20058705

This is to certify that the

dissertation entitled

Selection of common bean (Phaseolus vulgaris L.)
genotypes with enhanced drought tolerance and
biological nitrogen fixation.

presented by

Jorge Alberto Acosta Gallegos

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Plant Breeding and
Genetics - Crop and
Soil Sciences

M. W. Adams
Major professor

Date May 5, 1988

SELECTION OF COMMON BEAN (PHASEOLUS VULGARIS L.) GENOTYPES WITH ENHANCED DROUGHT TOLERANCE AND BIOLOGICAL NITROGEN FIXATION

BY

JORGE ALBERTO ACOSTA GALLEGOS

A DISSERTATION

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

DOCTOR OF PHILOSOPHY

Plant Breeding and Genetics Program - Crop and Soil Science

1988

Th

fixatio

investi

45 and

biologi

III gr

was in

a low

popula

parent

cultiv

genera

bean p

to th

gener

water

seed

the

more

culti

ABSTRACT

SELECTION OF COMMON BEAN (PHASEOLUS VULGARIS L.) GENOTYPES WITH ENHANCED DROUGHT TOLERANCE AND BIOLOGICAL NITROGEN FIXATION

By

Jorge Alberto Acosta Gallegos

The potential for improvement for drought adaptation and N_2 fixation concurrently in the same population of dry beans was investigated in this research. Parental genotypes, Lef-2-RB, I1900-5-M-45 and N81017, showed an acceptable level of drought tolerance and biological nitrogen fixation (BNF). Mexican parental genotypes (type III growth habit) proved to be photoperiod sensitive. Their sensitivity was initially expressed as a delay in flowering, and after flowering, as a low rate of partitioning to the developing fruits. Segregating populations were produced from crosses involving Michigan and Wisconsin parents (type II growth habit) and unadapted (type III) Mexican cultivars. Selection on the basis of nodule mass was conducted for two generations in these populations in the greenhouse by growing inoculated bean plants in a N-free medium. The segregant genotypes were compared to the check cultivar (UW 21-58) with superior BNF. Two additional generations of evaluation and selection were conducted under moderate water stress in the field where the primary bases for selection were seed and biomass productivity per unit land area. During selection in the field, segregants with the characteristics of the type II's were more adapted to the environment in Michigan.

Nineteen selected F7 families, six parental genotypes and a check cultivar were evaluated for BNF under controlled conditions, and for

dro
Mic
pre
che
dis
gov
for
ass
pla
an
The
fam
enh
val
obs
to
for
hab
and
at
dis
dro
sin
dec
dis
Pha

drought tolerance in the field at two locations (Durango, Mex. and Michigan). The results under controlled conditions indicated the presence of promising families with BNF superior to the parents and the check cultivar PUE 152. The best nitrogen fixers were those families displaying a longer vegetative phase. It seems that the genetic system governing photoperiod sensitivity, which sets the developmental stage for assimilate partitioning in beans, also affects BNF. A close association between biomass and nitrogen assimilated (N_2 fixed) per plant suggested that preliminary selection for BNF can be done by using an estimation of biomass of segregant families grown in a N-free medium. The results obtained in the field in Michigan indicated that recombinant families were produced with adaptation to this environment and with enhanced drought tolerance. In general, under stress, the metrical values of the recorded and calculated variables decreased. It was observed that morphologically different genotypes responded differently to water stress. The grouping of the genotypes in a final evaluation for drought adaptation upon the basis of their phenology and growth habit is likely to facilitate data interpretation. Under drought stress and non-stress, the type III genotypes proved to be the most productive at the location in Mexico. In conclusion, recombinant families which displayed adaptation to the Michigan environment had enhanced BNF and drought tolerance. Further enhancement of those two traits into a single genotype is believed to be feasible, but since BNF is readily decreased by water stress, these two traits must be expressed at different developmental stages, i.e. BNF during the early vegetative phase and drought tolerance during the reproductive phase.

I
guida
His
along
studi

commi
resea
matte

Drs.
sugg

grea
thr
pro

uns
Rec
ack
hel
ti

ACKNOWLEDGMENTS

I wish to express my gratitude to Dr. M. Wayne Adams for his guidance and encouragement during my stay in Michigan State University. His helpful suggestions through the different phases of this research along with his patience were instrumental for the completion of my studies. His critical reviews of the manuscript are deeply appreciated.

I would also like to thank Dr. Jim Kelly for serving in my committee and for his positive criticisms during the conduction of this reseach. The long and illustrative discussions we had on bean breeding matters were very helpful.

I am truly grateful to the other members of my guidance committee Drs. Frank Dazzo, Amy Iezzoni and Irwin Widders, for their helpful suggestions and good will, much thanks

The assistance of Mr. Jerry Taylor, and Mrs. Betsy Bricker is greatly appreciated. The work in Durango, Mexico, was made possible through the cooperation of the technical and field personnel of the bean program of the Center for Forestry and Agriculture research in Durango.

Special thanks to Mireille Khairallah and Susan Sprecher, for their unselfish help and moral support. I also appreciate the help of Barb Recchio during my first year at Michigan State. I gratefully acknowledge Mrs. Darlene Johnson for all her valuable administrative help. I extend thanks to many precious friends, who made the hard times at Michigan State more bearable.

I

Instit

from t

I deeply appreciate the financial support from the National Institute for Forestry and Agriculture Research (INIFAP) in Mexico and from the Bean-Cowpea Collaborative Research Support Program (MSU).

TABLE OF CONTENTS

LIST OF TABLES

Page

CHAPTER 1

CHAPTER 2

CHAPT

CHAPT

CHAPT

CHAPTER 2 (CONTINUED)

CHAPTER 3

CHAPTER 4

CHA

1

1

1

1

1

1

1

CHAPTER 4 (continued)

CHAPTER 4 (continued)

LIST OF FIGURES

CHAPTER 1

CHAPTER 2

CHAPTER 4

APPENDIX C

INTRODUCTION

Pulses, such as common beans (Phaseolus vulgaris L.), are a major source of proteins and calories throughout the world. Common beans are especially important in developing countries, where they are consumed by people of all social strata. The crop is generally grown for its mature seeds but its immature pods and leaves are also consumed as a vegetable in some African countries (Adams et al., 1985).

Common beans originated in the Americas (Gentry, 1969), however, they are grown and consumed in all continents. They are particularly important in Latin America and Eastern Africa. In these bean producing areas, the bean crop is constrained by different sets of biotic and abiotic factors. Some of those factors are widespread, like high or low temperatures, diseases, insects and weeds, while other factors are more site specific, such as marginal soils with a low content of essential plant nutrients or the lack of moisture at different times during the growing cycle.

In semi-arid areas of North-Central Mexico, where the common bean is an important crop, shallow soils with poor nutrient and organic matter content increase the chance for drought damage to occur. The bean crop is grown during the portion of the year when precipitation is expected to occur, but alternate wet and dry periods of varying lengths which affect production can be expected.

An examination of climate data for 110 production areas in Latin America indicates that almost 60 per cent of the crop experiences mo

In

to

du

li

re

re

wh

19

yea

cer

mod

par

bre

in

yie

incr

stab

envi

unpr

ofte

limi

expe

consi

surpr

moderate to severe water deficits after flowering (Laing et al., 1984). In spite of this, P. vulgaris is considered to be a crop with poor tolerance to severe water deficits (Laing et al., 1984). Although during the past decade, common beans have been studied extensively, little research has been directed towards breeding for drought resistance. An old concern in bean research, to which much effort and resources have been lately channeled, is to overcome the yield plateau which experimentally ranges from three to five tons/ha (Temple and Long, 1980; White, 1987). Yields of common beans have been static for many years, whereas notable yield increases have been realized in several cereal crops. Increased cereal yields were attributed largely to the modification of plant morphology, improvement in grain/straw partitioning and an increased use of fertilizer (Coyne, 1980).

Traditionally, advances in crop yields have been obtained through breeding and crop management. However, in some instances, particularly in developing countries, bridging the gap between actual and potential yields in variable environments can be more valuable than efforts to increase the yield potential of the crop. In other words, yield stability achieved through breeding for adaptation to adverse environmental stress is a more realistic approach to increase yields in unpredictable environments.

The bean crop in most producing areas in developing countries is often confined to marginal lands where available soil nitrogen is limited and nitrogen fertilizer is either difficult to obtain or too expensive to purchase (Graham, 1981; Bliss, 1985). Beans are generally considered poor in nitrogen fixation (Piha and Munns, 1987) and show surprisingly variable response to inoculation in field experiments. The

var
var
var
to

pla
est
is
(Gr
fol
bec
lik
nat
cer
to

moi
wit
eff
bre
is
wit

Rese
Proj
to
conc

variable responses obtained with field experiments are due in part to variable environmental conditions (Sprent, 1982), and genetic variability among both Rhizobium strains and bean genotypes for ability to efficiently fix biological nitrogen (Graham, 1981).

Common beans grown in rainfed areas of the Mexican plateau are planted after soil moisture is considered adequate to assure the establishment of the crop. Biological nitrogen fixation in common beans is favored during vegetative growth peaking at the flowering stage (Graham and Rosas, 1977; Rennie and Kemp, 1981a,b). The peak is followed by a sharp decline thought to be due to the developing fruits becoming a strong competitive sink for photosynthates. Thus, it is likely that bean genotypes which could readily enter into symbiosis with native or introduced rhizobia at early growth stages and which possess a certain degree of drought tolerance would be the most suitable genotypes to use in drought prone environments on marginal soils.

It is axiomatic that the productivity of a crop grown under moisture stress will be much less than its productivity when it is grown with an ample supply of water. Therefore, biological immunity to the effects of drought is not a possibility (Quisenberry, 1982). However, breeding for enhanced biological nitrogen fixation and drought tolerance is an attractive approach to stabilizing and/or increasing bean yields without increasing inputs.

As a part of the National Institute for Forestry and Agriculture Research INIFAP (Mexico) - Michigan State University, Bean/Cowpea CRSP project, this research was conducted to determine whether it is possible to select for drought tolerance and the ability for high BNF concurrently in the same population, and determine whether genotypes va

va

va

to

pla

est

is

(Gr

fol

bec

like

nat

cert

to

mois

with

effe

bree

is

with

Rese

Proj

to

conc

variable responses obtained with field experiments are due in part to variable environmental conditions (Sprent, 1982), and genetic variability among both Rhizobium strains and bean genotypes for ability to efficiently fix biological nitrogen (Graham, 1981).

Common beans grown in rainfed areas of the Mexican plateau are planted after soil moisture is considered adequate to assure the establishment of the crop. Biological nitrogen fixation in common beans is favored during vegetative growth peaking at the flowering stage (Graham and Rosas, 1977; Rennie and Kemp, 1981a,b). The peak is followed by a sharp decline thought to be due to the developing fruits becoming a strong competitive sink for photosynthates. Thus, it is likely that bean genotypes which could readily enter into symbiosis with native or introduced rhizobia at early growth stages and which possess a certain degree of drought tolerance would be the most suitable genotypes to use in drought prone environments on marginal soils.

