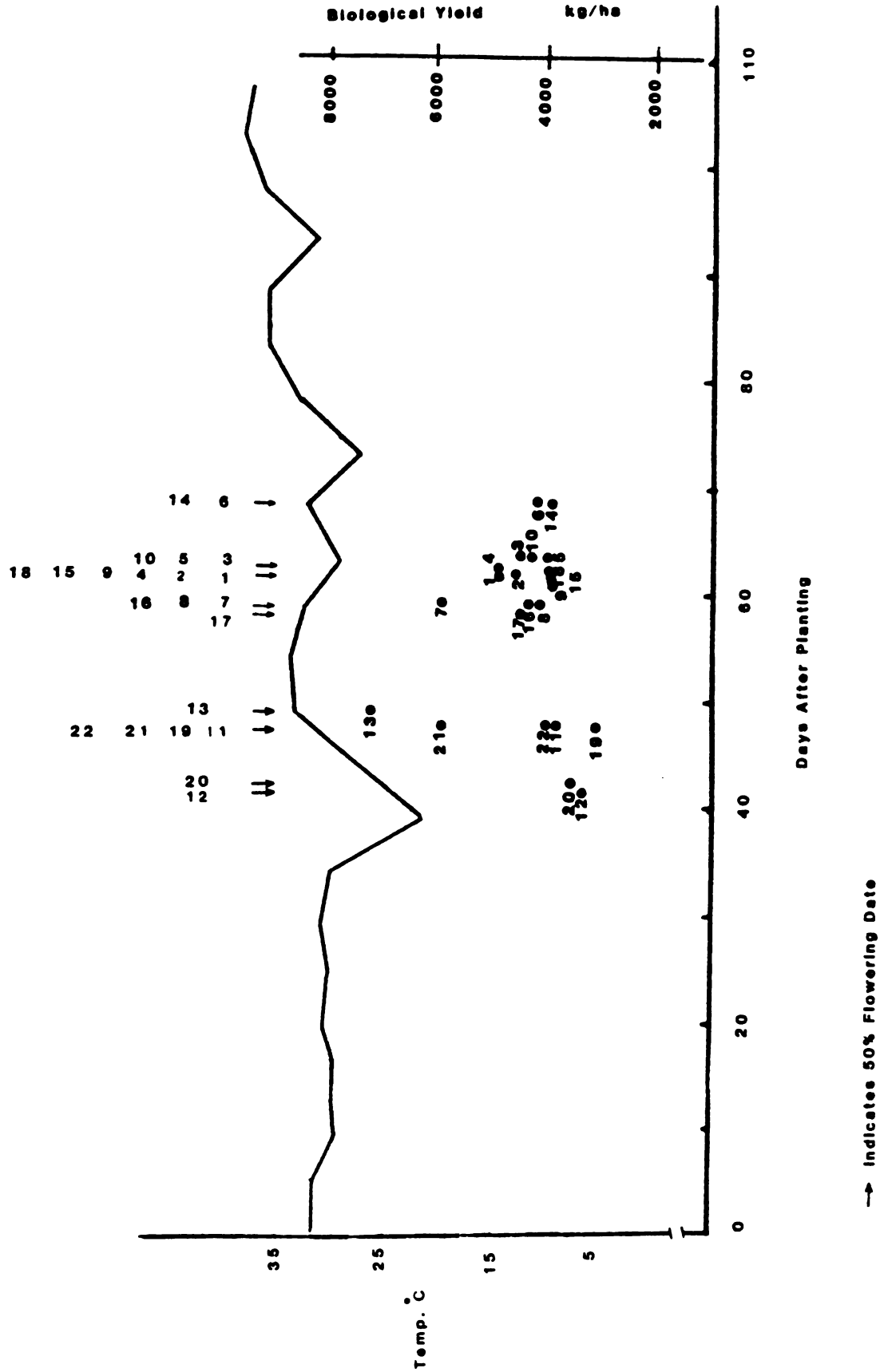
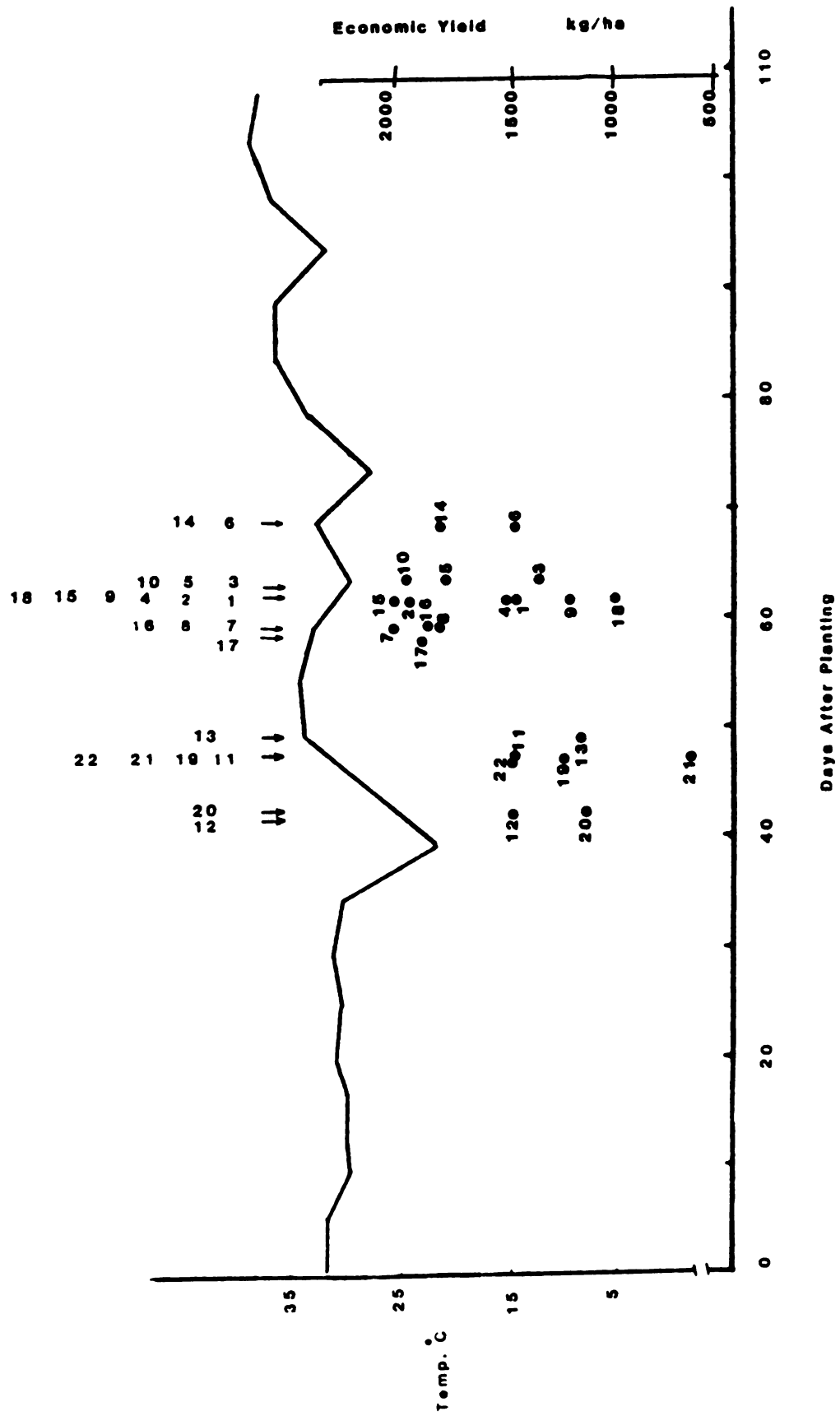


Figure 4. Economic Yield Under Irrigation and Flowering
dates. Iguala, 1982-3.

1=Wisc 23-61, 2=Wisc 21-58, 3=Wisc 21-54, 4=Neptune, 5=61065,
6=800122, 7=81017, 8=800205, 9=790131, 10=LEF-2-RB, 11=1213-2,
12 = C-5, 13 = Bayo Madero, 14=BAT 332, 15=BAT 85, 16=BAT 47,
17= A-162, 18=BAT 798, 19=Pinto Nacional, 20=Durango 222,
21=Ojo de Cabra, 22=Tepary.



→ Indicates 50% Flowering Date

severe periods of adversity. Faster development allows the completion of the reproductive stage before the soil water is exhausted.

The length of the vegetative stage, expressed as the number of days between planting and 50% flowering, is expected to be closely associated with the accumulation of total dry matter. One would also expect a positive correlation between Biological Yield and days to flower in the irrigated cultivars, since the longer they grow the greater the possibility for accumulation of dry matter . Figure 3 illustrates this point, and shows that only 2 of the 7 cultivars that flowered in less than 50 days after planting had a high Biological Yield, while all the late flowering cultivars had a high Biological Yield.

A greater accumulation of dry matter before the onset of stress might act as a reserve pool of assimilates that can be drawn upon when photosynthesis is reduced. If pre-anthesis assimilates are being utilized to fill the seeds, the cultivars that have a longer vegetative growth would be expected to have a greater source of assimilates and maybe a greater potential to buffer adverse environmental effects. Figure 4 shows that the top yielding cultivars from this experiment are all within the group that flowered 60 days or more after planting.

G. Leaf Dropping

Significant effects for the water treatment as well as significant differences between cultivars were detected by the AOV. All twenty two entries, without exception, had a significant increase in the leaf dropping score under stress (Table 7), which simply reveals that plants under stress had early defoliation. However, it is important to note that different degrees of defoliation were expressed. The leaf dropping scores under the irrigated plots ranged between 2.3 and 3.8 (little to moderate defoliation), while the scores for the water stress plots ranged from 2.8 to 4.8 (moderate to almost complete defoliation). Under water stress, varieties such as Ojo de Cabra, LEF-2-RB and Neptune had corresponding scores of 2.8, 3.1 and 3.3 while BAT 85 , 1213-2 and C-5 had respective values of 4.8, 4.7 and 4.6. Defoliation occurred in all cultivars under water stress and its correlation with economic yield turned out to be a non significant -0.161.

H. Plant Dry Weight at Physiological Maturity

Significant differences between cultivars were detected by the AOV for total plant dry weight. When individual components of total plant weight expressed as percent of the total dry weight were examined, not only significant differences between cultivars were evident, but also the

Table 7. Leaf dropping under two water treatments. Iguala, 1982-3. ^{*1}

Entry No.	Identification	Irrigated	Stress
1	Wisc 23-61	2.7	3.6 **
2	Wisc 21-58	2.8	3.5 **
3	Wisc 21-54	2.5	3.8 **
4	Neptune	2.5	3.3 **
5	61065	3.0	3.6 *
6	800122	2.0	3.5 **
7	81017	2.5	3.8 **
8	800205	3.0	3.6 **
9	790131	3.6	4.5 **
10	LEF-2-RB	2.6	3.1 *
11	1213-2	3.3	4.7 **
12	C-5	3.8	4.6 **
13	Bayo Madero	2.5	3.8 **
14	BAT 332	2.6	3.5 **
15	BAT 85	3.5	4.8 **
16	BAT 47	2.3	3.3 **
17	A-162	2.3	4.0 **
18	BAT 798	3.1	3.6 *
19	Pinto Nacional 1	3.6	4.8 **
20	Durango 222	3.8	4.5 **
21	Ojo de Cabra	2.3	2.8 *
22	Tepary	2.3	4.1 **

^{*1} Based on a scale from 1 to 5, where 1= No defoliation and 5= Complete defoliation.

* = LSD at 0.10 (0.5)

** = LSD at 0.05 (0.6)

water effects were significant for stem and leaf % of total dry weight. One must be cautious in interpreting these data. It is important to remember the inexplicable increase of total dry matter in the cultivars 800122 and LEF-2-RB under stress (Table 1). One must be aware that the % values may reveal some trends not shown by the total dry matter data.

In Table 8, one can see that of the 10 genotypes sampled only three had significant differences for stem % of total dry weight between the stress and the non-stress treatments. LEF-2-RB had a significant reduction of stem weight under water stress, while 800122 and Bayo Madero had a significant stem weight increase under stress. The other seven cultivars sampled showed a tendency towards decreasing stem weight under water stress, with the exception of 790131 and BAT 85.

At physiological maturity, the stems of Bayo Madero and 800122 under normal irrigation constituted 22.3 and 27.4 % of the total plant dry weight, indicating a high accumulation of dry matter in the stems. Their corresponding values under stress were 33.3 and 30.0 %; these figures might indicate that these two genotypes do not have the capacity to remobilize the stored assimilates from stems to the seeds. This inability to remobilize then could be the cause of the significant reduction of economic yield under stress for both Bayo Madero and 800122. However, this could also mean that the reduction of seed number under stress, although not statistically significant, resulted in

Table 8. Stem and Pod % of total dry weight at Physiological Maturity under two water treatments. Iguala, 1982-3.

Identification	Stem % ^a		Pod % ^b	
	Irrigated	Stress	Irrigated	Stress
Wisc 23-61	17.27	15.95	70.83	71.63
61065	17.35	17.94	71.90	71.00
800122	27.40	33.39	56.93	51.61
790131	17.37	17.46	66.20	70.85
LEF-2-RB	18.12	15.31	68.55	74.09
1213-2	14.40	13.65	70.09	77.05
Bayo Madero	22.33	30.04	65.48	54.60
BAT 332	18.10	16.53	69.39	72.61
BAT 85	15.19	16.12	70.96	71.67
Durango 222	16.12	15.84	70.75	72.67

a * = LSD at 0.10 (1.86)
 ** = LSD at 0.05 (2.23)

b * = LSD at 0.10 (3.78)
 ** = LSD at 0.05 (4.52)

a sink demand insufficiently strong to require remobilization.

The high yielding cultivar LEF-2-RB had a different behavior; under no stress the stem weight corresponded to 18.1 % of the total dry weight, while under stress it was only 15.3 %. The changes in dry weight induced by the stress, though not large by these figures, may be enough to sustain the seed filling process temporarily and as a consequence economic yield under stress was not significantly reduced.

Pod % of total plant dry weight showed a significant reduction under minus water in the low yielding cultivars 800122 and Bayo Madero, indicating that reduction in economic yield in these two cultivars probably was due not only to the decrease in single seed weight but also to the reduction of seed number.