It is axiomatic that the productivity of a crop grown under moisture stress will be much less than its productivity when it is grown with an ample supply of water. Therefore, biological immunity to the effects of drought is not a possibility (Quisenberry, 1982). However, breeding for enhanced biological nitrogen fixation and drought tolerance is an attractive approach to stabilizing and/or increasing bean yields without increasing inputs.

As a part of the National Institute for Forestry and Agriculture Research INIFAP (Mexico) - Michigan State University, Bean/Cowpea CRSP project, this research was conducted to determine whether it is possible to select for drought tolerance and the ability for high BNF concurrently in the same population, and determine whether genotypes superior in both characteristics simultaneously could be produced.

Effe

many

ulti

mois

vulg

the

the

the

spec

of t

deve

preve

tole

disc

Sulli

field

Proce

devel

Point

Yield

LITERATURE REVIEW

Effect of drought stress on plant growth

Water deficits which occur during the growth of common beans affect many physiological and morphological characteristics associated ultimately with seed yield. The species is considered vulnerable to moisture stress (Laing et al., 1984). In terms of seed yield, in *P. vulgaris*, as well as in most pulse crops, the duration and intensity of the moisture deficit as well as the phenological stage of the crop at the time the stress occurs will determine the amount of damage done to the crop.

There are essentially three mechanisms used by different plant species to overcome or survive periods of low water availability. Two of those involve the avoidance of large water deficits, either through developmental timing or by the plant surviving moisture deficits by preventing tissue dehydration. The third mechanism involves the tolerance of low tissue water potentials. These mechanisms are discussed in detail elsewhere (Blum, 1979; Turner, 1979; Levitt, 1980; Sullivan, 1983; Boyer, 1985).

The gradual development of water deficits by plants growing in most field situations allows slow and continual adjustment in physiological processes, eventually manifested as alterations in growth and development (Jordan, 1983). This review discusses, from a practical point of view, morphological, phenological, partitioning, and economic yield responses of common beans and related pulse crops to drought stress and the effects of soil moisture stress on biological nitrogen fixation in the legume-rhizobia symbiosis.

Shoot development

Leaf area index, the most often used measure of canopy development, is very sensitive to water deficit, which results in a decrease in leaf initiation and expansion and an increase in leaf senescence and shedding, or both (Hsiao, 1973; Karamanos, 1978; Elston and Bunting, 1980; Hebblethwaite, 1982; Sheriff and Muchow, 1984). Leaf expansion is more sensitive to water deficits than are stomatal closure or photosynthesis (Hsiao, 1973). Leaf senescence does not appear to be as sensitive as leaf expansion (Sheriff and Muchow, 1984). However, in the field, the most obvious morphological response to a sudden or prolonged water stress is leaf loss by accelerated senescence.

The reduced rate of leaf area accumulation usually associated with growth in dryland environments may be associated with a smaller size of individual leaves or with production of fewer leaves (Jordan, 1983). Bonnano and Mack (1983) evaluated the effect of differential irrigation on plant growth and development of two snap bean cultivars. They observed that the difference between treatments in total leaf area per plant occurred earlier in the season than the difference between treatments in total plant weight. The observed decrease in leaf area was due to a decrease in area per leaf rather than by a reduction in leaf number. In field beans, Karamanos (1978) found that after a period of 46 days the total leaf area of well-watered plants was about double that of the non-watered ones. He showed that the difference between treatments in total leaf area was mainly produced by the mechanisms determining leaf size rather than those associated with leaf initiation and maintainance, namely leaf production, unfolding and death. Thus, it seems that the reduction in leaf area in grain legumes is due mainly to the reduction in size of individual leaves.

With respect to leaf senescence, many researchers consider this accelerated senescence as a drought avoidance mechanism in plants (Kramer, 1983). In regions where an extended growing season is feasible, cultivars with an indeterminate growth habit may compensate later for the loss of leaf area by producing new leaves. However, for a short lived crop, such as the bean crop in the semi-arid highlands of Mexico, which rarely displays optimum LAI values of 4.0 (Laing et al, 1983) at bloom stage, a heavy loss of leaves may be counter-productive. Differences in leaf abscission rates and yield among soybean cultivars growing under differential degrees of water stress were reported by Caviness and Thomas (1980). Vidal and Arnoux (1981), in a screening program involving 15 soybean cultivars and utilizing 19 morphological, physiological, and biochemical responses to drought stress, found that reduction in leaf expansion and petiole growth were the characteristics most highly correlated to the reduction in seed yield and canopy.

Acosta and Kohashi (1988) found that the responses in yield of indeterminate bean cultivars to water stress, imposed at late vegetative and early bloom stages, could be explained by the decrease in LAI measured at bloom stage. Elston and Bunting (1980) pointed out that in faba bean, dry episodes affect final yield not by decreasing the rate of assimilation per unit area so much as by decreasing the rate of expansion of leaves; as a consequence, the total leaf area duration of the crop is reduced. In an experiment involving nine species of grain

legu
inte
prop

onto
wate
revi
of w
sene
a s
lowe

cove
evap
beco
Pass
via
Pla
to
spr
fit
reg
and

the
not
occ

legumes, Laing et al. (1983), showed that leaf area duration (LAD, the integral of time course of LAI) alone explained a remarkably large proportion (R^2=0.99) of the variation in seed yield.

The rate of natural leaf senescence is likely to change during crop ontogeny. An increase in natural leaf senescence is a common effect of water deficit during grain filling. As pointed out earlier in this review, the reduction in yield is dependent on the timing and duration of water deficit and the growth stage and type of crop. Increased leaf senescence caused by water deficit near physiological maturity has only a small effect on yield since senescence tends to occur first in the lower part of the canopy (Sheriff and Muchow, 1984).

Usually, early water deficits reduce yield only when full ground cover is not achieved before flowering. Thus, soil water loss by direct evaporation occurs when crops are building up leaf area, and the losses become small once the leaf area index exceeds about 2.5 (Ritchie, 1983). Passioura (1986) indicates that the best prospect to avoid water loss via direct soil evaporation is to have a vigorous establishment of plants with a postrate, rather than erect, growth habit. It is important to establish an LAI approaching 2 as fast as possible, with leaves well spread out. Type III bean and indeterminate prostrate cowpea cultivars fit this description and are the most widely used in drought prone regions in the Mexican highlands and in semiarid zones of Africa (Hall and Patel, 1985; Acosta and Kohashi, 1988).

Various mechanisms, particularly increses in leaf angle, can reduce the solar irradiance absorbed by leaves, so that stomatal closure does not result in metabolic damage. In beans, adjustment in leaf angle occurs rapidly in response to stress conditions (Dubetz, 1969). A d

i

u

re

pr

whi

may

long

wate

the

remov

1980).

c

which

branc

seasc

occur

Pinto

second mechanism in reducing the solar irradiance absorbed by leaves is by a decrease in leaf absorptivity. Leaf hairs, waxes and leaf color can reduce leaf absorptivity leading to lower leaf temperatures and transpiration rates (Schultze et al., 1987). Variation for all these traits seems to be present in beans, but does not appear to have been studied in relation to drought stress.

Crop growth habit and phenology

The time between sowing and maturity may be shortened or lengthened depending on the intensity and timing of water deficits. For example, intermediate maturing cowpeas and common beans flower and mature earlier under moderate levels of water deficits, but severe water deficits delay reproductive activity (Turk and Hall, 1980; Samper, 1984). This provides those crops with two possible adaptive responses.

Under moderate water deficits, mid-season cultivars produce grain which may mature before the soil water is depleted. Such early maturity may be advantageous in dry years (Hall and Patel, 1985) and yet permit a longer season and larger yields under wetter years. With early severe water deficit, the crop remains in a quiescent vegetative stage but has the ability to continue reproductive activity if the water deficit is removed as long as lethal deficits are not reached (Turk and Hall, 1980).

Other forms of developmental plasticity observed in legume crops which may be advantageous under water deficits include indeterminacy and branching. Where periodic water deficits occur during the growing season, the indeterminacy of certain grain legumes permits fruiting to occur in flushes during favorable periods. Such is the case of Colorado pinto bean cultivar San Juan Select (Adams, 1984; personal communication), selected in a region with sporadic rainfall during the growing season. Cowpeas recover after drought with a flush of flowers which produce a significant yield provided environmental conditions are then conducive to growth (Turk and Hall, 1980).

The climatic characterization of the environment of the target area is basic to determining the kind of cultivar to be produced in a plant breeding program. Severe moisture stress occurring later in the growth cycle favors earliness, while mild stresses relatively early will favor later maturing cultivars with capability for recuperative growth (Singh and White, 1988).

Wide adaptation in common beans, as in most crops, is one of the aims of bean breeders. Here, it is considered that genotypes with wide adaptation are those which possess individual or populational physiological and/or phenotypic plasticity that help them to cope with variable environments. Studies with common beans grown in variable environments have demonstrated that indeterminate growth types exhibit more yield stability than determinate ones (Beaver et al., 1985; Kelly et al., 1987). The latter types are also less productive (Laing et al., 1984).

Developmental plasticity facilitates the matching of crop growth and development to the constraints of the environment, especially in minimizing the occurrence of the critical reproductive phase during periods of severe water deficit. In agronomic terms, in developed countries, it may raise difficulties of uneven maturity of the crop in capital-intensive agriculture. In labor-intensive agricultural systems of the tropics, such plasticity substantially reduces the risk of complete crop failure for subsistance farmers (Sheriff and Muchow, 1984).

Comparing grain legume species, Wien et al. (1979) found that cowpeas which mature 17-20 days after anthesis were more likely to avoid environmental water deficits than soybeans, which mature 40-60 days after anthesis. One disadvantage of matching crop cycle length by using early cultivars is that they are conservative, so that higher yields are not produced in moist years.

Where a species like common bean has colonized a range of habitats it seems reasonable to expect to find various adaptations to those environments. Since habitats are subjected to continual fluctuation and change, adapted species must have considerable developmental plasticity (Summerfield, 1981). Furthermore, it is unlikely that any single attribute can provide all the adaptations that may be required to meet the complex array of possible ecological conditions that occur from time to time and from place to place (Bunting, 1985). It is clear that if drought tolerance exists in common beans, it is unlikely that it would be due to a single attribute.

Partitioning and remobilization

In most species only a distinct part of the plant, often a storage organ, is the economic yield. Economic yield (Y_e) is the function of total dry matter production, the biological yield (Y_b) and the harvest index (HI), so that $Y_e = Y_b \times HI$. Therefore, problems of partitioning of assimilates and the use of photosynthates for growth and storage (source-sink relationship) must be considered in the final yield (Apel, 1984). Furthermore, the size as well as activity of the photosynthetic apparatus and the pattern of assimilate distribution are genetically determined and also depend on changing environmental conditions and adaptation to a given environment.

In indeterminate grain legume crops, reproductive and vegetative growth phases overlap. When the lower nodes begin to produce flowers and set pods, the plant is still expanding and producing vegetative growth which competes for assimilates with flowers and young pods in the lower parts.

From a review of the subject in field bean (*Vicia faba*), El-Foudty (1982) concluded that:

a. During the entire flowering period pods and young seeds are competing with vegetative parts.

b. From the middle of the flowering period, pods are competing with each other within the same inflorescence.

c. During maturity, there is competition between pods according to their position on the plant.

Acosta and Kohashi (1988) mentioned that in common beans inter and intra-ovary competition takes place under both stress and nonstress conditions. Under stress, this competition may be responsible for the reduction in the number of pods per plant and seeds per pod of certain cultivars.

A widely used index of photosynthate partitioning, the harvest index (HI), was first defined by Donald and Hamblin (1976) as the ratio of seed yield to biological yield. Although it has been claimed that the rise in cereal yields in the last several decades is due largely to an improvement in HI, in common bean contradictory results have been reported (Wallace and Munger, 1966; Laing et al. 1984; White, 1987; Acosta and Kohashi, 1988).

For many crops, it appears that further substantial improvements in HI are unlikely (Sinclair et al., 1984). White (1987) recently pointed out that increase of the yield potential in beans through an improvement in the HI is not a feasible approach. He considers that common bean already possesses a high HI and reported that dry bean cultivars growing in the tropics have shown a lack of variability for this trait. He mentioned that in most yield trials a lack of correlation between HI and yield has been found. In addition, he considers that this lack of correlation is actually worse due to the statistical artifact introduced by correlating two components of the same end product. Increases in HI when the bean crop has been exposed to moisture stress have also been reported (Tosso, 1979; Couto, 1978).

Plants produce many storage compounds that can be changed back to forms that can be translocated to other parts of the plant. The movement of compounds from a site where they were deposited to a site where they can be utilized is referred to as "remobilization" (Gardner et al., 1985).

Water deficit during grain filling reduces grain yield through stomatal control of transpiration which reduces photosynthesis. Thus the demand for grain filling requires the use of stored assimilates, which results in a much higher proportional contribution by remobilization. In many crops, the economic yield is only a part of the total biomass. There is evidence in the literature that, for a number of crops, reallocation of carbohydrates produced before a stress period can partially alleviate the effects of the water deficit in terms of seed yield (Johnson and Moss, 1976; Bidinger et al., 1977; Gallagher and Biscoe, 1982; Aparicio and Boyer, 1983).

Samper et al. (1984) grew common beans in a greenhouse study with incorporated $^{14}CO_2$ and, by monitoring dry weight changes of different plant parts, demonstrated that assimilates from storage organs (mainly leaves) were remobilized to developing fruits. They showed evidence for differences in remobilization due to drought treatment versus non-stress and to genotype, with remobilization being more pronounced under water deficit.

Economically, only the usable portion of a crop plant is important; however, in a biological sense, all plant dry matter is made through photosynthesis. Therefore, the production of total dry matter determines the response of a genotype to drought stress (Quisenberry, 1982). Quisenberry (1982) considers that under drought conditions, partitioning should be a second objective for improvement. As Adams (1986) pointed out, in common beans, high yields under moisture stress result from partitioning of a greater biomass not merely from a high partitioning ratio *per se*. Thus, it is the ability to accumulate biomass and to partition it to the seed, under stress, that distinguishes top yielders from low yielders.

Although photosynthesis and nitrogen fixation during growth are two different processes, they cannot be separated since, in most legumes, remobilization of stored starch and nitrogen compounds from the leaves to the protein rich seeds plays an important role in the final yield and composition of the seeds (Summerfield, 1981).

Yield and yield components

It is well established that in any crop the effect of water stress on growth and yield depends on the degree of the stress, the stage of growth at which the stress occurs and the duration of the stress period.

In the case of common beans, there is general agreement in the literature that the reproductive stage is the most sensitive to water stress, affecting seed yield by reducing the number of pods set and single seed weight (Robins and Domingo, 1956; Dubetz and Mahalle, 1969; Stoker, 1974; Stansell and Smittle, 1980; Bonnano and Mack, 1983; Samper, 1984, Ibarra, 1985, Elizondo, 1987, Acosta and Kohashi, 1988).

Reductions in seed yield of up to 80 % for drought sensitive bean cultivars as compared to 40 % reduction for tolerant ones were reported by Sponchiado (as cited by Singh and White, 1988). Stoker (1974) obtained a yield reduction of 20 % when water stress occurred at early or late vegetative phases of growth, and a reduction of 50 % when stress was applied at early pod filling. Similar figures for a group of three indeterminate bean cultivars were reported by Acosta and Kohashi (1988).

The yield of common beans may be considered as the product of its components: number of pods per plant, number of seeds per pod and individual seed weight. According to Adams (1967), there is no genetic interdependence among yield components in beans since correlations between components was essentially zero under non-competitive conditions. However, yield reductions in common beans due to water stress can be attributed to its effects on one or more components according to the stage of growth of the crop, and intensity and duration of the stress.

Multiple reports in the literature have shown that if water stress occurs during vegetative growth, number of pods per plant is reduced; if water stress occurred during flowering, number of pods and number of seeds per pod are significantly reduced; if water stress occurs late during the pod filling stage, seed weight is reduced (Robins and

Domingo, 1956; Dubetz and Mahalle, 1969; Acosta and Kohashi, 1988). This would indicate that different components are being laid down sequentially during development.

Effect of drought stress on biological nitrogen fixation

In temperate climates, variability for nitrogen fixation is due mainly to the environment and evidence is accumulating that nitrogen fixation is more sensitive to stress than is the uptake of mineral nitrogen (Sprent, 1982). Graham (1981) pointed out that moisture stress is one of the environmental factors affecting nitrogen fixation in common beans; however, little research has been conducted on the matter.

Sprent (1981) and Finn and Brun (1980) have suggested that water stress reduces nitrogen fixation in soybeans by a direct effect on nodule physiology, but may be aggravated by the inability of stressed leaves to supply photosynthates to the nodules. Other evidence suggests that reduction in photosynthates during water deficits causes the observed reductions in nitrogen fixation (Huang et al., 1975a,b).

Nitrogen fixation has also been shown to decrease as nodule number and leaf water potentials decrease (Pankhurst and Sprent, 1975; Finn and Brun, 1980).

Bennett and Albrecht (1984), working under greenhouse conditions, found that after 10 days of withholding water, nitrogen fixation was reduced, and nitrogenase activity declined to zero as stress became progressively more severe. Their data indicate the sensitive nature of nitrogen fixation to reductions in the water content of the soil and further suggest that nodules surrounded by dry soil may dessicate to water potentials lower than those observed for leaf tissue. Nitrogen fixation appeared to be more sensitive to drought stress than was photosynthesis (Weisz et al. 1985), suggesting that some drought yield reductions may reflect the effects of nitrogen deficiency.

Saito et al. (1984) conducted a glasshouse experiment with the bean cultivar Carioca and found that soil water content affected nodulation, N_2 fixation and the utilization of mineral nitrogen by the plants. Plants grown in wet soil produced twice as much biomass as those grown in dry soils. Nodule weight and activity were five to ten times greater than those from dry soil. Decreases in soil water content were accompanied by decreases in growth, and in nitrogen accumulation by the plant.

Recently, Durand et al. (1987) studied the effects of water deprivation on the activity of nodules of soybeans. During a seven-day period of water deprivation there was a close relationship between decreases in leaf and nodule water potential. Nitrogenase activity showed a 70 % decrease during the first four days, whereas photosynthesis declined by only 5 %. They suggested that water stress exerts an influence on nitrogenase activity which is independent of the rate of photosynthesis; it acts directly on nodule activity through increases in the resistance to oxygen diffusion to the bacteroids. The data suggest that the linear relationship between oxygen diffusion resistance and water potential is more important than any reductions in photosynthate supply.

Abdel-Ghaffar et al., (1982) conducted an experiment in which common beans were planted, then irrigated every 7, 12, 17, or 22 days during the growing season. They found that water stress inhibited nodulation, depressed nitrogenase activity and decreased the yield of bean plants. Maximum yields were obtained when plants were irrigated every 7-12 days.

Briefly, it is believed that the combination of drought tolerance and high ability to fix nitrogen in a single bean cultivar can occur, but optimum expression of each will depend upon differential timing in development.

Concluding remarks

In the grain legumes in general, and with common beans in particular, there is no single factor or unique characteristic which is sufficient alone to account for "adaptation to drought-prone environments". Traditional bean cultivars in Latin America seem to be adapted to cropping systems which imply sacrificing yield potential in exchange for reduced risk, production costs and other problems (White, 1987).

Improvement in plant production need not rest solely on increases in genetic potential but should also emphasize ways of bringing productivity closer to the existing genetic potential through management techniques. Plant types that are productive with lower inputs should be readily accepted by the farmers (Boyer, 1982). Therefore, as pointed out in the introduction, selection for increased stability in variable environment should be assigned high priority in research centers.

Where unpredictable water deficits occur, maximum productivity should be the goal, whereas conservation of water using a shorter growing season crop should be the goal where terminal water deficits occur. Maximum productivity will be achieved where leaf expansion and senescence are relatively insensitive to water deficit, where leaf expansion recovers quickly upon relief of water deficits, and where minimum dry matter is partitioned into immobile root reserves.

Crop water use efficiency is in nature a conservative approach (Sinclair et al., 1984), and selection for wide adaptation and/or yield stability has been considered to be defensive breeding. The improvement of bean cultivars for ability to fix atmospheric nitrogen and display tolerance to soil moisture deficits will undoubtely benefit peasant farmers in those regions where the bean crop relies on uncertain rainfall patterns for its growth.