I. Plant Dry Weight Changes: Remobilization

Figure 5 shows the changes in stem, root, leaf and pod dry weights over the three different sampling times (Flowering, 15 days after Flowering and P.Maturity) for six different cultivars. From Flowering to 15 d.a.f. stem weight increased in all cultivars, however, the size of this increment varied among cultivars. One can see fairly large increments in cultivars such as 61065 and BAT 85, while 790131, 1213-2 and Bayo Madero showed only a relatively small

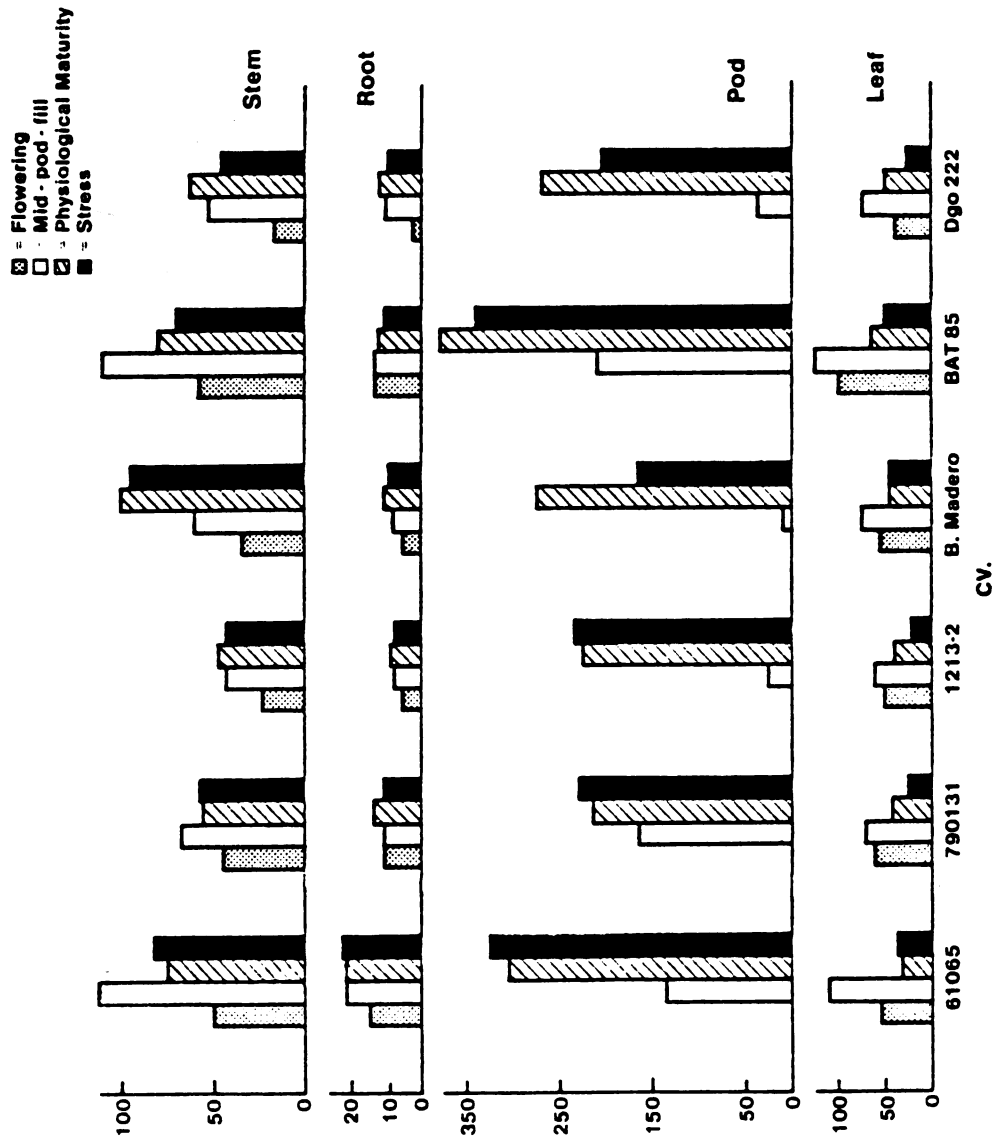


Figure 5. Stem, Root, Pod and Leaf dry weights (grs/mt²) over three physiological stages. Iguala, 1982-3.

increase. The changes from 15 d.a.f. to P.Maturity differed in the sampled cultivars. BAT 85, 61065 and 790131 had a reduction in stem dry weight, while Durango 222, 1213-2 and Bayo Madero had an increase.

When comparing the stem dry weight reduction in the water stress versus the non-stress plots, one can observe a general tendency towards a greater reduction in dry weights under the stress treatment. Durango 222 and 1213-2 incurred a reduction of dry weight under the stress treatment, while no reduction occurred under the plus water conditions. Bayo Madero showed an increase in stem dry weight at P.Maturity with respect to 15 d.a.f., however, the increment was slightly smaller under stress. BAT 85, as noted before, incurred a reduction in stem dry weight from 15 d.a.f. to P.Maturity, the reduction being greater under stress. 790131 had a small reduction from 15 d.a.f. to P.Maturity but no differences were seen between the stress and the non-stress treatments.

The high yielding lines BAT 85 and 61065 had the largest stem weights at 15 d.a.f. Their respective losses from 15 d.a.f. to P.Maturity might indicate that remobilization of stored assimilates had taken place.

The low yielding line Bayo Madero, although it had high values for stem weight at 15 d.a.f., apparently did not remobilize its stored carbohydrates to the seeds. In the case of Durango 222 remobilization occurred only under stress. The lack of remobilization under non-stress conditions was probably due to the lack of need to utilize

the stored carbohydrates because assimilate demand by the seeds was being satisfied by currently produced photosynthates. Only when photosynthesis is adversely affected would the seed filling process depend upon the stored assimilates and their reallocation .

A significant correlation of 0.394 between root weight at flowering time and economic yield points out the importance of the root system in relation to yield. However, one must be careful when interpreting these results, because a low correlation even though statistically significant, still leaves a great deal of yield variance unaccounted for that has to be explained by other factors. The top yielding cultivars BAT 85 and 61065 had the highest values for root dry weight at flowering, while the bottom yielding line Durango 222 had the smallest value. No significant correlations were found between economic yield and root weight at either 15 d.a.f. or P.Maturity. Large values of leaf weight at flowering and at 15 d.a.f. represent a large photosynthetic area and therefore a substantial carbohydrate manufacturing site. The data show that the highest values for leaf weight at these physiological stages were produced by the top yielding lines BAT 85 and 61065. Changes in leaf weight from 15 d.a.f. to P.Maturity show that under stress the reduction of leaf weight is greater as compared to the non-stress values. However, as pointed out before when describing the leaf dropping results, economic yield and defoliation did not show a significant correlation.

In general one can observe that the pod dry weight data presented in Fig. 5, as expected, are in broad agreement with the economic yield data given in Table 2. Small discrepancies such as the higher pod weight in BAT 85 which was outyielded by cultivar 61065 (Table 2) might indicate a greater dry weight of the pod walls in BAT 85 which are not included in the economic yield data. Nevertheless, these discrepancies are small and not statistically significant.

J. Starch Analysis

Significant cultivar differences for the amount of starch present at flowering, 15 d.a.f. and physiological maturity in the stems, roots and pods were detected by the AOV. Table 9 shows the starch percentage (mgrs of starch per gr of dry weight) for the different plant components at three physiological stages. The estimated values are very low as compared to starch determinations previously reported for dry beans (30,40). These low values might be the result of the lack of sensitivity of the method used, starch being determined by the colorimetric method already described, or from high respiration rates caused by high temperatures that prevailed during the growing season. Figures 6 and 7 illustrate the changes in starch content in the stems and pods over the 3 sampling times. One can see that the starch content is always lower under the stress treatment as compared to the irrigated plots. The AOV

Table 9. Mean values of starch (mgrs / gr dry wt.) at three different physiological stages under two water treatments. Iguala 1982-3.

Identification	Stage*	Stems		Roots		Pods	
		Irrigated	Stress	Irrigated	Stress	Irrigated	Stress
Wisconsin 21-34	P	20.8		1.7			
	MPP	---		---		---	
61065	PM	8.6	7.1	0.9	1.1	12.5	11.4
	P	21.4		2.1			
800122	MPP	25.0		2.3		9.4	
	PM	7.8	4.4	0.4	0.5	13.2	12.1
790131	P	18.7		1.5		---	
	MPP	---		---		---	
LEF-2-RB	PM	8.4	8.4	1.2	0.7	11.8	11.0
	P	32.8		1.7			
1213-2	MPP	27.9		2.3		11.3	
	PM	20.5	7.4	1.7	1.5	12.2	11.5
Bayo Madero	P	39.0		2.1		---	
	MPP	---		---		---	
BAT 332	PM	19.9	13.7	2.4	1.4	14.1	14.0
	P	36.8		1.4			
BAT 85	MPP	124.5		4.3		5.7	
	PM	40.0	24.5	3.9	4.2	13.2	12.1
Durango 222	P	21.4		1.5			
	MPP	63.7		3.6		3.0	
BAT 332	PM	56.4	50.2	3.8	3.3	12.1	12.2
	P	36.7		2.5		---	
BAT 85	MPP	---		---		---	
	PM	12.5	7.5	2.9	0.9	11.8	11.7
Durango 222	P	40.5		2.7			
	MPP	49.5		2.6		9.7	
BAT 332	PM	7.3	4.9	1.0	0.8	12.6	11.2
	P	18.6		1.9			
BAT 85	MPP	58.1		7.7		4.8	
	PM	41.4	25.7	4.1	4.9	12.1	12.3

* P= flowering
MPP= mid-pod filling
PM = physiological maturity

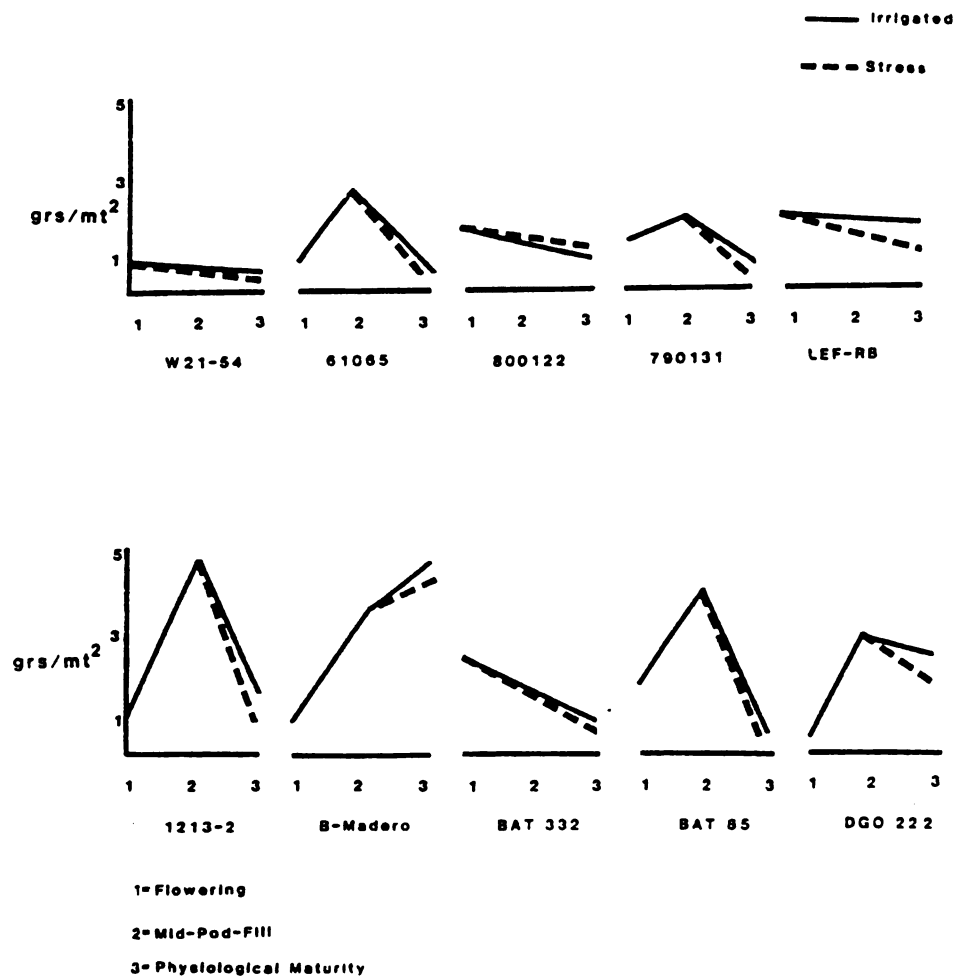


Figure 6. Changes in Stem - Starch Contents (grs/mt²) Over Three Physiological Stages Under Two Water Treatments. Iguala, 1982 - 3.

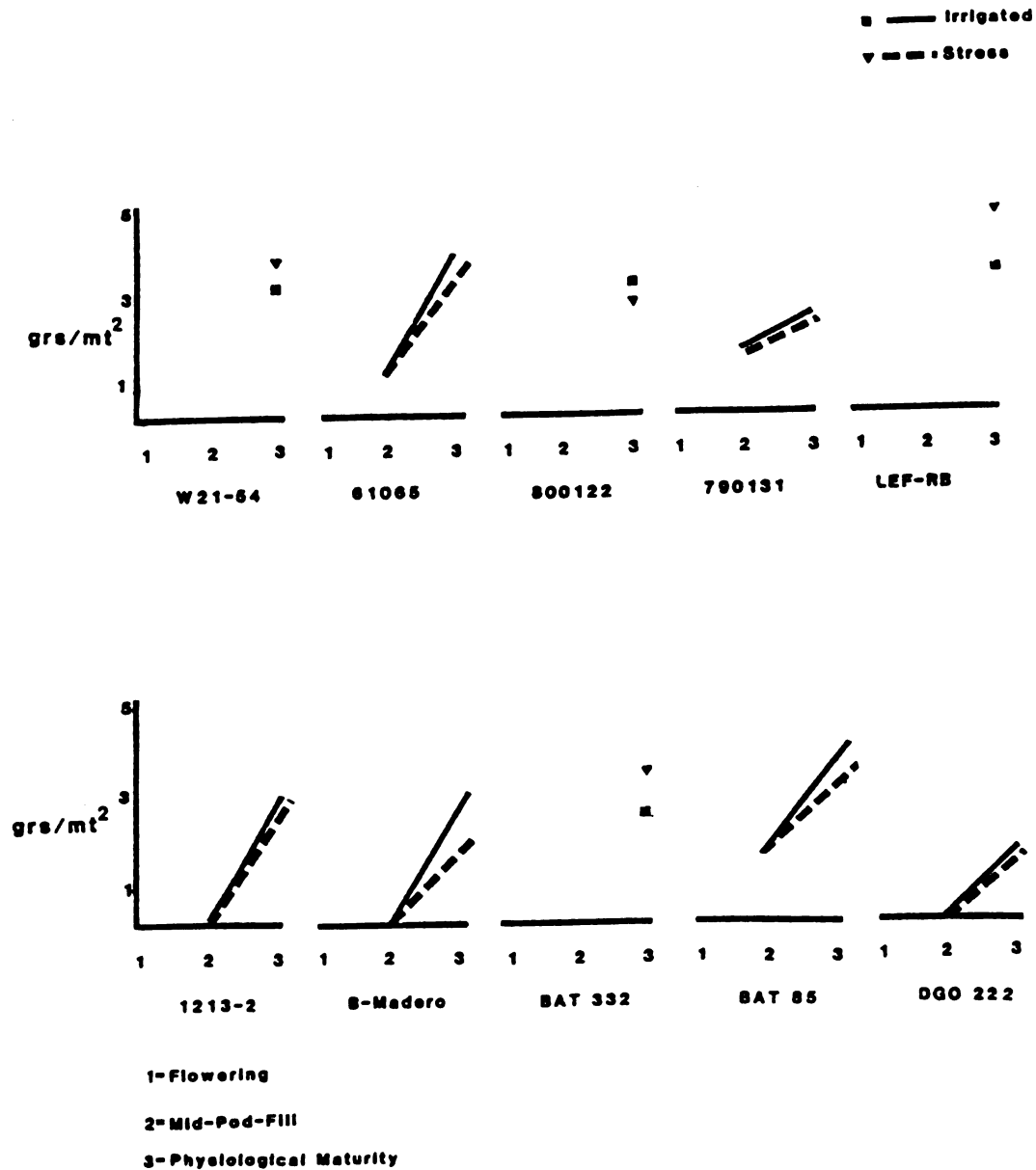


Figure 7. Changes in Pod - Starch Contents (grs/mt²) Over Three Physiological Stages Under Two Water Treatments. Iguala, 1982 - 3.

revealed significant cultivar and treatment differences for the amount of starch present in the stems at physiological maturity. Figure 6 illustrates the seasonal variation in starch content in the stems. Bayo Madero was the only cultivar that had an increment in the amount of starch in the stem from m.p.f. to PM, and this increment was smaller under the water stress treatment. A greater utilization of assimilates stored in the stems under water stress may constitute a strategy by which the plants cope with adverse environmental effects. A negative and significant correlation between the starch present in the stems at P.M. and seed yield supports this hypothesis. The calculated correlation was -0.5 under water stress, while under irrigation the corresponding value was -0.3 . This might indicate that the seed filling process, when photosynthesis is adversely reduced, utilizes the stored carbohydrates, and that the greater the capacity to remobilize them, the higher the seed yield would be. Under irrigation, when photosynthesis is not drastically reduced, there is a continuous supply of assimilates so the plant does not have to draw upon the reserves so heavily.

K. Twenty Upper and Lower Pods: Seed Number and Size

Significant differences were found among cultivars for seed number in both the upper and lower pods, but no significant water effect was indicated by the AOV. When the

number of seeds of the upper pods versus the lower pods was compared, no significant differences were observed (Table 10). However, for seed weight the AOV revealed a significant cultivar effect as well as a significant water by cultivar interaction. Seed weight in the upper and lower pods was reduced under the minus water treatment (Tables 4 and 11) , seeds from the upper pods being smaller than those from the lower pods. Since the lower pods are the first ones to be formed during the plant's developmental processes , they were at a more advanced seed filling stage when the stress became effective. This probably implies that either they did not have to rely upon the stored carbohydrates to fill their seeds because they were being filled with currently made photosynthates, or due to closer proximity they were the first ones to use the stored carbohydrates; they had essentially completed filling before the stress became severe.

Table 10. Seed number of 20 upper and lower pods under two water treatments. Iguala, 1982-3.

Identification	20 lower pods ^a		20 upper pods ^b	
	Irrigated	Stress	Irrigated	Stress
Wisc 23-61	102	113	111	119
61065	104	114	109	111
800122	109	107	108	112
790131	71	68	73	65
LEF-2-RB	87	106**	95	108
1213-2	61	56	70	61
Bayo Madero	57	61	62	65
BAT 332	96	108	84	99
BAT 85	106	107	113	106
Durango 222	50	45	52	52

a * = LSD at 0.10 (17)

** = LSD at 0.05 (20)

b * = LSD at 0.10 (16)

** = LSD at 0.05 (19)

Table 11. Seed weight (mgrs/seed) of 20 upper and lower pods under two water treatments. Iguala, 1982-3.

Identification	20 lower pods ^a		20 upper pods ^b	
	Irrigated	Stress	Irrigated	Stress
Wisc 23-61	210.7	199.9	193.5	188.5
61065	190.5	186.7	174.2	165.6
800122	163.9	158.5	168.5	153.1
790131	230.1	231.1	218.1	217.5
LEF-2-RB	251.2	254.0	242.2	242.9
1213-2	360.6	341.2	347.0	354.1
Bayo Madero	446.0	391.1**	409.7	373.3**
BAT 332	171.7	163.3	169.2	161.1
BAT 85	219.2	209.6	211.7	181.7**
Durango 222	519.4	422.8**	481.2	469.8

a * = LSD at 0.10 (27.7)

** = LSD at 0.05 (33.1)

b * = LSD at 0.10 (19.9)

** = LSD at 0.05 (23.8)

II. Nitrogen Effects

A secondary objective of this experiment was to determine the nitrogen fixation potential of the 22 cultivars, and to relate their potential with the effect of drought stress imposed during the latter part of the seed filling period and with the ability to translocate non-structural carbohydrates. To accomplish this objective, the twenty two cultivars were planted under two contrasting nitrogen levels and under two water regimes. As described in the Materials and Methods section, the experimental plots were on a Silty Clay soil in which the organic matter and total N contents were low (% of organic matter = 1.05, total N = 0.112 ppm). Before planting the so called plus N plots were fertilized with 40 kgs of N per hectare, applied in the form of urea, while the minus N plots did not receive any N fertilizer. At the time of planting all plots, except 2 border rows that ran the length the field, were inoculated with a commercial granular Rhizobium inoculant.

We expected to see differences due to the N treatment, but we could not observe any visual symptoms of N deficiency in the non-fertilized plots; also, the observed nodulation throughout the season was considered fairly poor for plants grown under the two different N treatments. The only clear N deficiency symptoms, such as severe yellowness and reduced growth, were observed in the two border rows that had neither fertilizer nor inoculant. We have no definite

explanations for the lack of difference between the plus and minus N treatments. Whether the soil analysis was faulty and the actual content of N in the soil was higher than shown by the analysis is unknown. We can't answer this question now because after harvesting this experiment the soil was plowed and uniformly fertilized for the next crop to be planted. Another possible explanation, though it may be remote, might be found in the levels of NO_3 present in the irrigation water. If such levels were high enough to provide the plants with sufficient N for their vegetative growth, it is possible that no N treatment differences did in fact exist. The fact that only two border rows, which were at the end of the field and therefore did not receive as much water as the other plants did, supports this assumption.

The quality of the applied inoculant turned out to be poor, having only 5.8×10^4 rhizobia per gram. A good quality inoculum should have at least 10^8 rhizobia per gram. Nevertheless, this does not imply that there were not enough bacteria in the soil sufficient to have established a symbiotic relationship with the host plants. Countings of the native Rhizobia population existing in the soil before inoculation ranged from 1.8×10^3 to 1.7×10^7 colonies per gram of soil.

Since the water stress was not effective until the late pod filling stage and the data herein described refers to earlier physiological stages, the results are based on only one water treatment.

A. Non-significant effects

The individual AOVs for Biological Yield, Economic Yield, Harvest Index, Weight of 100 seeds, Length of seed filling period, Leaf dropping, Seed number and weight from the 20 upper and lower pods and % of Nitrogen did not show a significant Nitrogen effect. However, some Nitrogen x Cultivar interactions as well as Nitrogen x Water and Nitrogen x Water x Cultivars interactions were significant. These interactions will be referred to in the next section.

The effect of added Nitrogen on N-fixation depends on the specific cultivar; different cultivars show different responses to N fertilizer. In the section, Interaction Effects, the differential response of the genotypes used in this study will be discussed and I will attempt to reach some conclusions from this experiment.

B. Plant dry weight

The AOV for total plant dry weight at the three sampling times (Flowering, 15 d.a.f., and Physiological Maturity) did not detect any significant differences due to N effect. However, with respect to the individual components of plant dry weight over the three different samples, a significant Nitrogen effect was given for stem % of total

plant dry weight at flowering time.

Figure 8 illustrates the differential responses of the 10 sampled cultivars over the two different levels of Nitrogen. In genotypes such as BAT 332, 61065, and 800122, the stem constituted over 42 % of their total plant dry weight, while in Durango 222 the corresponding value was less than 30 %. Even though the correlation between stem % of dry weight at flowering and Economic yield was expressed as a significant r value of 0.408, the data show that in high yielding lines such as BAT 85 the stem % of total dry weight was approximately the same as in the low yielding lines Bayo Madero and 790131.

Different cultivars showed different responses to N fertilizer. A line previously selected for high BNF potential, Wisconsin 23-61, showed an increase in stem weight when N was not added; BAT 332, also previously reported by CIAT to be a good N-fixer, showed an opposite response. No conclusions can be drawn from these results except that if stem % of total dry weight is positively correlated with yield, good N-fixers should have high stem weights at flowering time. The carbohydrates that are stored in the stems can be remobilized and utilized in the later stages of plant development when photosynthetic activity is reduced, particularly in the lower (shaded) portion of the canopy where carbohydrates might be needed for supporting N-fixation. In the case of N-fixation, a great amount of photosynthate is required by the nodules in order to

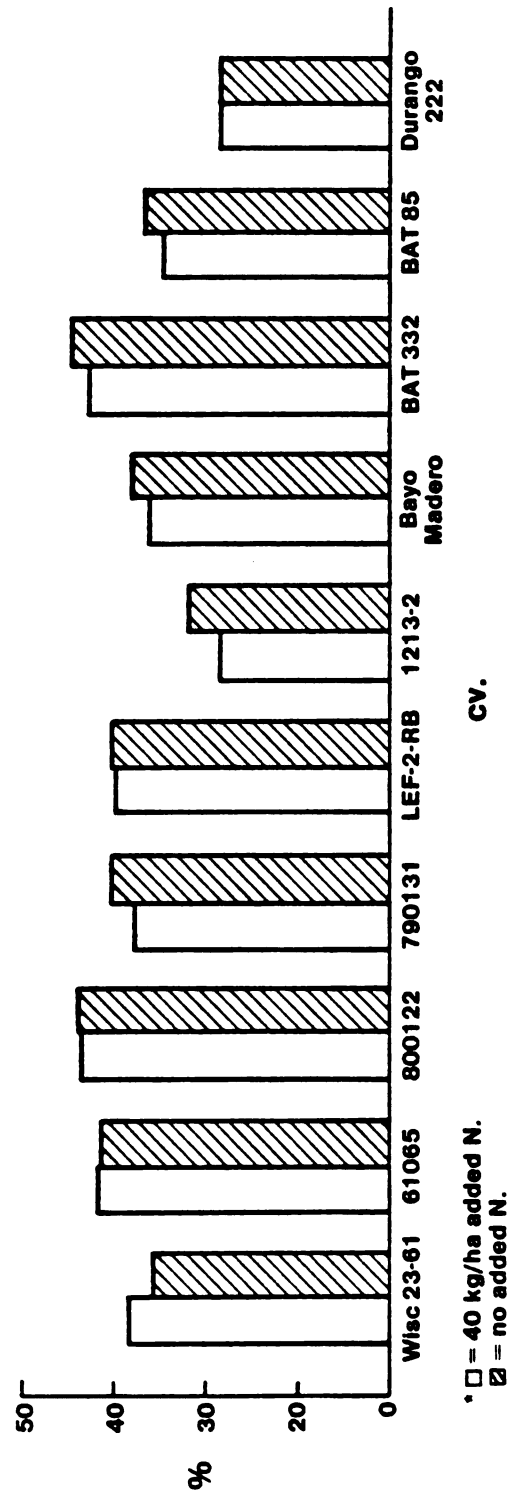


Figure 8. Stem % of total plant dry weight at flowering time. *Igualea 1982,3.

maintain their growth and to facilitate the organic binding of the fixed Nitrogen. Since the nodules store very few reserves, they depend on the supply of assimilates that is available to them. Genotypes like BAT 332, 61065 and 800122 should have a greater BNF potential than 1213-2 and Durango 222.

The roots constitute a potential site for carbohydrate storage and a possible supplier of assimilates to the nodules. A positive and significant correlation between the economic yield and the root weight at flowering time (when N-fixation is supposed to be at its maximum activity) was found, the calculated r-value being a significant 0.394.

C. Plant dry weight changes: remobilization

Figure 9 shows the changes in stem, root, leaf and pod dry weights that occurred from flowering to 15 d.a.f., the time that we consider to be the middle of the pod filling stage. This figure illustrates the differences in dry weights of six genotypes under added N as well as under non added N.