REFERENCES

Acosta Gallegos, J.A. and J. Kohashi Shibata. 1988. Effect of water stress on growth and yield of indeterminate dry bean (Phaseolus vulgaris L.) cultivars. Submitted : Field Crops Research. The Netherlands

Abdel-Ghaffar, A.S., El-Altar, H.A., El-Halfawe, M.H. and A.A. Abdel Salam. 1982. Effects of inoculation, nitrogen fertilizer, salinity and water stress on symbiotic N_2 fixation by Vicia faba and Phaseolus vulgaris. In: P.H. Graham and S.C. Harris (Eds.), BNF Technology for Tropical Agriculture. CIAT, Cali, Colombia pp.153-159

Adams, M.W. 1967. Basis of yield component compensation in crop plants with special reference to the field bean Phaseolus vulgaris L. Crop Sci. 7:505-507

Adams, M.W., Coyne, D.P., Davis, J.H.C., Graham, P.H. and C.A. Francis. 1985. Common bean (Phaseolus vulgaris L.). In: R.J. Summerfield and E.H. Roberts (Eds.), Grain Legume Crops. William Collins and Sons & Co. Ltd pp. 433-476

Adams, M.W. 1986. Improving resistance to environmental stress in beans through genetic selection for carbohydrate partitioning and efficiency of biological nitrogen fixation. Bean-Cowpea-CRSP Report on the INIFAP (Mexico)-MSU Project p.24

Aparicio, T.P.M. abd J.S. Boyer. 1983. Significance of accelerated leaf senescence at low water potentials for water loss and grain yield in maize. Crop Sci. 23:1198-1202

Apel, P. 1984. Photosynthesis and assimilate partitioning in relation to plant breeding. In: P.V. Bose and S.G. Blixt (Eds.), Crop Breeding. A Contemporary Basis. Pergamon Press pp.163-182

Beaver, J.S. Paniagua, C.V., Coyne, D.P. and G.F. Freytag. 1985. Yield stability of dry bean in the Dominican Republic. Crop Sci. 25:923-926

Bennett, J.M. and S.L. Albrecht. 1984. Drought and flooding effects on N_2 fixation, water relations and diffusive resistance of soybean. Agron. J. 76:735-740

Bidinger, F., Musgrave, R.B., and R.A. Fischer. 1977. Contributions of stored preanthesis assimilate to grain yield in wheat and barley. Nature 270:431-433

Bliss, F.A. 1985. Breeding for enhanced dinitrogen fixation potential of common bean (*Phaseolus vulgaris* L.). In: P.W. Ludden and J.E. Burris (Eds.). Nitrogen Fixation and CO$_2$ Metabolism. Proc. 14th Steenbock Symposium, 17-22 June 1984, University of Wisconsin, Madison. Elsevier Science Publishing Co., pp. 303-310

Blum, A. 1979. Genetic improvement of drought resistance in crop plants: A case for sorghum. In: H. Mussell and R.C. Staples (Eds.), Stress Physiology in Crops Plants. John Wiley and Sons Inc. pp. 429-445

Bonanno, A.R., and H.J. Mack. 1983. Yield components and pod quality of snap beans growth under differential irrigation. J. Amer. Soc. Hort. Sci. 105:869-873

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443-448

Boyer, J.S. 1985. Water transport. Ann. Rev. Plant Physiol. 36:473-516

Bunting, A.H. 1985. What is this thing called drought ? Workshop on drought, Bean-Cowpea CRSP, Durango, Mexico, 26-28 August p.9

Caviness, C.E. and J.D. Thomas. 1980. Yield reduction from defoliation of irrigated and non-irrigated soybean. Agron J. 72:977-980

Coyne, D.P. 1980. Modification of plant architecture and crop yield by breeding. Hortscience 15:244-247

Couto, L. 1978. Effects of water stress on growth, reproductive development, dry matter partitioning and yield components of beans (*Phaseolus vulgaris* L.) in the field. Ph.D. Thesis. University of California, Davis

Donald, C.H. and J. Hamblin. 1976. The biological yield and harvest index of cereals as agronomic and plant breeding criteria. Adv. Agron. 28:361-405

Dubetz, S. 1969. An unusual photonastism induced by drought in *Phaseolus vulgaris*. Can. J. Bot. 47:1640-1641

Dubetz, S. and P.S. Mahalle. 1969. Effect of soil water stress on bush beans *Phaseolus vulgaris* L. at three stages of growth. J. Amer. Hort. Sce. 94:479-481

Durand, J.L., Sheehy, J.E. and F.R. Minchin. 1987. Nitrogenase activity, photosynthesis and nodule water potential in soyabean plants experiencing water depravation. J. Exp. Bot. 38:311-321

El-Fouty, M.M. 1982. Flower and pod drop. In: G. Hawtin and C. Webb (Eds.), Faba Bean Improvement. ICARDA. Martinus Nijhoff, The Netherlands pp.177-184

Elizondo-Barron, J. 1987. Characteristics related to yield of dry bean (Phaseolus vulgaris L.) under water stress conditions. M.S. Thesis Michigan State University, East Lansing p. 73

Elston, J. and A.H. Bunting. 1980. Water relations of legume crops. In: R.J. Summerfield and A.H. Bunting (Eds.), Advances in Legume Science. Royal Botanic Garden, Kew pp.37-42

Finn, G.A. and W.A. Brun. 1980. Water stress effects on CO_2 assimilation, photosynthate partitioning, stomatal resistance and nodule activity in soybean. Crop Sci. 20:431-434

Gallager, J.N. and P.V. Biscoe. 1982. A physiological analysis of cereal yield. II. Partitioning of dry matter. Agricultural Progress 53:51-70

Gardner,, F.P., Pearce, R.B. and R.L. Mitchell. 1985. Physiology of Crop Plants. Iowa State University press, Ames pp. 58-75

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

Graham, P.H., and J.C. Rosas. 1977. Growth and development of indeterminate bush and climbing cultivars of Phaseolus vulgaris L. inoculated with Rhizobium. J. Agric. Sci. Camb. 88:503-508

Graham, P.H. 1981. Some problems of nodulation and symbiotic nitrogen fixation in Phaseolus vulgaris L. : a review. Field Crops Res. 4:93-112

Hall, A.E. and P.N. Patel. 1985. Breeding for resistance to drought and heat. In: S.R. Singh and K.O. Rachie (Eds.), Cowpea: Research, Production and Utilization. John Wiley & Sons pp 137-151

Hebblethwaite, P. 1982. The effects of water stress on the growth, development and yield of Vicia faba L. In: G. Hawtin and C. Webb (Eds), Faba Bean Improvement. ICARDA. Martinus Nijhoff, The Netherlands. pp. 165-175

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570

Huang, C.Y., Boyer, J.S. and L.N. Vanderhoef. 1975a. Acetylene reduction (nitrogen fixation) and metabolic activities of soybean having various leaf and nodule water potentials. Plant Physiol. 56:222-227

Huang, C.Y., Boyer, J.S. and L.N. Vanderhoef. 1975b. Limitation of acetylene reduction (nitrogen fixation) by photosynthesis in soybean having low water potentials. Plant Physiol. 56:228-232

Ibarra, P.F. 1985. Effects of water stress on the relationships between root and shoot characteristics in dry beans. M.S. Thesis, Michigan State University, East Lansing p. 114

Johnson, R.R., and D.N. Moss. 1976. Effect of water stress on $^{14}CO_2$ fixation and translocation in wheat during grain filling. Crop Sci. 16:697-701

Jordan, W.R. 1983. Whole plant responses to water deficits: an overview. In: H.M. Taylor, W.R. Jordan and T.R. Sinclair (Eds.), Limitations to Efficient Water Use in Crop Production. ASA, CSSA, SSSA. pp.289-317

Karamanos, A.J. 1978. Water stress and leaf growth of field beans (*Vicia faba* L.) in the field: leaf number and total leaf area. Ann. Bot. 42:1393-1402

Kelly, J.D., Adams, M.W. and G.V. Varner. 1987. Yield stability of determinate and indeterminate dry bean cultivars. Theor. Appl. Genet. 74:516-521

Kramer, P.J. 1983. Water relations of plants. Academic Press, Inc. pp.342-389

Laing, D.R., Kretchmer, P.J., Zuluaga, S. and P.G. Jones. 1983. Field bean. In: W.H. Smith and S.J. Banta (Eds), Symposium on Potential Productivity of Field Crops Under Different Environments. Los Banos, Philippines, 1980 (Proceedings) IRRI pp.227-248

Laing, D.R., Jones, P.G. and J.H.C. Davis. 1984. Common bean (*Phaseolus vulgaris* L.)In: P.R. Goldsworty and N.M. Fisher (Eds), The Physiology of Tropical Crops. John Wiley & Sons Ltd. pp.305-351

Levit, J. 1980. Responses of Plants to Environmental Stress. 2nd. ed. Vol. 2 Academic Press, New York

Pankhurst, C.E. and J.I. Sprent. 1975. Effects of water stress on the respiratory and nitrogen-fixing activity of soybean root nodules. J. Exp. Bot. 26:287-304

Passioura, J.B. 1986. Resistance to drought and salinity: avenues for improvement. Aust. J. Plant Physiol. 13:191-201

Piha, M.I., and D.N. Munns. 1987. Nitrogen fixation potential of beans (*Phaseolus vulgaris* L.) compared with other grain legumes under controlled conditions. Plant and Soil 98:169-182

Quisenberry, J.E. 1982. Breeding for drought resistance and plant water use efficiency. In: J.W. Christiansen and C.F. Lewis, (Eds.), Breeding Plants for Less Favorable Environments. John Wiley and Sons, Inc. pp. 193-212

Rennie, R.J., and G.A. Kemp. 1981a. Selection for dinitrogen-fixing ability in *Phaseolus vulgaris* L. at two low-temperature regimes. Euphytica 30:87-95

Rennie, R.J., and G.A. Kemp. 1981b. Dinitrogen fixation in pea beans (*Phaseolus vulgaris*) as affected by growth stage and temperature regime. Can. J. Bot. 59:1181-1188

Ritchie, J.T. 1983. Efficient water use in crop production: discussion on the generality of relations between biomass production and evotranspiration. In: H.M. Taylor, W.R. Jordan and T.R. Sinclair (Eds.), Limitations to Efficient Water Use in Crop Production. ASA, CSSA, SSSA. pp.29-44

Robins, J.R., and C.E. Domingo. 1956. Moisture deficits in relation to the growth and development of dry beans. Agron. J. 48:67-70

Saito, S.M.T., Nazareth, M., Montanheiro, S., Victoria, R.L. and K. Reichardt. 1984. The effect of N fertilizer and soil moisture on the nodulation and growth of Phaseolus vulgaris. J. Agric. Sci. Camb. 103:87-93

Samper, C. 1984. Effects of water stress imposed at mid-pod filling upon yield and dry matter partitioning in dry beans (Phaseolus vulgaris L.). M.S. Thesis, Michigan State University, East Lansing p. 131

Samper, C., Adams, M.W., Hanson, A.D., and E. Watt. 1984. Contribution of stored assimilates to the seed following a drought stress in dry beans. Agronomy Abstracts 76:87

Sheriff, D.W. and R.C. Muchow. 1984. The water relations of crops. In: P.R. Goldsworthy and N.M. Fisher (Eds.), The Physiology of Tropical Field Crops. John Wiley and Sons Ltd. pp.39-83

Shultze, E.D., Robichaux, R.H., Grace, J., Rundel, P.W., and J.R. Ehleringer. 1987. Plant Water Balance. BioScience 37:30-37

Sinclair, T.R., Tanner, C.B. and J.M. Bennett. 1984. Water-use efficiency in crop production. BioScience 34:36-40