Stem weight increased in all cultivars, from flowering to 15 d.a.f. but the size of the increment varied for the different cultivars. The incremental changes were essentially the same for N-fertilized and non-fertilized treatments. Root weights remained approximately the same from flowering to 15 d.a.f.; only 61065 and Durango 222

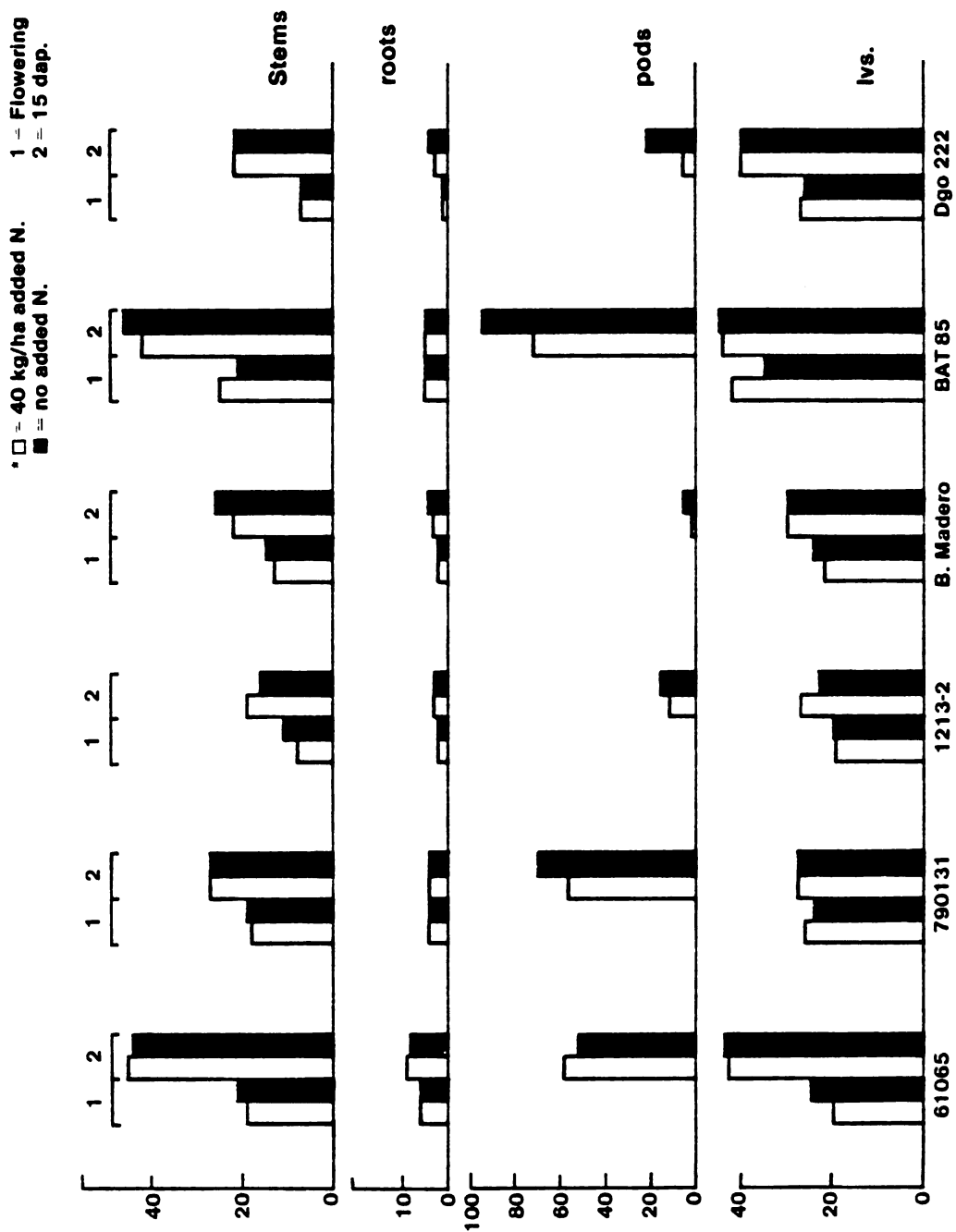


Fig. 9 Stem, Root, Pod and Leaf weights at Flowering and at 15 dap. under two different levels of added Nitrogen. 'Iguala 1982-3.

showed a noticeable increase in root dry weight, but no overall differences were seen between the two N treatments. With respect to pod weight at 15 d.a.f., a general tendency towards a greater pod weight under no added N was observed. These data suggest that in this experiment N fixation or soil N supply was sufficient to maintain a large number of flowers which developed into pods. Leaf weight increased over time, but again no differences due to N source were seen.

Since no differences were observed between N treatments for the individual components of plant dry weight, a Shoot:Root ratio (S:R) was calculated in order to try to understand the behavior of the different genotypes. This ratio, as a measure of the pattern of differential growth, can provide an index for the performance of each plant organ under different growth conditions. An increase in the S:R ratio might be the result of a greater utilization of carbohydrates by the shoot at the expense of the root, possibly bringing about a shortage in carbohydrate supply to the nodules that will translate into poor or reduced N-fixation. The effects of added N on S:R ratio as shown in Table 12 varied with plant genotype and stage of development. When reading this table one must be aware that very high values of S:R ratio probably reflect very incomplete harvest of the root system.

At flowering time, the cultivars 61065, 1213-2 and Bayo Madero had a higher S:R ratio under non-added N, while

Table 12. Shoot:Root ratio under two Nitrogen treatments
at two physiological stages. Iguala, 1982-3.

Identification	Stage ^{#1}	Treatment ^{#2}	S:R ratio
61065	F	+	6.7
		-	8.0
	MPF	+	17.0
		-	17.6
790131	F	+	9.9
		-	10.1
	MPF	+	25.9
		-	29.6
1213-2	F	+	14.9
		-	17.5
	MPF	+	18.8
		-	18.9
Bayo Madero	F	+	17.3
		-	19.8
	MPF	+	16.9
		-	16.2
BAT 85	F	+	12.7
		-	10.8
	MPF	+	32.3
		-	41.6
Durango 222	F	+	22.5
		-	21.6
	MPF	+	16.6
		-	17.0

*1 F= flowering
MPF= mid-pod filling

*2 + = added N
- = non-added N

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Durango 222 and 790131 remained the same. Only BAT 85 had a higher S:R ratio under added N at flowering time.

At 15 d.a.f. the cultivars 61065, 1213-2, Bayo Madero and Durango 222 showed no differences in S:R ratio due to added N. However, 790131, which showed no differences at flowering time, did show an increase of S:R ratio at 15 d.a.f. under non-added N. Also, BAT 85 had an increase of S:R ratio at 15 d.a.f. under the non fertilized treatment. Higher S:R ratios at flowering, under non-fertilized conditions, are caused by an increase in shoot dry weight. Shoot growth was enhanced when no N was added and it was diminished under added N. One possibility is that the applied dosage of N fertilizer (40 kgs/ha) was enough to inhibit N fixation but at the same time it was not enough to maintain a continued vigorous growth. On the other hand, the plants that were grown under non-added N conditions were able to maintain high levels of N-fixation which resulted in shoot growth. A second possible explanation is that temperatures were too high for maintaining high levels of the enzyme Nitrate Reductase, whose presence and activity is necessary for the utilization of N-fertilizer. In the case of BAT 85, the applied dosage of N fertilizer was either enough to satisfy the plant's requirements and promote optimum growth, or it acted as a "starter" and stimulated nodulation and plant growth at flowering time. However, in a later stage of development, BAT 85 had a higher S:R ratio under non added N as compared to the N-fertilized plots. This illustrates that the effect of N fertilizer varies not

only among cultivars but also between stages of development within the same cultivar.

The data presented herein suggest that N availability in both N-fertilized and inoculated plants was sufficient to support vegetative growth. Economic yield was not affected by N treatments for any of the sampled cultivars, nevertheless, small differences were seen between different combinations of genotype and N treatment.

DISCUSSION

One of the main purposes of this experiment was to try to identify physiological changes during the course of the growing season that can be responsible for maintaining normal yields under stress conditions. It seems reasonable to think that a better understanding of the basis of differences among cultivars and the relationship between these differences and their yield potential should provide basic information that would be very valuable in choosing a drought tolerance breeding strategy. As suggested by Duncan et al. (16), three plausible explanations for differences in yield between cultivars can be given. The first one is a difference in photosynthetic efficiency of leaf canopies, which would result in differences in the amount of carbon fixed over the growing season. This efficiency could result from better canopy geometry resulting in better light interception, or from greater leaf area duration. A second reason for yield differential could be the proportion of daily produced assimilates that is partitioned to the economic sink. It is likely that a higher yielding cultivar either partitions more of the daily assimilate production to the seeds or is capable of utilizing stored assimilates to fill the seeds. As a result, a greater number of seeds (increased sink size) and heavier seeds can be attained. The third reason could be the duration of the vegetative and reproductive periods, the latter commonly known as the seed

filling period. Seed yield is the result of the rate and duration of the filling period times the size of the economic sink. With this experiment we sought to answer the following questions: 1. Is there storage capacity in the stems of all cultivars ? 2. When stem weight declines, does this correspond to a non-structural carbohydrate loss? 3. What proportion of the seed dry weight increase can be accounted for by changes in dry weights, particularly by stem dry weight loss? 4. Are there cultivar and treatment differences in the contribution of storage assimilates to seed yield? With these questions in mind, the following discussion is organized around the three possible reasons for yield differences that were mentioned above.

1. Crop Growth Rate

Ground cover by the leaf canopy and rate of accumulation of dry weight generally increase exponentially until light interception is complete (16). In dry beans a fully closed canopy is achieved at around flowering time, and this was the case for the 22 cultivars planted in this experiment. Given that after reaching a closed canopy full light interception is attained, a further increase in LAI should not have any effect on light interception. The data presented here show that total leaf area (expressed as total leaf dry weight) continued to increase after flowering. However, for the reasons stated above, no further gains in

light interception were expected after flowering time.

Total dry matter accumulation or net photosynthesis, expressed as kgs of dry matter per hectare, is simply the difference between the total amount of carbon fixed by photosynthesis and the respective carbon losses due to growth and maintenance respiration. Net photosynthesis as well as average crop growth rates for 10 different cultivars during the vegetative stage are given in Table 13. It is evident that the late flowering cultivars had both a greater accumulation of dry matter and a higher growth rate during their vegetative phase of development. However, the CIAT line BAT 85 stands out for its high photosynthetic efficiency (expressed as kgs. of dry matter accumulated per hectare per day) given that it was not included among the late flowering cultivars, and that the cultivars that flowered at the same time as BAT 85 (63 to 64 days after planting) had lower crop growth rates. The efficiency of BAT 85 can not be explained further with our current data; we can not determine whether high photosynthetic capability, low respiratory losses or both are responsible for the high dry matter accumulation that occurred during the vegetative phase. The photosynthates accumulated during the reproductive stage of development and the crop growth rates for that period for the 10 sampled cultivars are given in Table 14. Crop growth rates increased in all cases in the reproductive stage as compared to the vegetative stage. Cultivar responses to the stress differed: BAT 332, LEF-2-

Table 13. Average Crop growth rates(kg/ha/day) from planting to flowering. Iguala, 1982-3.

Identification	Days to Flower	Total dry matter at Flow. (kg/ha)	Average growth rate from planting to Flow.
Wisc 23-61	64	1198	18.7
61065	64	1286	20.1
800122	70	1969	28.1
790131	63	1309	20.7
LEF-2-RB	64	1369	21.3
1213-2	48	838	17.4
Bayo Madero	50	1022	20.4
BAT 332	70	1910	27.3
BAT 85	63	1816	28.8
Durango 222	43	688	16.0

Table 14. Average Crop growth rates (kg/ha/day) from flowering to maturity under two water treatments. Igualea, 1982-3.

Identification	Total dry matter at PM (kg/ha)		Average Crop growth rates from Fl. to PM	
	Irrigated	Stress	Irrigated	Stress
Wisc 23-61	4464	3536	88.2	68.7
61065	3908	4012	74.9	80.1
800122	4305	5280	68.7	97.3
790131	4021	3457	90.4	76.7
LEF-2-RB	4360	5298	76.6	98.2
1213-2	3853	2952	71.7	52.8
Bayo Madero	7592	3371	126.3	48.9
BAT 332	3862	4044	65.0	73.5
BAT 85	4049	3482	67.6	52.0
Durango 222	3642	3288	59.0	55.3

RB, 800122 and 61065 had higher growth rates under the minus water treatment as compared to the irrigated plots. The other 6 cultivars had lower crop growth rates under stress. It becomes evident from these data that not only do cultivar differences for crop growth rate exist but also that different cultivars react differently under water stress.

Net photosynthesis is the result of a biological input-output system that has several constraints. Identifying and quantifying the relevant constraints would help the plant breeder achieve a maximization of photosynthetic production. Physiological and morphological components which determine the crops efficiency of light conversion in a particular environment, such as rapid establishment of a closed leaf canopy, efficient canopy photosynthesis and effective distribution of assimilates to the relevant economic sinks for as long a period as possible, and the genetic variation associated with them, should be the focus of detailed study.

2. Partitioning

The most important determinant of economic yield, as Donald and Hamblin (15) stated, is not total crop photosynthesis, but the way in which assimilates are distributed within the plant, either for continued vegetative growth or for accumulation in storage organs,

seeds or fruits. However, it is not clear how this allocation is regulated. It can be regulated by the supply of assimilates (source strength), by the ability of the sink to make use of the assimilates (sink strength) or by the rate of translocation. How far sink strength can influence photosynthetic rate is still an unanswered question. The term partitioning, as used here, indicates the allocation of assimilates between reproductive and vegetative plant parts. It is a dynamic day-to-day process, that differs with cultivars and with physiological stages such as early or late pod filling. The partitioning of assimilates between new vegetative tissue and storage can be very important for plant performance under environmental stresses such as temperature or water stress.

Table 15 illustrates the fruit growth rates of the 10 sampled cultivars under irrigated and stress conditions. Differences not only among cultivars but also among treatments were obtained. This indicates that the daily partitioning of assimilates to the fruits was determined by the genotype and the water treatment. When comparing the data shown in Table 14 (Crop growth rates - CGR-) with the corresponding values in Table 15, one can see that Fruit growth rates -FGR- exceeded CGR in 7 cultivars under water stress, while under irrigation FGR exceeded CGR in 5 cultivars.

One of the basic questions to be answered is whether or not the water stress treatment induces a greater partitioning of stored assimilates to the fruit. The

Table 15. Average Fruit growth rate from flowering to physiological maturity (kgs/ha/day) under two water treatments. Iguala, 1982-3.