Singh, S.P. and J.W. White. 1988. Breeding common beans for adaptation to drought conditions. In: G. Hoogenboom, F. Ibarra, S.P. Singh, J.W. White and S. Zuluaga (Eds.), Research on Drought Tolerance in Common Beans. CIAT, Cali, Colombia. In press

Sprent, J.I. 1981. Nitrogen fixation. In: L.G. Paleg and D. Aspinall (Eds.), The physiology and Biochemistry of Drought Resistance in Plants. Academic Press pp.131-142

Sprent, J.I. 1982. Nitrogen fixation in grain legumes in the U.K. Phil. Trans. R. Soc. Lond. 296:387-395

Stansell, J.R., and D.A. Smittle. 1980. Effects of irrigation regimes on yield and water use of snap bean (Phaseolus vulgaris L.). J. Amer. Soc. Hort. Sci. 105:869-873

Stoker, R. 1974. Effect on dwarf beans of water stress at different phases of growth. N. Z. J. Exp. Agric. 2:13-15

T

T

Tu

Vid

Wal

Weis

Whit

Wien,

Sullivan, C.Y. 1983. Genetic variability in physiological mechanisms of drought resistance. Iowa State J. Res. 57:423-439

Summerfield, R.J. 1981. Adaptation to environments. In: C. Webb and G. Hawtin (Eds.). Lentils. ICARDA, Page Bross (Norwich) Ltd. pp 91-110

Temple, S.R. and L. Long. 1980. Crop improvement and genetic resources in Phaseolus vulgaris for the tropics. In: R.J. Summerfield and A.H. bunting (Eds.), Advances in Legume Science. London, HMSO pp.365-373

Tosso, J.E. 1979. Effects of different levels of applied water on the vegetative growth, yield and water production function in dry beans (Phaseolus vulgaris L.). Ph.D. Thesis, University of California, Davis p. 125

Turner, N.C. 1979. Drought resistance and adaptation to water deficits in crop plants. In: H. Mussell and R.C. Staples (Eds.), Stress Physiology in Crop Plants. John Wiley and Sons, New York pp.343-372

Turk, K.J. and A.E. Hall. 1980. Drought adaptation of cowpea. III. Influence of drought on plant growth and relations with seed yield. Agron. J. 72:428-433

Vidal, A. and M. Arnoux. 1981. Drought tolerance processes in soybean. Biol. Plant. 23:434-441

Wallace, D.H. and H.M. Munger. 1966. Studies of the physiological basis of yield differences. II. Variation in dry matter distribution among aerial organs for several dry bean varieties. Crop Sci. 6:503-507

Weisz, P.R., Denison, R.F. and T.R. Sinclair. 1985. Response to drought stress of nitrogen fixation (acetylene reduction) rates by field grown soybeans. Plant Physiol. 78:525-530

White, J.W. 1987. Strategies at CIAT for increasing yield potential of common beans -- finishing the domestication process. In: Symposium on Breeding for Higher Yields in Common Beans. XXXIII meeting of the PCCMCA, Guatemala, C.A. CIAT-B/C CRSP-ICTA p. 34

Wien, H.C., Littleton, E.J. and A. Ayanaba. 1979. Drought stress of cowpea and soybean under tropical conditions. In: H. Mussell and R.C. Staples (Eds.), Stress Physiology in Crop Plants. John Wiley and Sons, New York pp.283-301

b

D

ni

su

imp

Kol

Fel

1986

CHAPTER 1

BIOLOGICAL NITROGEN FIXATION AND DROUGHT TOLERANCE OF A GROUP OF BEAN GENOTYPES, *Phaseolus vulgaris* L.

INTRODUCTION

Leguminous plants use two principal sources of nitrogen in their nutrition : soil nitrate and atmospheric nitrogen. Legume symbiosis is governed by factors and processes independently inherited in the host and bacterium; these interact to produce a joint phenotype (Nutman, 1981). The involvement of host genetic factors in root nodule symbiosis was first suggested by Wilson in 1939 (Nutman, 1981). He showed that the host ranges of different strains of *Rhizobium* was not only related to properties of the bacteria but also to the hosts' characteristics (Nutman, 1981).

Most cultivated legumes are able to fix nitrogen, but differences in the efficiency of nitrogen fixation between species of legumes has been observed (Schubert and Evans, 1976: Piha and Munns, 1987). Differences have also been observed within species. Measurements of nitrogen fixed and various parameters of nitrogen fixation suggest sufficient variability among cultivated dry bean germplasm to allow improvement through selection (Graham and Rosas, 1977; Westerman and Kolar, 1978; Rennie and Kemp, 1981a,b; Mc Ferson, 1983; Rosas, 1983; Felix et al., 1984; Pacowsky et al., 1984; Bliss, 1985; St. Clair, 1986).

of

red

bio

pro

Zab

198

meta

nitr

to

(Alb

exis

1984

of

anthe

analy

matu

conc

the

comm

Sinc

BNF

if

gen

were

In most legume crops it has been demonstrated that the occurrence of a water deficit drastically reduces nitrogen fixation. This reduction can be either by a direct effect on the physiology and/or biochemistry in the nodule tissue or indirectly by affecting the production of photosynthates in the host plant (Sprent, 1981; Zablotowicz et al., 1981; Beadle and Long, 1985; Myers Jr. et al., 1986), since the energy for nitrogen fixation is derived from root metabolism of photosynthates. Recent findings seem to indicate that nitrogenase activity is much more sensitive to nodule dehydration than to reduction in photosynthesis due to a fall in leaf water potential (Albrecht et al. ,1984).

On the other hand, it has been demonstrated that genetic variation exists in common beans for traits related to drought tolerance (Samper, 1984; Elizondo, 1987). Elizondo (1987) studied the response of a group of 11 common bean cultivars to a mild water stress period imposed after anthesis. A principal factor analysis and stepwise multiple regression analysis performed on 27 traits showed that biomass at physiological maturity made the largest contribution to seed yield variance. He concluded that genotypes best adapted to drought were those possessing the greatest biomass at physiological maturity.

The objective of this research was to rank a selected group of common bean genotypes for BNF related variables and drought tolerance. Since the literature shows that plant growth and development as well as BNF are affected by water deficits, the main objective was to determine if drought tolerance and ability for BNF could be combined in a single genotype. In order to achieve those objectives BNF related variables were evaluated early during the life cycle of the crop and water stress related variables were evaluated after flowering, when the stress was imposed.

MATERIALS AND METHODS

To accomplish the stated objective, two experiments were conducted; a greenhouse experiment where variability in fixing atmospheric nitrogen was assessed within a selected group of bean genotypes, and a field experiment where a subgroup of selected cultivars was evaluated for drought tolerance and BNF capacity.

Greenhouse experiment. A group of 11 cultivars (Table 1) previously selected as drought tolerant, capable of good nitrogen fixation, or high yielding, were planted in January, 1985 in a greenhouse at Michigan State University (MSU), East Lansing, MI. Uniformly sized seeds were over-inoculated with one of two strains of *Rhizobium phaseoli*, CIAT 899 (isolated by P. Graham at CIAT) and J025 (isolated by J. Maya, provided by F. Dazzo from the Brazil-UW-MSU, CRSP project). In addition to treatments inoculated with two *Rhizobium* strains, two other treatments without inoculant were included, one with nitrogen fertilizer (positive check) and the other without nitrogen fertilizer (negative check). For each cultivar, two seeds per pot were planted in 8x12 cm plastic pots containing a sterilized pure silica sand medium. After emergence, seedlings were thinned to one per pot. Depending on treatments, pots were irrigated each week day with a Hoagland solution with or without nitrogen.

The four treatments obtained by testing the two *Rhizobium* strains and both checks on the 11 cultivars, were distributed in a Completely Randomized Design (CRD) with eight replicates. Each experimental unit was a single pot containing one plant. At 25 and 50 days after planting

Table 1. Characteristics of bean genotypes grown in greenhouse (G) and/or field (F) experiments. East Lansing, MI. 1985

Genotype	Pedigree	Origin*	Seed color	Plant type[1]	Experiment
UW.21-58	P. sint/Pue 152	UW	black	II	GF
UW.23-61	Ex-Rico 23/Pue 152	UW	white	II	F
A411	BAT 461/(G879xG2337)	CIAT	brown	II	G
BAT 336	51052/Cacahuate	CIAT	cream	II	G
N81017	Kent/Nep2//Pijao/Bunsi	MSU	white	II	GF
N81064	Bunsi/Nep2	MSU	white	II	GF
B76001	Nep2/BTS	MSU	black	II	G
LEF-2-RB	(Ver 10/Chis 143)/Pue 144	INIFAP	black striped	III	G
Mex.1213-2	Unknown	INIFAP	pinto	III	GF
Dgo.222	Durango 222	INIFAP	white	III	G
Bayo Madero	Bayo RGZ/C-102	INIFAP	cream	III	GF
II900-5-M-45	Pinto Amer./C-14	INIFAP	brown striped	III	GF
Pinto Nal.1	local Durango	INIFAP	pinto	III	F

* UW = University of Wisconsin
MSU = Michigan State University
CIAT = Internatinal Center for Tropical Agriculture, Colombia
INIFAP = National Institute for Forestry and Agriculture Research, Mexico

1- Type II = indeterminate-bush, erect stem and branches.
Type III = indeterminate-bush, postrate main stem and branches.

(DAP), plants were harvested by cutting them at the sand level. Shoots were placed in paper bags and dried in a forced dry air oven at 60 °C for 72 hours. Dry matter per plant was determined.

Roots were carefully washed and the nitrogenase activity of plants in each treatment, at 25 DAP, except those under positive check, was determined by the acetylene reduction assay. Each root system with attached nodules was placed in a 50 cc flask which was sealed. A 10 ml volume of air was withdrawn with a syringe and replaced by 10 ml of acetylene. After 30 min incubation, 2 ml of gas were taken from the flask and injected into a calibrated gas chromatograph using nitrogen as a carrier gas at a flow rate of 25 ml/min at 80 °C. After nitrogenase activity was determined, nodules were detached from the roots and their fresh weight was recorded.

Analyses of variance were performed on the recorded variables following a CRD as a two factor factorial 4 x 11. Simple correlations were calculated among recorded variables by using genotype averages over treatments.

Field experiment. This experiment was planted in June 1985 on a Marlette fine-loamy soil (mixed, mesic, Glassoboric Hapludolfs) (USDA, Soil Conservation Service) at the Crops Research Farm of MSU in East Lansing, MI. A group of eight cultivars previously selected as drought tolerant or with outstanding BNF ability were tested in the field by using a Randomized Complete Block Design arranged as a split-split plot with three replications. Each experimental plot consisted of four rows of 4m length, spaced 50 cm apart. Plant density was 20 plants per m^2. Treatments were as follows:

Factor A: 1- drought stress imposed at flowering time ad

the

dep

the

fer

row

that

were

(DAP

of s

Blis

matt

Phys

fill

2- rainfall and complementary irrigation

Factor B: 1- commercial inoculant (no N fertilizer)

2- N fertilizer, 40 kg/ha

Factor C Genotype: 1- UW 21-58

2- UW 21-54

3- N81017

4- N81064

5- Mex.1213-2

6- Bayo Madero

7- II900-5-M-45

8- Pinto Nal.1

Planting was done following rain, when soil moisture was considered adequate for germination (Table 1, Appendix A). In order to establish the treatments, planting was done using a hoe to open rows and depositing the seeds and abundant commercial inoculant in the bottom of the furrow then immediately covering them with moist soil. Nitrogen fertilizer was applied in a similar fashion 10 cm apart from the seeded row. To create the stressed treatments, advantage was taken of the fact that the experimental site had a relatively strong slope (3 %). Rows were designed to be parallel to the slope and at 45 days after planting (DAP), black plastic stripes (0.4 X 6 m) were placed between the rows of stressed treatments.

At 45 DAP, a visual nodulation score as described by Rosas and Bliss (1986) (Table 2, Appendix A) was recorded and total plant dry matter taken at two sampling times 45 and 70 DAP, was collected. Physiologically related variables were measured at flowering and mid-pod filling stages which correspond with the initiation and 25 days after

c
w
d
l
we
at
we
Fi
int
sus

exp
moi
and
out,
coll
hour
weig
anal
fiel
agri
seas

drought treatment was imposed. The recorded variables were: leaf water potential (LWP), using the pressure chamber technique; leaf conductance (LC), using a diffusion porometer; leaf area index (LAI), with the use of a leaf area meter. The relative crop growth rate and leaf specific weight were also calculated. Leaf elongation in each treatment was determined after drought treatment was imposed by tagging three young leaves and recording the length of the central leaflet every day for two weeks. Leaf nitrogen content was determined by microKjeldahl procedure at 45 DAP. At physiological maturity, seed yield and yield components were recorded and a harvest index (HI) was calculated. The method of Fischer and Maurer (1978) (Appendix A) was used to calculate the drought intensity index (DII) for the site and the individual drought susceptibility index (DSI) per genotype.

Soil moisture was monitored regularly in six different plots in the experiment at four depths: 0-15, 16-30, 31-45, and 46-60 cm. The soil moisture content of each plot was recorded at two different depths: 0-15 and 16-30 cm on the same day that pressure bomb readings were carried out, at two different depths: 0-15 and 16-30 cm. Soil samples were collected, weighed and immediately placed into an oven at 110 °C for 24 hours. The soil moisture content was expressed as a percentage on dry weight basis (Table 3, Appendix A). All measured variables were analyzed, following the design used to distribute the treatments in the field, with the aid of the MSTAT microcomputer statistical package for agricultural sciences. Data on rain and temperature during the growing season are presented in Table 1 of Appendix A.

RESULTS AND DISCUSSION

In both experiments, genotype UW 21-58, which possessed an increased ability to fix atmospheric nitrogen (Bliss, 1985), was utilized as a check cultivar for comparison when looking at nitrogen fixation related variables.

Greenhouse experiment. In this experiment, results were recorded for samples taken at 25 DAP and emphasis was put on the variation of the 11 bean genotypes. Samples taken at 50 DAP were discarded due to *Rhizobium* contamination.

The genotypes A 411 and N81064 showed the highest and lowest values, respectively, for nodule fresh weight per plant. For plant dry matter, cultivar Dgo. 222 showed the highest value for this trait, whereas N81064 showed the smallest value (Table 2).

The activity of the enzyme dinitrogenase quantified by the acetylene reduction (AR) assay at 25 DAP is presented in Table 2. As we were mainly interested in the BNF ability of the bean genotypes, which accounted for most of the observed variation for AR, we will not present results for the treatments. Thus, on a per plant basis Lef-2-RB was the genotype which fixed more N; with respect to nodule specific activity, Lef-2-Rb, N81017 and the check cultivar UW 21-58 showed the highest values for this trait.

Values for phenotypic correlations between pairs of variables are presented in Table 3. Plant biomass showed a significant positive correlation with all variables studied. At this stage of development (25 DAP), nodule fresh weight was highly correlated with nodule specific activity. Nodule fresh weight values showed the highest r value when correlated to plant dry matter.

Table 2. Genotype average value for biomass per plant and nitrogen fixation related variables. East Lansing, MI. 1985

Genotype	Plant biomass(1)	Nodule fresh weight(2)	AR per plant/ hour(3)	Nodule specific activity(4)
UW 21-58	1.14 b@	410 bc@	3593 ab@	8.8
A 411	1.11 b	560 a	3336 abc	5.9
BAT 336	0.79 c	310 de	1837 e	5.9
N81017	1.00 b	370 bcd	3324 abc	9.0
N81064	0.75 c	270 e	1824 e	6.8
B76001	1.04 b	430 bc	2877 bcd	6.7
LEF-2-RB	1.04 b	440 bc	4140 a	9.4
Mex.1213-2	1.09 b	350 cde	2479 cde	7.1
Dgo-222	1.35 a	460 b	2524 cde	5.5
Bayo Madero	1.05 b	380 bcd	2303 de	6.0
II900-5-M-45	1.08 b	450 b	3202 bcd	7.1
Average	1.04	403	2859	7.1

1- g, average of 32 pots.
2- mg/plant, average 24 pots.
3- nm/plant/hour, average 24 pots.
4- nm/mg nodule tissue/plant/hour, average 24 pots.
@ Duncan's Multiple Range Test (0.05).

Table 3. Correlations between biomass per plant and nitrogen fixation variables. East Lansing, MI. 1985

	Nodule fresh weight	Nitrogenase activity per plant	Nodule specific activity (1)
Plant biomass g/plant	0.57**	0.36**	0.45**
Nodule fresh weight mg/plant	----	0.47**	0.82**
Nitrogenase activity per plant nm/p/h	----	----	0.45**

** highly significant (P<0.01).

(1) nm/mg nodule tissue/plant/h

Field experiment. In this experiment, the moisture stress treatment was not started until 45 DAP, thus analyses of variance for samples taken at 45 DAP included only the effects of nitrogen rate, genotype and their interaction (Tables 5, Appendix A).

The addition of 50 kg/ha of nitrogen fertilizer increased significantly the weight of all above-ground plant parts ($P<0.05$), thus, the growth of the plant was N limited. The effect of the genotype was significant only for root and stem dry weights ($P<0.05$). No significant effect was found for the nitrogen x genotype interaction (Table 5, Appendix A).

In Figure 1, total dry matter and dry matter of different plant parts under two nitrogen sources at 45 DAP are presented. The genotypes UW 23-61, Bayo Madero and Pinto Nal.1 showed a significant response to the added nitrogen fertilizer. Genotype I1900-5-M-45 gave the highest total dry matter (TDM) yield without added fertilizer. In the treatment without nitrogen fertilizer a commercial inoculant along with phosphorus fertilizer was uniformly applied to the whole experiment; thus, assuming a low N content in the soil, dry matter yield and total leaf nitrogen content under this treatment could be used as an indicator of BNF. In general, at this stage of development, the type III unadapted cultivars were superior in total dry matter yield to adapted type II cultivars under both nitrogen sources. Cultivar I1900-5-M-45 was outstanding under inoculation. Graham and Rosas (1977) previously reported the superiority in BNF of indeterminate type III growth habit versus type II cultivars.

It was noticed when digging roots in the sampled strata, that type III genotypes showed a much more branched root system than type II's.

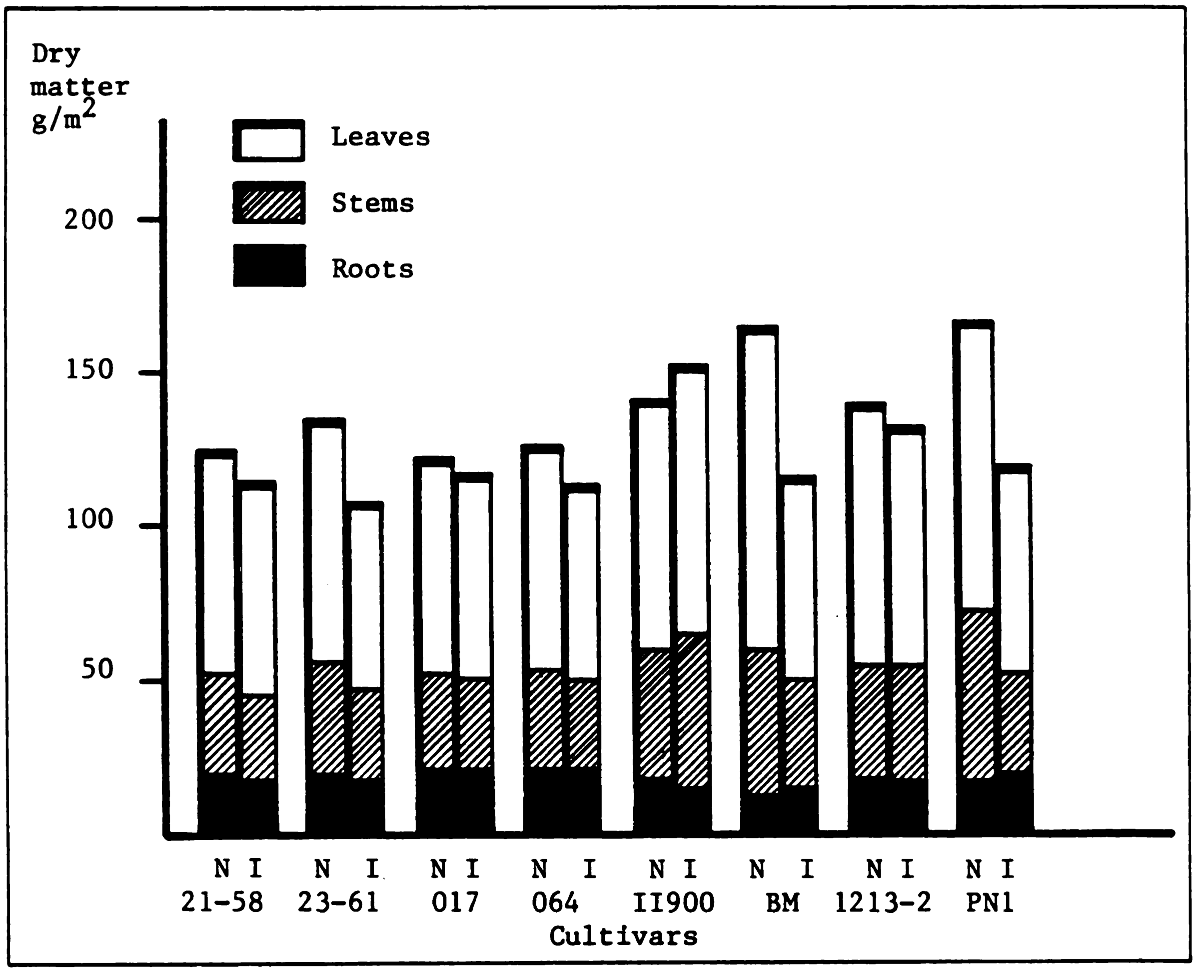


Figure 1. Dry matter of different plant parts of eight bean cultivars under two nitrogen sources (N=50kg/ha nitrogen, I=inoculated) at 45 days after planting. East Lansing, MI. 1985.