Identification	Irrigated	Stress
Wisc 23-61	80.6	109.8
61065	94.0	101.5
800122	84.2	86.4
790131	77.0	88.6
LEF-2-RB	77.5	116.9
1213-2	56.9	62.5
Bayo Madero	56.7	37.3
BAT 332	91.0	123.2
BAT 85	123.0	109.4
Durango 222	57.6	46.8

division of FGR by CGR during a given period of time gives the average fraction of net photosynthate partitioned to fruit growth. If all fruit growth can be explained by current photosynthesis, net accumulation of dry matter should be greater than or equal to fruit growth; if not, one can assume that fruit growth was sustained in part with photosynthates that were fixed in an earlier developmental stage. A calculated partitioning factor, shown in Table 16, indicates that in 7 out of the 10 sampled cultivars under stress, the calculated partitioning ratio exceeded 100%, and under irrigation in 5 entries the ratio exceeded 100%. Whether this can be extrapolated to the extent that we can be sure that water stress induces a greater partition of assimilates to the fruit is not clear, but it is clear that treatment and cultivar differences in partitioning exist.

A greater partition of assimilates can be the result of a greater fruit load, or what was called before, namely "sink strength". We have no conclusive evidence to say that this in fact is the case, but the data show a very consistent trend in which the cultivars with a high partitioning factor such as BAT 332 and BAT 85 had between 149 and 231 grs of seed/mt², while in cultivars with a low partitioning factor such as Durango 222 and Bayo Madero sink size varied from 80 to 111 grs of seed/mt².

Considering the change in plant dry matter between anthesis and maturity as an indicator of net plant photosynthesis during this period, and comparing this

Table 16. Partitioning Factor under two water^{#1} treatments. Iguala, 1982-3. Calculated %

Identification	Irrigated	Stress
Wisc 23-61	91.4	159.7
61065	125.5	126.6
800122	114.9	88.7
790131	85.2	115.5
LEF-2-RB	101.0	119.0
1213-2	79.3	118.3
Bayo Madero	44.9	76.2
BAT 332	139.8	167.4
BAT 85	181.7	210.1
Durango 222	97.5	76.4

^{#1} % = (fruit growth rate / crop growth rate) x 100

increment with the corresponding increment in fruit weight, seems to be a reasonable way of illustrating the proportion of pre-anthesis and post-anthesis assimilates that were utilized for fruit growth under the 2 water treatments. In Figures 10 and 11, plus water and minus water treatments respectively, the X-axis is the net post-anthesis photosynthesis expressed in kgs/ha and the Y-axis is the fruit growth from anthesis to maturity also expressed in kgs/ha. The 1:1 line shows the position where a cultivar would lie if all the assimilate produced after anthesis had gone into the grain. A cultivar that lies further from and below the line is fixing more carbon and it is using it for fruit growth at a slower rate than it is produced. On the other hand in a cultivar that is positioned above the 1:1 line fruit growth exceeds total growth for that period, implying that the pods had to be receiving assimilates produced and stored in an earlier stage of development, which in this case would be pre-anthesis assimilates. If the water stress treatment induces a greater partition of pre-anthesis assimilates to grain growth in some genotypes, their position with respect to the 1:1 line should differ under the plus water and minus water treatments. In fact, when comparing Figures 10 and 11, one can see that cultivars 1 (Wisc 23-61), 4 (790131) and 6 (1213-2) were below the line under the plus water treatment but under the minus water treatment they are positioned above the line. On the other hand, cultivar 7 (Bayo Madero) is below the line under the 2 water treatments, but its position changed, being much

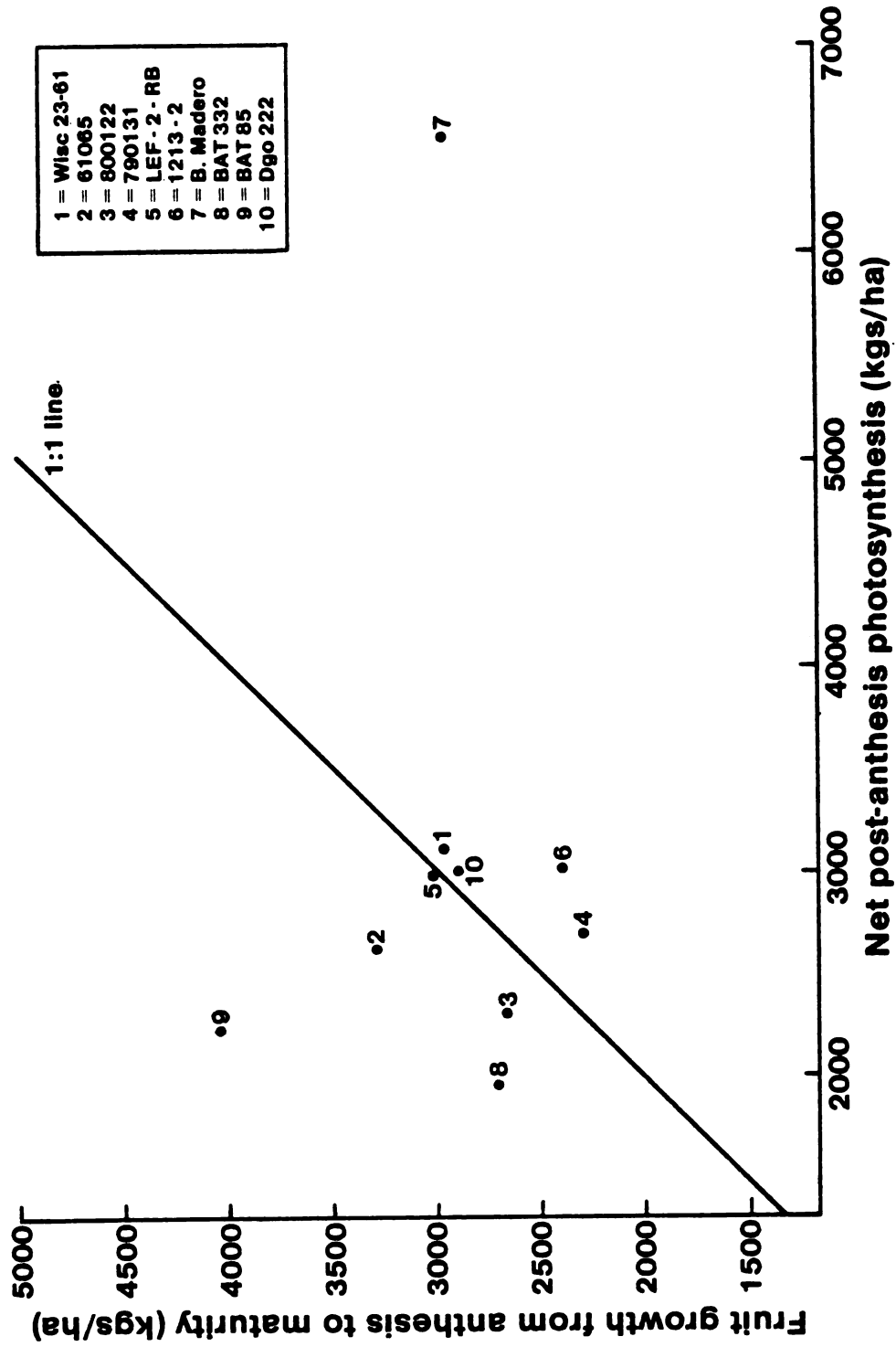


Fig. 10 Proportion of fruit growth that can be accounted for by post-anthesis photosynthesis under irrigated conditions. Iguala, 1982-3.

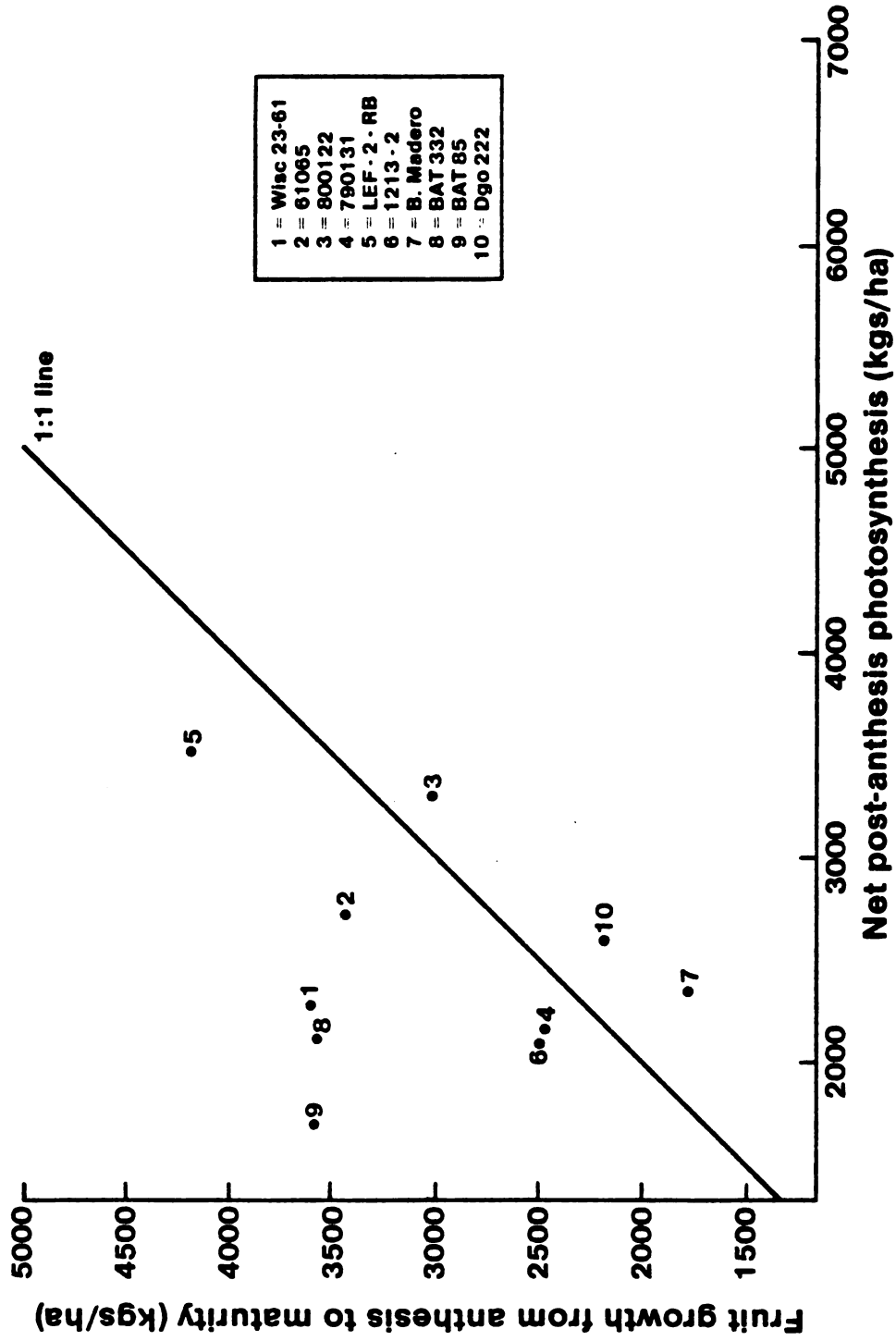


Fig. 11 Proportion of fruit growth that can be accounted for by post-anthesis photosynthesis under stress conditions. Iguala, 1982-3.

closer to the line under the minus water treatment. The proximity to the 1:1 line is another indication of the proportion of assimilates utilized for grain growth, the further from the line the smaller the partition and vice versa. Cultivar 10 (Durango 222) also remained below the 1:1 line under the stress treatment; its position did not change drastically, being a little further from the line under the stress conditions. In the case of cultivar 3 (800122), its position changed from above the line under the irrigated treatment to below the line under stress. We do not know if this is a real treatment effect, but we can speculate and say that this cultivar might be a more efficient remobilizer under well-watered conditions.

The fact that all cultivars showed leaf deterioration and defoliation before pod growth stopped, a condition that was accentuated under water stress, might also be considered as support for the hypothesis that a redistribution of carbon and nitrogen from the vegetative parts to the reproductive organs was taking place. Partitioning of more assimilates to the fruit leaves less to be used for growth and renewal of the foliage. If assimilate is not partitioned to the fruit, as was the case for the cultivar Bayo Madero, especially under irrigation, more assimilates are available for vegetative growth. This seems a reasonable explanation for the high dry matter accumulation of Bayo Madero at maturity, which widely exceeded the corresponding values of the other 9 cultivars.

An increase in the rate of loss of vegetative dry matter (stems and leaves) before maturity, especially under water stress, might correspond to the remobilization of assimilates from the vegetative organs to the seeds. In Figures 12 and 13 the change in stem and leaf weight from anthesis to maturity is plotted against grain yield. The importance of remobilization of stored material under water stress is shown in Figure 13. A close relationship (calculated significant correlation coefficient = 0.5), between grain yield and the change in stem and leaf dry weight applies for all cultivars and treatments; the calculated regression slopes are -0.45 under the plus water treatment and - 0.70 under the minus water treatment. Cultivars grown under stress lost more dry weight than their corresponding irrigated plots, however, we can not be sure if these losses reflect differences between treatments in respiration. Nevertheless, it is still reasonable to conclude that a fair proportion of the differences between yields of treatments and cultivars are due to differences in the availability and partitioning of assimilate reserves.

3. The Filling Period

The main function of a vegetative canopy is to provide an appropriate crop structure on which to carry the optimum number and size of fruits. A mutual adjustment of source and sink strength is therefore vital for the maximization of

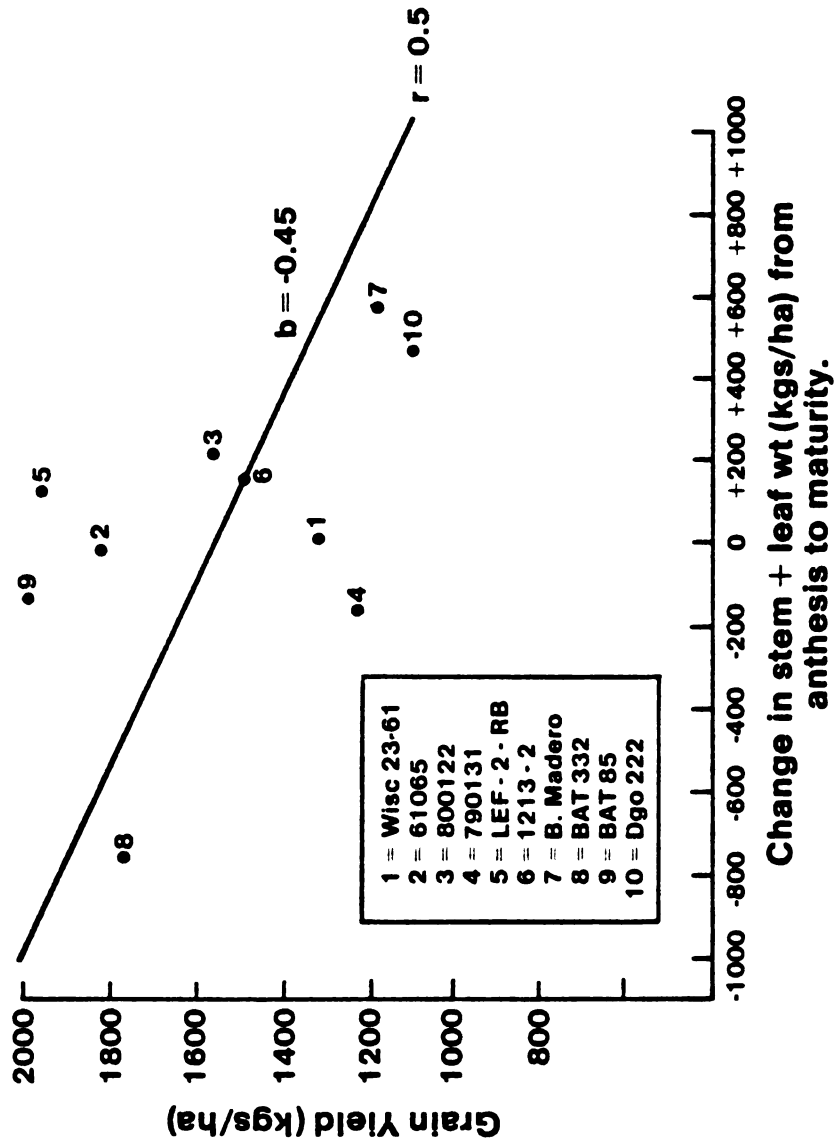


Fig. 12 Relationship between change in stem and leaf weight from anthesis to maturity and grain yield under irrigated conditions. Iguala, 1982-3.

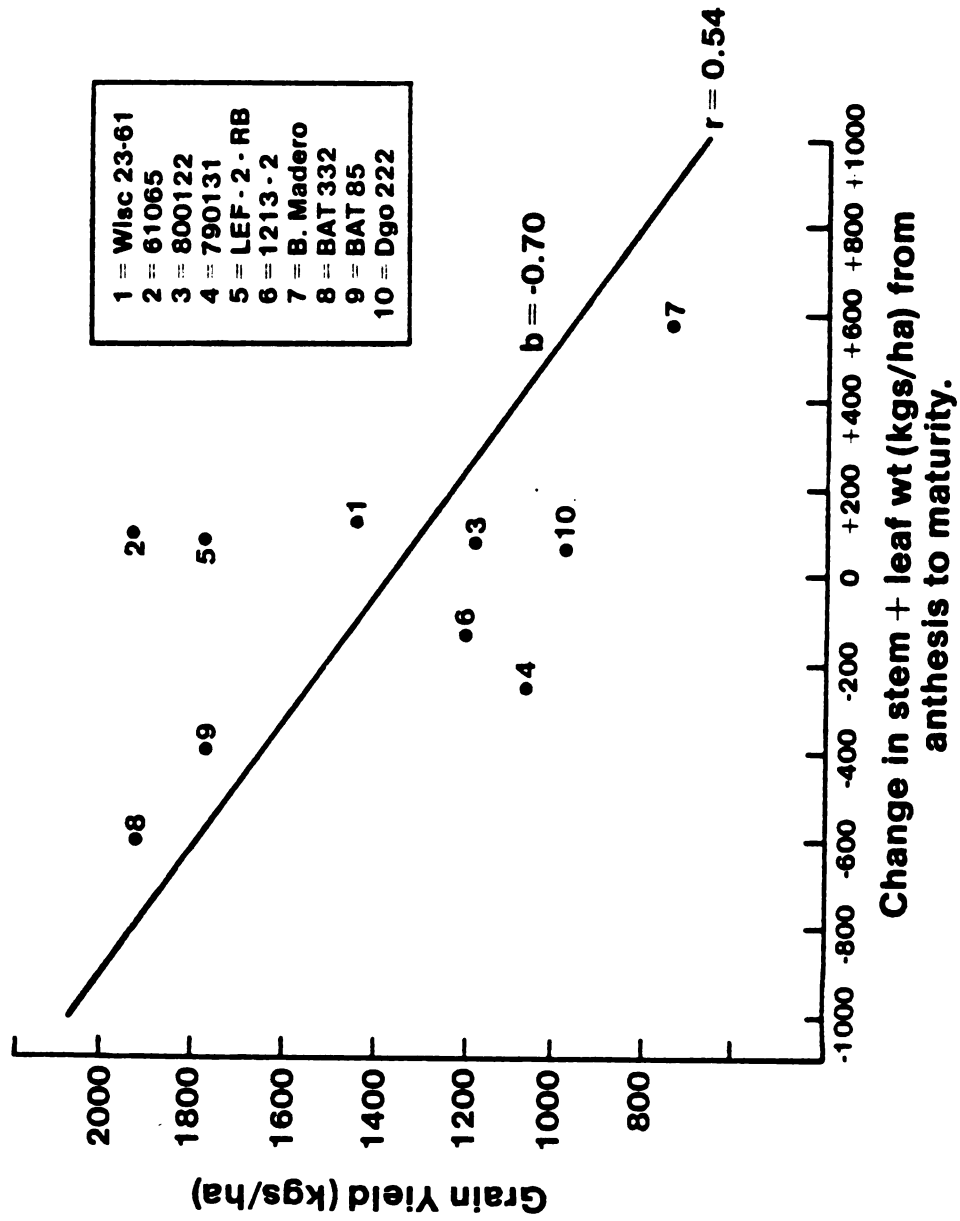


Fig. 13 Relationship between change in stem and leaf weight from anthesis to maturity and grain yield under stress conditions. Iguala, 1982-3.

grain yield. The duration of seed development is often restricted, but we cannot be sure whether these restrictions are caused by the low availability of assimilates (source limited) or by a low demand for assimilates from the fruits (sink limited). The length of the grain filling period rather than the rate of filling has been repeatedly cited (13,30) as a more important determinant of varietal differences in grain yield. A rapid initial growth and an increased longevity of the photosynthetic tissue capable of maintaining the seed filling process would seem a desirable plant strategy for maximizing seed yield.

The data presented in Table 17 arrange the 10 sampled cultivars into three different subgroups according to their grain yield, FGR and seed number. What appears interesting is that none of the cultivars that were included in group I had a significant reduction in the length of the seed filling period due to stress (data presented in Table 6). The calculated means of grain yield, FGR and seed number for irrigated and stress conditions are relatively high in group I, intermediate for group II and low in group III. When the length of the seed filling period was not reduced, as in the case of cultivars included in group I, grain yield under stress did not differ from the irrigated plots. An increment in the FGR under stress can probably explain the lack of yield reduction. In groups II and III, the length of the seed filling period was reduced under water stress. In the case of cultivars included in group II, even though the FGR was higher under water stress, this did not prevent a

Table 17. Comparison between Grain yield, Fruit growth rate, Seed number and Effective seed filling period under two water treatments. Iguala, 1982-3.

		Grain Yield (kg/ha)	FGR (kg/ha/day)	Seed No. (seeds/mt ²)	ESFP (days)
<u>Group I</u>					
BAT 332	Ir*	1779	91.0	1052	30
	St	1919	123.2	1181	29
BAT 85	Ir	1966	123.0	949	33
	St	1751	109.4	894	33
61065	Ir	1851	94.0	994	35
	St	1938	101.5	1108	34
$\bar{X}$, s.d.	Ir	1853, 99	102.6, 17.6	998, 52	33, 3
	St	1869, 103	111.3, 10.9	1061, 149	32, 3
<u>Group II</u>					
LEF-2-RB	Ir	1964	77.5	732	39
	St	1775	116.9	735	36
790131	Ir	1225	77.0	534	30
	St	1064	88.6	474	28
800122	Ir	1571	84.2	957	34
	St	1178	86.4	787	34
WIS 23-61	Ir	1536	80.6	842	37
	St	1500	109.8	862	33
$\bar{X}$, s.d.	Ir	1574, 303	79.8, 3.3	766, 180	35, 4
	St	1379, 322	100.4, 10.0	714, 168	33, 3
<u>Group III</u>					
DGO 222	Ir	1102	57.6	221	50
	St	985	46.8	216	47
1213-2	Ir	1514	56.9	421	42
	St	1200	62.5	347	40
B.Madero	Ir	1183	56.7	269	52
	St	742	37.3	178	48
$\bar{X}$, s.d.	Ir	1266, 218	57.0, 0.5	304, 104	48, 5
	St	976, 229	48.8, 12.7	247, 87	45, 4

* Ir= Irrigated
St= Stress

reduction in grain yield. In group III, FGR was lower under the stress treatment and a reduction in grain yield under the stress treatment was observed. The data presented here indicate that the length of the seed filling period and the rate of filling are both important determinants of varietal differences in grain yield. A higher FGR accompanied by a filling period that showed no significant differences in length between the water treatments, even though it was not a very long one, resulted in the highest yielding cultivars under both treatments.

YIELD POTENTIAL AND DROUGHT SUSCEPTIBILITY

Given the lack of reliable information on specific drought resistance mechanisms, plant breeders are still largely guided in their selection for drought resistance by grain yield and its stability under dry conditions. High yields could be the result of drought escape or high yield potential, rather than the possession of specific drought resistance mechanisms that favor yield performance under water stress. The identification and separation of the influence of these mechanisms upon yield under drought would facilitate breeding and selection.

Utilizing the data from the Iguala experiment, as well as the data collected in a similar experiment planted in Durango, Mexico in July of 1983, I will concentrate in this section upon the economic yield results, their adjustment for drought escape and the separation of effects due to differences in yield potential. A brief description of the Durango experiment and the data collected are given in Appendix A.

1.Drought Susceptibility Index

The relationship between stress yield and control yield is generally positive and strong. A poor yielder in the control treatment cannot give by any means a good yield

under stress. However, as stated in the CIAT's 1982 Annual Report (10), the degree of correlation between control and stress yield probably depends on the severity of the stress.

Differential yield reduction due to stress has been commonly used as a criterion for selecting cultivars with tolerance to water stress. This strategy can be counterproductive because of the likelihood of selecting generally low yielding cultivars whose yield differential ($Y_c - Y_s$) is relatively small.

A dimensionless slope termed Drought Susceptibility Index (S) was suggested by Fischer and Maurer (19) as a useful way of comparing cultivar performances between drought levels and experiments. This slope is calculated from the following formula:

$$Y_s = Y_p (1 - SD)$$

where D is defined as the drought intensity and calculated by $D = (1 - \bar{X}_s / \bar{X}_p)$, $\bar{X}_s$ being the mean yield of the stress plots and $\bar{X}_p$ the mean yield of the well watered plots. D ranges from 0 to 1. Y_s is the yield under stress and Y_p (yield potential) is the yield under well watered conditions. This equation expresses the separate effects of yield potential and drought susceptibility on yields under drought, and in these terms lower drought susceptibility is considered synonymous with higher drought resistance. Although S should be independent of drought intensity, its exact value will depend on the cultivars included in calculating the drought intensity index (D); for this

reason, when comparing a group of cultivars grown under different environments for their drought susceptibility, it is better to base the comparison on their ranking rather than on the absolute S values.

Drought susceptibility indices were calculated for the individual cultivars as well as for the cultivar groups of the Durango and Iguala experiments. Grouping was done according to cultivar origin. The cultivars planted in the Durango experiment were subdivided into 4 groups: group I - Mexican cultivars, group II - CIAT cultivars, group III - Wisconsin cultivars and group IV - Michigan cultivars previously selected for high yields. The cultivars planted in Iguala were subdivided into 5 groups: groups I, II and III correspond to Mexican, CIAT and Wisconsin cultivars, while group IV includes Michigan cultivars previously selected for high yields and group V includes Michigan lines previously selected for low yields. Cultivar names and the calculated S values appear in Tables 18 and 19. Variation of the drought susceptibility indices between groups is as great as within groups, so associations between cultivar origin and drought tolerance are not apparent. While the Mexican cultivars appeared to have a lower S value in Durango than in Iguala, the opposite was observed for the CIAT lines. Fischer and Maurer (19) assert that despite differences in drought intensity, S values should be consistent for a given cultivar grown in different experiments. Environmental differences between the two experiments, such as temperature, nutrient availability,

Table 18. Individual cultivar drought susceptibility indices. Iguala 1982-3 and Durango 1983.

Cultivar	Iguala Experiment ^{*A}	Durango Experiment ^{*B}
LEF-2-RB	1.20	
1213-2	2.59	1.45
C-5	2.66	
Bayo Madero	4.65	1.02
Pinto Nacional 1	3.68	
Durango 222	1.32	0.98
Ojo de Cabra	-1.29*	
BAT 332	-0.98*	
BAT 85	1.36	
BAT 47	0.42	0.85
A-162	0.60	
BAT 798	0.43	1.32
Wisc 23-61	0.29	
Wisc 21-58	0.95	0.55
Wisc 21-54	-1.02*	
Neptune	-0.96*	
61065	-0.85*	0.89
800122	3.12	0.84
81017	0.51	
800205	2.29	
790131	1.64	

*A D = 0.08

* negative values because $Y_s > Y_c$

*B D = 0.29

Table 19. Group drought susceptibility indices - S -
Iguala 1982-3 and Durango 1983.

Iguala Experiment			Durango Experiment		
Group	Cultivars	S	Group	Cultivars	S
I	LEF-2-RB 1213-2 C-5 Bayo Madero Pinto Nacional Durango 222 Ojo de Cabra	2.30	I	1213-2 Bayo Madero Durango 222	1.18
II	BAT 332 BAT 85 BAT 47 A-162 BAT 798	0.39	II	BAT 47 BAT 798	1.05
III	Wisc 23-61 Wisc 21-58 Wisc 21-54	0.19	III	Wisc 21-58	0.55
IV	Neptune 61065 800122 81017	0.42	IV	61065 800122	0.87
V	800205 790131	2.03			

radiation, etc might affect the expression of Y_p , but they should not alter the S values drastically, unless other factors besides water availability play an important role in determining yield.