However, the latter genotypes showed a strong main root with few secondary roots going deep into the soil profile. Thus, it is likely that the root system of erect type II genotypes is more suited to support a taller plant under Michigan conditions; whereas the root system displayed by type III genotypes seems more suited to explore more soil volume, mainly in the upper soil strata. Probably this latter type of root system plays an important role in the adaptation of type III cultivars to sporadic rainfall patterns of the semiarid highlands of Mexico.

At this stage of development (45 DAP), the leaves accounted for approximately two-thirds of shoot biomass (Figure 1). In the analysis of variance for leaf dry weight, no significant difference was found between genotypes; however, a highly significant difference among genotypes was found for LAI. Therefore, it is clear that the genotypes possess different leaf specific weights (Table 4). In general, type III cultivars were superior to type II's for LAI.

With respect to leaf water status at this stage of development (45 DAP), genotype Bayo Madero showed the least negative leaf water potential (LWP), which was significantly different (LSD 0.05) from the rest of the genotypes (Table 4). The same genotype gave the smaller value for stomatal conductance. Since the moisture stress treatment had not been applied at this time in development, genotypic variations for these physiological variables were probably obtained in response to the relatively high temperatures (Table 1, Appendix A) observed at mid-day.

Analyses of variance for nodule score and some physiological variables did not show significant differences for the effect of nitrogen rates nor its interaction with genotypes (Table 5, Appendix A).

Table 4. Average values for physiological related variables of eight bean cultivars under two nitrogen sources at 45 days after planting. East Lansing, MI. 1985

Genotype	LAI*	Stomatal Conduct. cm/s	LWP* bars	LSW* mg/cm	LAR*	Root/ Shoot
UW 21-58	1.41	0.278	-6.3	4.77	122.3	0.202
UW 23-61	1.28	0.239	-7.2	5.01	111.9	0.211
N81017	1.15	0.204	-6.7	5.76	97.6	0.226
N81064	1.31	0.209	-6.2	5.15	110.2	0.228
I1900-5-M-45	2.32	0.196	-6.1	3.69	157.1	0.138
Bayo Madero	1.82	0.168	-3.8	4.97	124.6	0.119
Mex.1213-2	1.84	0.209	-6.4	4.46	134.1	0.158
Pinto Nal.1	2.14	0.272	-6.1	3.82	147.4	0.151
LSD 0.05	0.51	____	2.3	____	32.3	0.041

* LAI = leaf area index.
LWP = leaf water potential.
LSW = leaf specific weight.
LAR = leaf area ratio.

Table 5. Nodule score and total leaf nitrogen content of eight bean genotypes grown under two nitrogen sources at 45 days after planting. East Lansing, MI. 1985

	Nodule Score (1)		Leaf Nitrogen Cont. (2)	
Genotype	Inoculant	N fertilizer	Inoculant	N fertilizer
UW 21-58	3.0	2.2	2.8	2.9
UW 23-61	1.5	1.5	2.5	3.4*
N81017	2.2	2.5	2.6	3.0*
N81064	1.5	1.8	2.8	3.3*
I1900-5-M-45	2.3	3.0	3.5	3.5
Bayo Madero	2.0	1.5	2.9	4.4*
Mex.1213-2	2.3	2.5	3.5*	3.3
Pinto Nal.1	2.7	2.3	2.8	3.9*
Average	2.2	2.1	2.9	3.5*

* LSD 0.05 between nitrogen sources.

(1)- Following Rosas and Bliss (1986).

(2)- Percentage on a dry weight basis.

Thus, average genotypic values across treatments are presented in Table 5. Scores for nodule mass were determined by comparing all cultivars to UW 21-58 check. Cultivar II900-5-M-45 displayed maximum average value for nodule score. Genotype N81017 and all type III cultivars were statistically similar to UW 21-58.

A second set of samples was taken at 70 DAP, stage R5 for adapted cultivars, which was 25 days after the moisture stress treatment was applied. The dry matter yield of different plant parts at 70 DAP is presented in Figure 2. The data were analized for plant grown under two different water regimes. A significant effect of moisture treatment was observed ($P<0.05$) for the dry weight of stems, leaves and developing pods; a significant effect of the genotypes for the same variables and dry weight of roots was observed (Table 6, Appendix A). None of the interactions among evaluated factors was significant.

With the exception of genotype UW 21-58, all genotypes showed a significant reduction in dry matter yield under stress (Figure 2). At this stage of development, type II cultivars were reallocating dry matter into developing pods at a much higher rate than type III cultivars (II900-5-M-45 and Bayo Madero) which started flowering about the same time as adapted cultivars. Cultivars Mex.1213-2 and Pinto Nal.1 did not start flowering at this time. Unadapted genotypes showed a striking variation in daylength sensitivity with II900-5-M-45 being the least sensitive (Table 6). Daylength sensitivity of unadapted genotypes was expressed as an increase in the number of days needed to reach R3 stage (50 % bloom) and a decreasing rate of dry matter partitioning into developing pods in those genotypes which reached R3 stage of development at the same time as adapted genotypes.

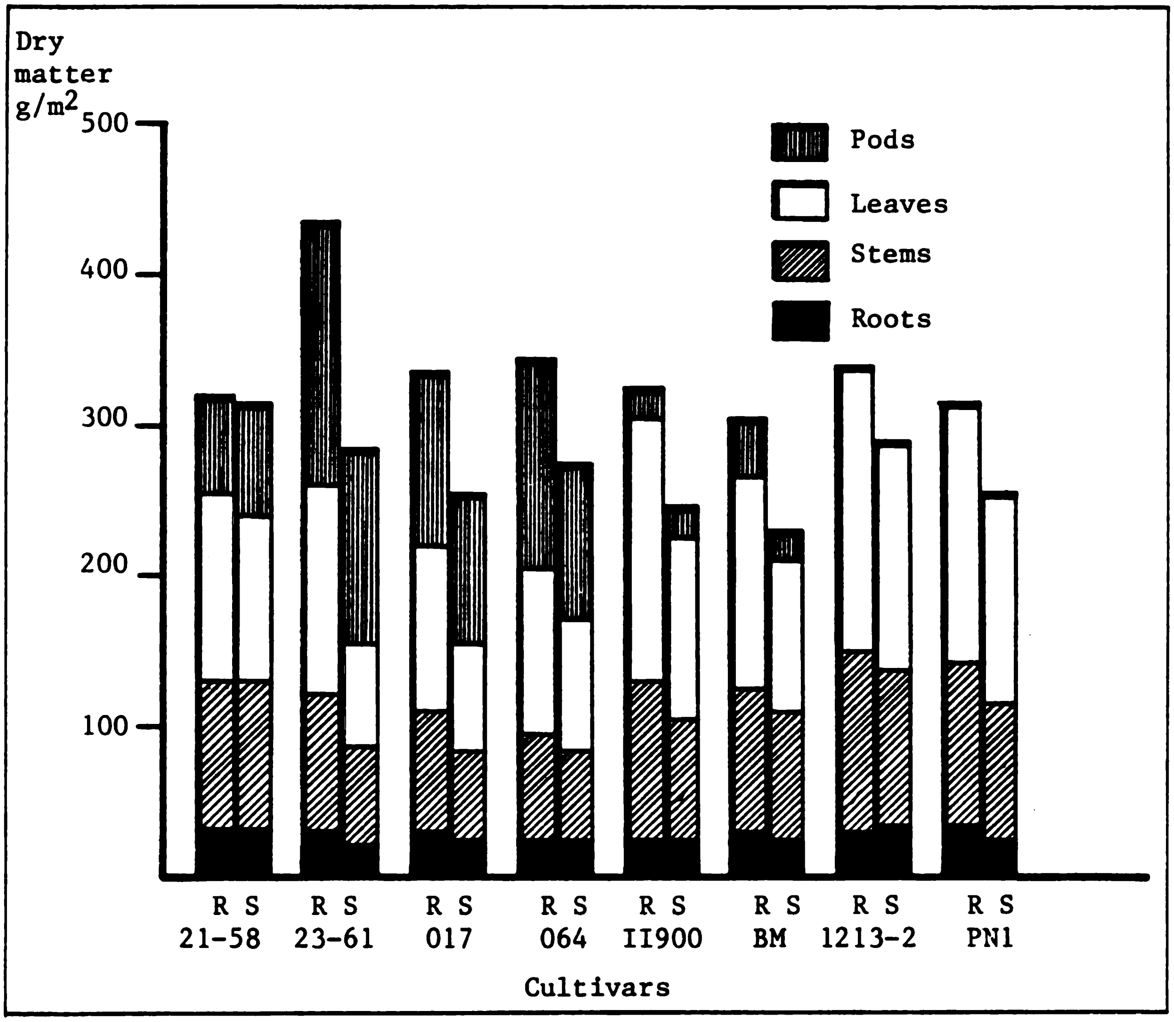


Figure 2. Dry matter of different plant parts of eight bean cultivars under two moisture regimes (R=rainfed, S=water stressed) at 70 days after planting. East Lansing, MI. 1985.

Higher yields of total dry matter of type III cultivars seemed associated with large plant growth, as measured at 45 DAP. This was associated with a slower reproductive development (Figure 2) where the allocation of assimilates to the developing pods procceded at a reduced rate as compared to type II cultivars.

Leaf area index of all genotypes, except UW 21-58, was significantly reduced under stress. No response of root/shoot ratio was observed for water and nitrogen treatments; however, the effect due to genotype was highly significant ($P<0.01$). Observed values for root/shoot ratio of different genotypes at this stage of development (70 DAP), were smaller than those observed at 45 DAP (Table 6).

Daily measurements taken of central leaflet length per cultivar are presented in Table 7. Central leaflet length measurements on all cultivars were initiated at 50 DAP, five days after black plastic stripes were placed between the rows to establish the moisture stress treatment. Under stress, genotypes N81017 and II900-5-M-45 showed the highest accumulated values for leaflet elongation. A significant difference ($P<0.05$) between stress and nonstress treatments was found for this trait during most of the days that measurements were recorded.

The above results are in agreement with findings reported for other legume crops, particularly soybeans and field beans (Karamanos, 1978; Myers et al., 1986). A relationship between LWP, leaf area expansion, and relative growth rate was demonstrated by Karamanos (1978). The relationship of leaf enlargement to turgor prompted Boyer and McPherson (1975) and Hsiao and Acevedo (1974) to propose that leaf elongation rate could be used as a negative index of drought sensitivity in plants.