Table 20 illustrates the group ranking by the S value. The consistency of the group ranking contrasts with the differences in ranking obtained for individual cultivars. (Data shown in Table 21). Drastic changes in ranking for cultivars such as 800122 and BAT 798 illustrate the importance of local adaptation when selecting for drought tolerance. Under the Iguala conditions, 800122 was considered very susceptible to water stress, while under the Durango environment it was drought tolerant. This apparent inconsistency simply says that one must be aware of the importance of other environmental factors in determining the overall plant performance in a given environment. However, if the drought conditions differ cultivar differences in ranking would probably reflect this. On the other hand, in cultivars such as BAT 47,1213-2, Bayo Madero and Durango 222, there was no apparent change in the ranking between the two experiments. One can probably say that these cultivars had a broader adaptation.

The lack of correlation between Y_p and S ($r = -0.03$) does not agree with the high correlation reported by Fischer and Maurer (19). As far as this experiment has shown, there is no association between yield potential and the drought susceptibility index. The diversity of the bean genotypes

Table 20. Group ranking by drought susceptibility index (S). Iguala 1982-3 and Durango 1983.

Group	Iguala Experiment	Durango Experiment
I	5	4
II	2	3
III	1	1
IV	3	2
V	4	

Table 21. Ranking by drought susceptibility index (S) of the eight cultivars planted in Iguala and Durango

Cultivar	Iguala	Durango
Wisc 21-58	4	1
61065	1	4
800122	7	2
BAT 47	2	3
BAT 798	3	7
1213-2	6	8
Bayo Madero	8	6
Durango 222	5	5

used in these experiments, which contrasts with the similarity of the genotypes used by Fischer and Maurer, probably can explain the difference in the results.

2.Relationship between control and stress yields

Figures 14 and 15 show the relationship between control and stress economic yields for the Iguala and Durango experiments. In Figure 14, all the cultivars that had a negative value for the $Y_c - Y_s$ differential are above the 1:1 yield line ($b=1$), while the cultivars that had a yield reduction under stress are below the 1:1 yield line. The distance between each individual point and the regression line is proportional to the yield differential. Points 13 , 6 , 19 and 8 which correspond to Bayo Madero, 800122, Pinto Nacional and 800205 are the farthest from the regression line, while 22 (Tepary), 1 (Wisc 23-61), and 18 (BAT 798) are the closest to it.

The distances from the regression line of points 18 and 1 are almost the same, however their yields under both stress and non stress are significantly different. Cultivar 1 (Wisc 23-61) outyielded cultivar 18 (BAT 798) by 415 kg./ha. Points 19 (Pinto Nacional) and 8 (800205) are at approximately the same distance from the regression line, however 800205 outyielded Pinto Nacional by more than 500 kg./ha. under stress conditions.

When looking at the distance from the regression line of

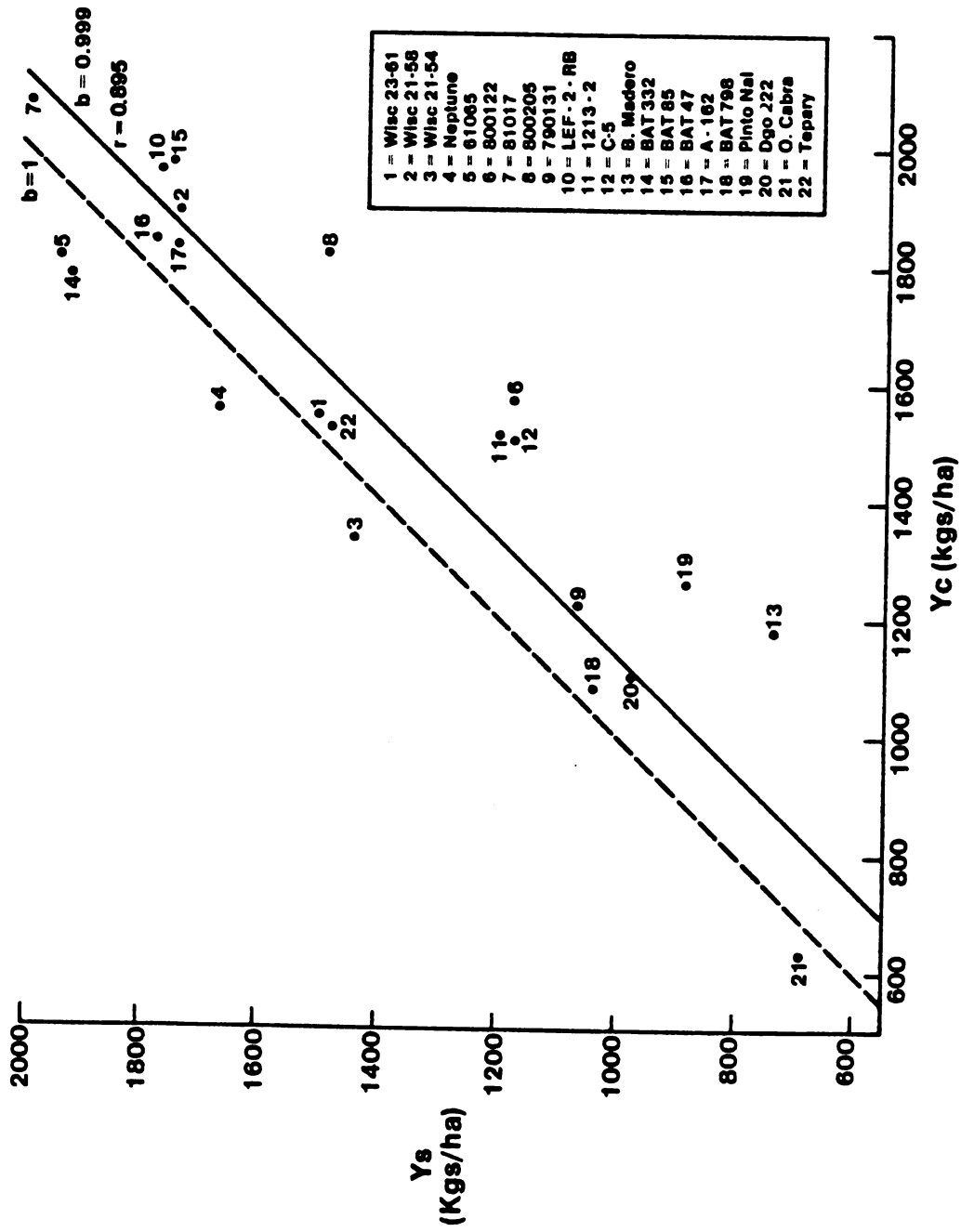


Figure 14. Relationship between Control and Stress Yield. Iguala, 1982-3.

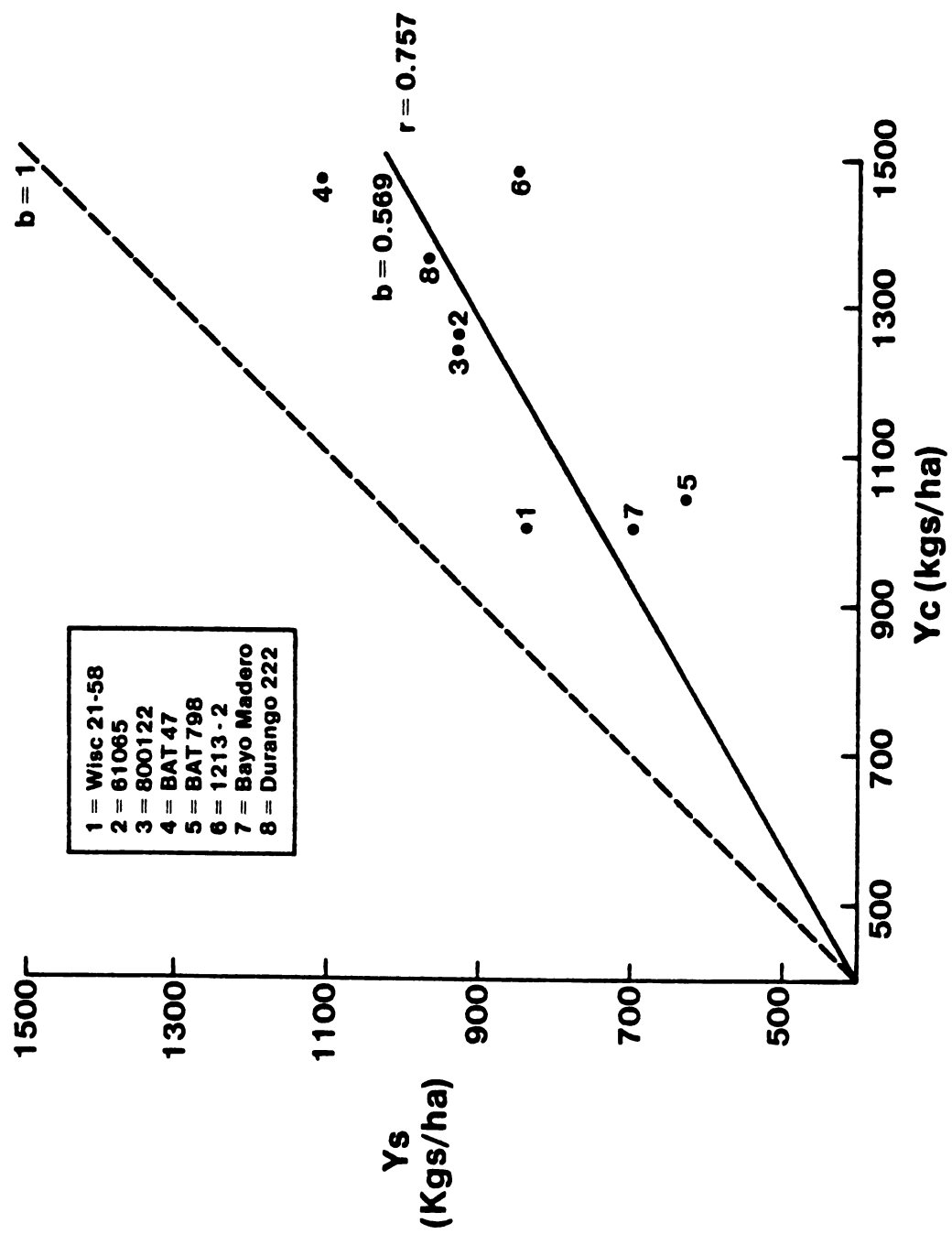


Figure 15. Relationship between Control and Stress Yield. Durango, 1983.

cultivar 7 (81017) and cultivar 17 (A-162), one can observe that A-162 is closer to the regression line. Nevertheless, the yield of 81017 under stress was over 250 kg./ha. higher than its homologue for A-162.

The distances between each individual point and the regression line for the Durango experiment are shown in Figure 15. Points 5 and 6 which correspond to BAT 798 and 1213-2 are the farthest from the regression line, while 8 (Durango 222), 2 (61065) and 7 (Bayo Madero) are the closest to it. The distance from the regression line of points 7 and 2 is almost the same, nevertheless their yields under both stress and non-stress differed by more than 200 kgs/ha. Cultivar 2 (61065) outyielded cultivar 7 (Bayo Madero).

From these data it becomes evident that when one examines the Y_c vs Y_s graph trying to select for tolerance to water stress, two important factors should be taken into consideration : (1) distance from the origin and (2) distance from the regression line. The distance from the origin is an indication of the yield potential of each individual cultivar ; the farther a particular cultivar is from the origin, the higher its yield potential. The distance from the regression line is an indicator of the reduction in yield under stress conditions.

3. Geometric mean of stress and control yield as a selection criterion for drought tolerance

The likelihood of selecting generally low yielding cultivars, when differential yield reduction due to drought is used as a criterion for selecting cultivars with tolerance to water stress, suggests the use of an alternative selection criterion. The geometric mean of stress and control yields, is probably a better option since the two critical factors, yield potential and yield differential, are both taken into account.

In this section, a comparison between the yield differential ($Y_c - Y_s$), the arithmetic mean, the geometric mean and the drought susceptibility index will be made. Calculated values for the yield differential and the arithmetic and geometric means for the Iguala and the Durango experiments are given in Tables 22 and 23. The negative values under the yield differential column in Table 22 indicate that for these particular cultivars the stress plots outyielded the control plots. However, as already stated (Table 2), these differences were not significant.

It is clear that the water stress when imposed late in the seed filling period under Iguala conditions did not affect yield significantly. Only six cultivars of the twenty two that were screened had significant yield reductions under stress (Table 2). The correlation between stress yield and control yield was positive and highly

Table 22. Yield differential, Arithmetic mean and Geometric mean for the Iguala experiment.*

Entry No.	Identification	$Y_c - Y_s$	$\frac{Y_c + Y_s}{2}$	$\sqrt{Y_c \times Y_s}$
1	Wisc 23-61	36	1519	1519
2	Wisc 21-58	145	1816	1814
3	Wisc 21-54	-109	1385	1384
4	Neptune	-120	1613	1612
5	61065	-124	1877	1876
6	800122	392	1375	1361
7	81017	85	2044	2044
8	800205	335	1655	1647
9	790131	162	1145	1142
10	LEF-2-RB	189	1870	1867
11	1213-2	314	1357	1348
12	C-5	320	1342	1332
13	Bayo Madero	441	963	938
14	BAT 332	-140	1850	1848
15	BAT 85	215	1859	1855
16	BAT 47	63	1812	1811
17	A-162	89	1789	1788
18	BAT 798	37	1063	1063
19	Pinto Nacional 1	372	1076	1060
20	Durango 222	117	1044	1042
21	Ojo de Cabra	-65	661	660
22	Tepary	37	1503	1503

* Yield data in kgs/ha

Table 23. Yield differential, Arithmetic mean and Geometric mean for the Durango experiment.*

Entry No.	Identification	$Y_c - Y_s$	$\frac{Y_c + Y_s}{2}$	$\sqrt{Y_c \times Y_s}$
1	Wisc 21-58	161	921	917
2	61065	327	1098	1086
3	800122	306	1089	1078
4	BAT 47	363	1289	1276
5	BAT 798	399	836	812
6	1213-2	625	1166	1123
7	Bayo Madero	299	854	840
8	Durango 222	391	1168	1151

*Yield data in kgs/ha

significant (calculated $r = 0.895$). This might indicate, as suggested by the CIAT 1981 Annual Report (9), that the degree of stress was not very high. For the Durango experiment, the correlation between control and stress yield was also positive and significant, but its calculated value ($r = 0.76$) was smaller than the one obtained for Iguala. One can then assume that the water stress was more severe in Durango, a result that is confirmed by the calculated drought intensity.

Comparing the calculated values under the arithmetic and geometric mean columns shown in Tables 22 and 23, one can see the greater conservativeness of the geometric mean, the calculated values always being smaller than or equal to the arithmetic means. Since the absolute values for yield differential and the calculated means differed in magnitude, a more illustrative comparison is given in Tables 24 and 25 based on the cultivar ranking when using different selection criteria ($Y_c - Y_s$, $(Y_c + Y_s)/2$, $\sqrt{Y_c \times Y_s}$ and S). Ranking based on the arithmetic and geometric means did not differ, except for a one position change in cultivars BAT 798 and Pinto Nacional 1 in the Iguala experiment. On the other hand, the results of ranking based on the yield differential are very similar to the results obtained when ranking cultivar performance based on their drought susceptibility index. However, the $Y_c - Y_s$ and S ranking was substantially different from the $(Y_c + Y_s)/2$ and $\sqrt{Y_c \times Y_s}$ ranking. The advantage of utilizing the geometric mean as a selection criterion rather than the yield differential is illustrated

Table 24. Cultivar ranking for the Iguala experiment
using four different selection criteria

Cultivar	Yield differential	Arithmetic mean	Geometric mean	Drought susceptibility index
Wisc 23-61	6	11	11	6
Wisc 21-58	13	6	6	12
Wisc 21-54	4	13	13	2
Neptune	3	10	10	4
61065	2	2	2	5
800122	21	14	14	20
81017	10	1	1	10
800205	19	9	9	17
790131	14	17	17	16
LEF-2-RB	15	3	3	13
1213-2	17	15	15	18
C-5	18	16	16	19
Bayo Madero	22	21	21	22
BAT 332	1	5	5	3
BAT 85	16	4	4	15
BAT 47	9	7	7	8
A-162	11	8	8	11
BAT 798	7	19	18	9
Pinto Nacional	20	18	19	21
Durango 222	12	20	20	14
Ojo de Cabra	5	22	22	1
Tepary	8	12	12	7

Table 25. Cultivar ranking for the Durango experiment
using four different selection criteria

Cultivar	Yield differential	Arithmetic mean	Geometric mean	Drought susceptibility Index
Wisc 21-58	1	6	6	1
61065	4	4	4	4
800122	3	5	5	2
BAT 47	5	1	1	3
BAT 798	7	8	8	7
1213-2	8	3	3	8
Bayo Madero	2	7	7	6
Durango 222	6	2	2	5

in Tables 26 and 27. When selecting the top 20 % of the cultivars by both criteria and comparing their yields under stress and non-stress conditions, the mean yields of the $Y_c - Y_s$ selected groups are lower than the mean yields of the $\sqrt{Y_c \times Y_s}$ group.

Table 26. Mean yields of the selected top 20 % cultivars, using two different selection criteria. Iguala experiment.

Selected group	Cultivars	Mean yield of selected cvs.* Irrigation	Stress
Top 4 by yield differential	BAT 332 61065 Neptune Wisc 21-54	1620	1743
Top 4 by geometric mean	81017 61065 LEF-2-RB BAT 85	1958	1867

*kgs/ha

Table 27. Mean yields of the selected top 20 % cultivars, using two different selection criteria. Durango experiment.

Selected group	Cultivars	Mean yield of selected cvs.* Irrigation	Stress
Top 2 by yield differential	Wisc 21-58 Bayo Madero	1002	772
Top 2 by geometric mean	BAT 47 Durango 222	1417	1039
*kgs/ha			

SUMMARY AND CONCLUSIONS

These experiments were designed to get a better understanding of agronomic and certain physiological responses of the bean crop to water stress. The studies are on-going and it is premature to draw lasting conclusions at this time, but we have obtained some information that allows us to speculate on the importance of certain characters and their relative contribution to the plant's ability to withstand an environmental stress.

The major findings of this thesis can be summarized as follows:

1. A relationship between grain yield and the change in stem and leaf dry weights from anthesis to physiological maturity ($b=-0.54$), a relationship that was accentuated under the minus water treatment ($b=-0.70$), implicates assimilate remobilization as an important contributor to seed yield, especially under late-season water stress.

2. The daily partition of assimilates to the fruits is determined by genotype and influenced by water treatment. A high partitioning ratio under water stress in 7 of the 10 sampled cultivars shows that treatment and cultivar differences in partitioning exist and that they probably represent a desirable character for plants grown under water stress.

3. The length and the rate of the seed filling period are important determinants of varietal differences in grain yield. The top yielding cultivars under stress and irrigated conditions were those which had a higher than average fruit growth rate -FGR- accompanied by a seed filling period that was not significantly different in length due to water treatments.

4. The environmental inputs and constraints in a particular environment are critical determinants that must be considered in the design of an appropriate "crop model" or ideotype to be used in developing improved varieties specifically intended for a particular production system. Simple observations and measurements in a given environment, such as dry matter production, flowering date, length of the vegetative and reproductive stages and leaf area index permit the investigator to reach useful conclusions underlying causes of yield differences. An understanding of the type of water limitation, along with a more complete quantification of the drought environment, are essential to the task of producing an appropriate ideotype.

5. Grain yield and its stability are the most widely used selection criteria when selecting for drought resistance. The utilization of the geometric mean of Y_c and Y_s as a selection criterion rather than the yield differential ($Y_c - Y_s$) or the drought susceptibility index, proved to be very advantageous. The mean yields of the groups selected by the

geometric mean. were higher than the mean yields of the groups selected on the basis of yield differential.

6. The relationship between cultivar yield performance (based on the geometric mean) and remobilization is evident. The two cultivars with the highest partitioning ratios (BAT 85 and 61065) were also in the top 20% of cultivars selected by the geometric mean.

7. Genotypic variation exists for many of the physiological characters that determine the net photosynthesis of the crop canopy and the distribution of assimilates to the grain, such as CGR, FGR, partitioning ratio and length of the vegetative and reproductive stages. It should be possible for the plant breeder to make use of this variation to develop improved varieties for water-limited regions.

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APPENDICES

APPENDIX A

A field experiment was planted in the second week of July of 1983 at the Campo Agricola Experimental Francisco Madero in the state of Durango, Mexico. The experimental station is at the meridian $104^{\circ} 20'$ longitude West and the parallel $24^{\circ} 20'$ latitude North. The altitude is 1932 m above sea level. The minimum temperature during the growing season was 4°C and the maximum was 35°C , with a season average of 20°C . The total precipitation between July 6th and October 30th was 402 mm, distributed as follows: 13 % during July, 63 % during August, 19 % during September and 5 % during October. The experimental plots were on a Silty Clay soil, with a pH of 6.5. Eight dry bean cultivars were selected from the Iguala experiment, on the basis of their good adaptation to the Durango conditions. They included:

1. One line from the Univ. of Wisconsin : Wisc 21-58
2. Two CIAT lines : BAT 47 and BAT 798
3. Three Mexican lines : 1213-2, Bayo Madero and Durango

222

4. Two Michigan State lines : 61065 and 800122

The experimental plots were arranged in a split plot design with 3 replications, the water treatment was the whole plot factor and cultivars were the split factor. Before planting, 35 kg./ha. of Phosphorous and 25 kg./ha. of Nitrogen were applied.

All plots were rainfed until flowering time, and thereafter only the so-called plus water plots received rain. A wooden structure was built around the stress plots, and every time that it rained a clear plastic sheet was placed over the structure to cover the plots and prevent them from getting water. Individual plots of each cultivar were treated as separate units for water management.

Each plot consisted of 4 rows 2 meters long; the distance between plants within a row was 10 cms. and the distance between rows was 0.75 cms.

Economic yield was taken at harvest time. Two rows of 2 meters each were harvested, grain yield adjusted to 10 % moisture was recorded. (Data given in Table A).

Table A. Economic Yield (kgs/ha) under two water treatments. Durango, 1983.

Entry No.	Identification	Rain-fed	Stress
1	Wisc 21-58	1001	840
2	61065	1261	934
3	800122	1241	935
4	BAT 47	1470	1106
5	BAT 798	1036	636
6	1213-2	1478	853
7	Bayo Madero	1003	703
8	Durango 222	1363	972

APPENDIX B

Starch contents were determined with a colorimetric method with perchloric acid (38). This technique involved the three following steps:

1. Reagents.

- a. Colorimetric Solution: 80 grs. of NaCl dissolved in 250 ml. of distilled water and 750 ml. of ethanol.
- b. Diluted perchloric acid: 300 ml. of perchloric acid (70%) and 224 ml. of distilled water.
- c. Iodine Potassium solution: 20 grs. of KI dissolved in 20 ml. of distilled water, and 2 grs. of Iodine diluted to 1 lt. with distilled water.

2. Calibration Curve.

One gram of starch is dissolved in 10 ml. of perchloric acid solution and diluted to 100 ml. with distilled water. Aliquots of 2,3,4,5,6,7,8,9 and 10 ml. are taken and 0.5 ml. of perchloric acid solution are added and diluted to 100 ml. with distilled water. The solutions will have 2, 3, 4, 5, 6, 7, 8, 9 and 10 mgms./ml. of starch. To 5 ml. of each solution 4.5 ml. of distilled water and 0.5 ml. of KI solution are added. The final concentrations being attained are then 100,150,200,250,300,350,400,450 and 500 μ gms. of starch in 10 ml. of solution. After 20 minutes, absorbance is read at 600 nm. with the spectrophotometer. The calibration curve (shown in Figure B) is plotted

calculating the mgs. of starch that correspond to one unit of absorbance (F).

3. Determination of starch in the sample.

Fifty mgs. of dry ground sample (duplicate samples) are taken; after centrifugation, 12.5 mls. of the colorimetric solution are added. The sample is placed in a water bath at 72°C for 10 minutes, and centrifuged for 10 minutes. The supernatant is discarded and to the residue 5 mls. of perchloric acid solution are added. After letting the sample stand for 10 minutes, 5 mls. of distilled water are added and then it is centrifuged for 20 minutes. An aliquot of the supernatant is taken and the color is developed as in the calibration curve. Then, absorbance is read at 600 nm. The amount of starch is expressed as grs./100 grs. of sample, and is calculated using the following formula:

$$\% \text{ of starch} = \frac{A \times F \times V \times D}{a \times m \times 10}$$

where A = absorbance

F = absorbance factor taken from the curve

V = volume

D = dilution

a = aliquot

m = sample weight

10 = conversion factor

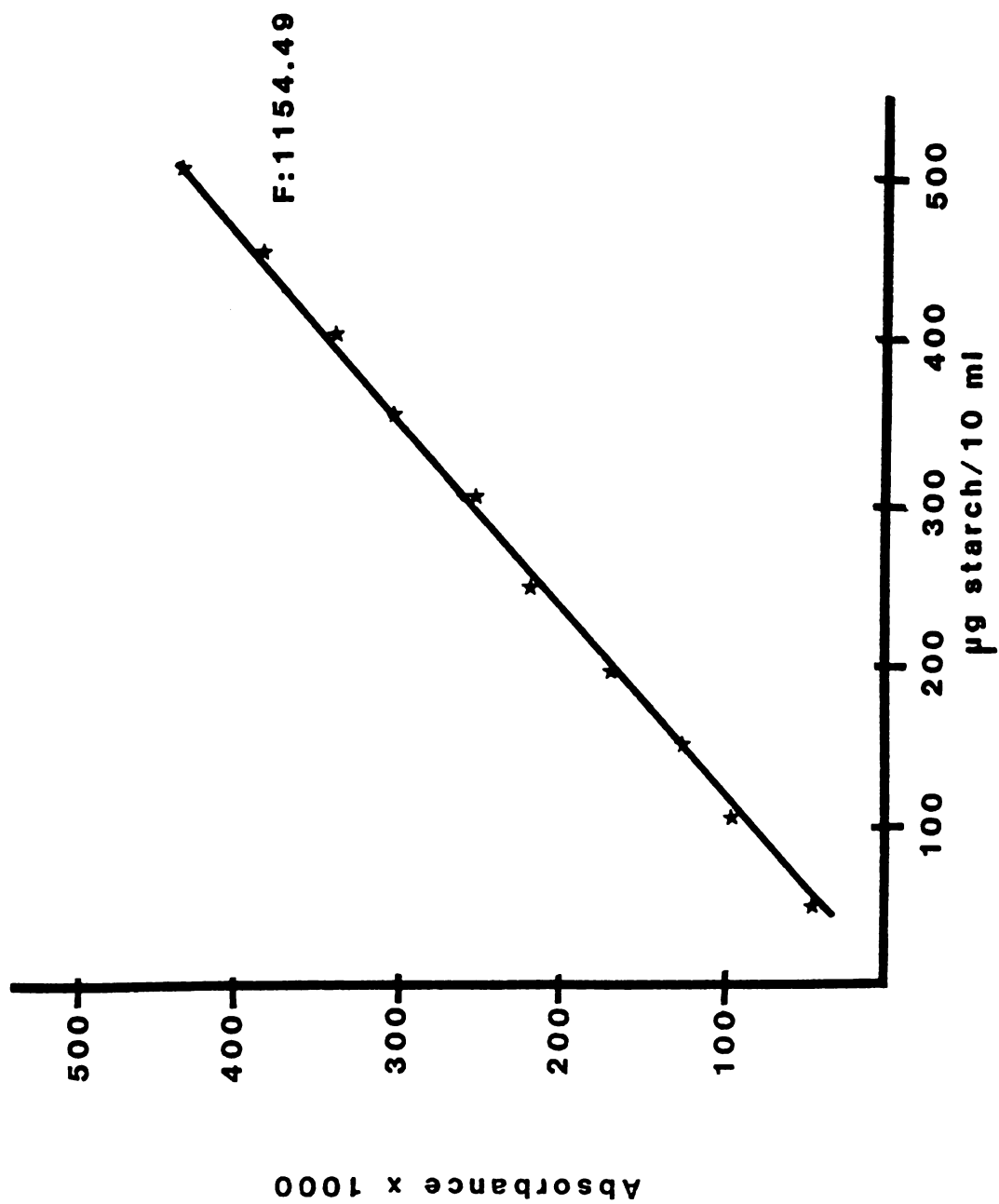


Figure B. Calibration curve. μ grs of starch vs. absorbance

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