Table 6. Number of days to flowering, LAI and root/shoot ratio of eight bean cultivars growing under two moisture treatments at 70 days after planting. East Lansing, MI. 1985

Genotype	Days to Flowering	LAI		Root/ shoot ratio
		Rainfed	Stressed	
UW 21-58	52	3.24	3.02	0.107
UW 23-61	46	3.21	1.68*	0.071
N81017	48	2.81	1.75*	0.098
N81064	46	2.43	2.04*	0.103
II900-5-M-45	51	4.21	3.36*	0.112
Bayo Madero	46	2.82	2.33*	0.125
Mex 1213-2	90	4.48	3.87*	0.134
Pinto Nal.1	90	3.99	3.44*	0.133
LSD 0.05	1	0.851	0.851	0.093

* LSD 0.05 between moisture treatments = 0.275

Table 7. Central leaflet length in mm of eight bean genotypes under two moisture regimes. East Lansing, MI. 1985

	Days after planting								
Genotype	51	52	53	54	55	56	57	58	59
Rainfall									
UW 21-58	7.4	14.4	22.5	33.2	38.4	41.9	46.6	51.7	54.7
UW 23-61	6.0	14.2	22.8	29.9	32.1	32.7	34.2	36.3	38.5
N81017	7.1	16.5	26.7	36.1	39.7	41.2	44.1	47.5	49.1
N81064	6.0	13.7	20.7	30.9	34.2	34.6	38.7	42.0	44.3
II900-5-M-45	5.7	11.9	23.2	32.2	37.6	38.2	44.1	48.7	53.3
Bayo Madero	4.3	9.9	15.7	22.5	24.5	24.5	24.9	28.4	30.4
Mex.1213-2	5.3	12.2	18.5	25.8	28.2	28.2	30.1	33.5	35.8
Pinto Nal.1	4.2	12.2	20.5	26.7	30.5	30.5	32.7	36.0	38.9
Average	5.7	13.1	21.3	29.7	33.1	34.0	36.9	40.5	43.1
Stress									
UW 21-58	4.7	9.15	15.8	23.2	25.6	26.0	29.1	33.0	35.3
UW 23-61	4.3	9.50	13.3	18.4	19.5	19.5	20.0	20.8	21.6
N81017	6.4	11.5	16.3	22.9	29.1	31.6	34.8	36.9	38.4
N81064	5.4	10.6	17.0	25.2	26.9	27.8	29.8	33.0	34.1
II900-5-M-45	4.7	9.90	16.3	24.3	28.1	28.9	32.7	36.8	40.4
Bayo Madero	4.4	6.75	10.1	16.2	17.8	17.8	18.8	21.3	24.1
Mex.1213-2	3.2	6.60	11.1	13.9	17.5	18.1	19.2	22.7	24.8
Pinto Nal.1	4.1	7.30	12.1	16.5	18.5	18.5	20.0	23.0	25.3
Average	4.6	8.9	14.0	20.1	22.9	23.5	25.5	28.4	30.5

Yield and yield components. Results do not include two of the unadapted cultivars, Mex.1213-2 and Pinto Nal.1, because they did not produce seed. These two genotypes started flowering at 90 DAP and were killed by freezing temperatures in late September. They proved to be highly sensitive to the extended daylength of the Northern latitudes.

The analysis of variance for seed yield showed significant differences for moisture ($P<0.05$) and genotype ($P<0.01$) effects. No significant effects were detected for nitrogen source or any of the interactions (Table 6, Appendix A). Therefore, in tables summarizing those results, data related to nitrogen rates is not presented. An average yield reduction of 27% was observed when the genotypes were subjected to mild drought stress, equivalent to a drought intensity index of 0.27 (Fischer and Maurer, 1978). In table 8, individual seed yields per genotype under both moisture conditions are presented, as well as the reduction per cultivar in percentage, arithmetic and geometric means and the drought susceptibility index of Fischer and Maurer (1978).

Genotypes UW 23-61 and II900-5-M-45 showed the highest yield reductions under stress. When looking at the arithmetic mean values, II900-5-M-45 together with UW 21-58, UW 23-61 and N81017 were statistically similar; however, the former showed the highest value for the geometric mean, which is considered more appropriate for comparison of genotypes under stress and non-stress conditions (Samper and Adams, 1985).

The percent seed yield reduction of a genotype when evaluated in favorable and unfavorable environments can mislead the interpretation of results (Table 8). Since different genotypes possess different yield

Table 8. Seed yield under rainfed and stressed conditions, reduction in percentage, arithmetic and geometric means and drought susceptibility index (DSI). East Lansing, MI. 1985

Genotype	Yield g/m^2		Reduction	Arith.	Geom.	
	Rainfed	Stressed	%	mean	mean	DSI(1)
UW 21-58	213*	161	24	187	185	0.81
UW 23-61	229*	117	49	173	164	1.63
N81017	181	163	10	172	172	0.33
N81064	136	125	8	131	130	0.27
II900-5-M-45	275*	150	46	213	203	1.51
Bayo Madero	166*	121	27	143	142	0.90
Average	200	139*	27	170	166	0.91

* LSD 0.05 between water regimes.

(1) Drought suscep. index of Fischer and Maurer, 1978; Appendix A.

potentials. Those genotypes which do not show a high reduction of yield under stress, like N81064, are not necessarily drought resistant. Since such genotypes possess a limited yield potential even under non-stress conditions as demonstrated by the arithmetic and geometric mean yield values, caution must be exercised when utilizing low percent seed yield reduction as a criterion for drought tolerance.

Within the adapted cultivars, N81017 showed a better than average seed yield under stress and an intermediate value for both the arithmetic and geometric means, and a low value for the drought susceptibility index. Therefore, those results would indicate that N81017 is the more drought tolerant of the evaluated adapted cultivars, which is in agreement with the finding of Samper (1984) and Samper et al. (1984).

Briefly, in using any criteria to select or decide which genotype(s) shows the maximum degree of stress tolerance, genotypes with values above the mean under both stress and nonstress conditions are the ones to select.

Moisture stress significantly reduced all the yield components ($P<0.05$) and the effect of genotype also had a significant effect on the yield components (Table 6, Appendix A). Interestingly not all the genotypes responded in the same way to the stress. For instance, cultivars N81017 and N81064 showed the same number of pods per m^2 and the same seed weight, but they differed significantly in the number of seeds per pod (Table 9). As a consequence of their difference in this yield component, they were significantly different for final seed yield per m^2. In the case of II900-5-M-45 and UW 23-61, which showed the highest percentage yield reduction under stress; the number of pods per

Table 9. Yield components of six bean genotypes under two moisture treatments. East Lansing, MI. 1985

Genotype	Pods/m^2		Seeds/pod		100 seed weight.	
	Rainfed	Stressed	Rainfed	Stressed	Rainfed	Stressed
UW 21-58	224	192	4.3	3.7	22.0	22.4
UW 23-61	290	200*	4.0	3.4	19.5	17.4*
N81017	206	190	4.1	4.0	21.2	21.2
N81064	220	192	3.1	3.2	20.1	20.4
II900-5-M-45	235	156*	4.7	3.8	25.1	25.3
Bayo Madero	162	134	2.5	2.4	40.2	37.0*
Average	223	177*	3.8	3.4	24.7	23.9*
LSD 0.05	63	63	---	---	1.5	1.5

* LSD (0.05) between moisture treatments.

m^2 was the yield component most affected by the stress. UW 23-61 also showed a significant reduction in seed weight. Finally, Bayo Madero had a significant reduction in seed yield due to a decrease in seed weight (Table 9).

The observed variability of the yield components between genotypes in response to the imposed mild water stress in this experiment could be due to the differences in timing and duration of different phenological phases of this small sample of genotypes in conjunction with the timing and intensity of the moisture stress. In general, the number of pods per m^2 was the component most affected by the stress. These findings are in agreement with previous reports (Robins and Domingo, 1956; Stoker, 1973; Stansell and Smittle, 1980; Bonnano and Mack, 1983).

A modified harvest index (HI) was calculated by dividing the economic yield by the TDM at physiological maturity which did not include the weight of the leaves. Cultivars N81064 and Bayo Madero showed the smallest values for this variable, and the latter was the only genotype showing a significant decrease for this trait under stress.

CONCLUSIONS:

1. Evaluated genotypes showed variation for BNF related traits and some of them proved to be as good fixers as the check UW.21-58, i.e. Lef-2-RB, II900-5-M-45, and N81017.

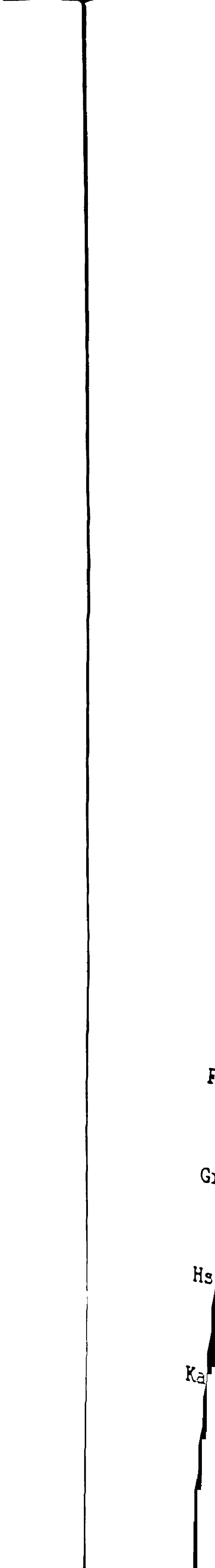
2. Significant differences among genotypes grown under stress and non-stress treatments were observed for seed yield and yield components as

well as for the different morphological and growth related variables recorded.

3. Genotypes from two different genetic backgrounds, namely adapted and unadapted to Michigan conditions, exhibited different morphological characteristics and they probably possess different mechanisms to partially avoid drought effects.

4. Mexican type III cultivars were photoperiod sensitive in varying degrees, as indicated by the number of days to initiate flowering and an extended reproductive phase. A relationship between larger total dry matter accumulation of unadapted type III genotypes seems to be associated with a slow development or partitioning into reproductive structures.

5. The results in this study indicated that genotypes N81017 and II900-5-M-45, are drought tolerant and possess a superior ability for BNF.


F
Gr
Hs
Ka

REFERENCES

Albretch, S.L., Bennet, J.M. and K.J. Boote. 1984. Relationship of nitrogenase activity to plant water stress in field-grown soybeans. Field Crops Res. 8:61-71

Beadle, C.L. and S.P. Long. 1985. Photosynthesis - is it limiting to biomass production ? Biomass 8:119-168

Bliss, F.A. 1985. Breeding for enhanced dinitrogen fixation potential of common bean (*Phaseolus vulgaris* L.). In: P.W. Ludden and J.E. Burris (Eds.). Nitrogen Fixation and CO_2 metabolism. Proc. 14th Steenbock Symposium, 17-22 June 1984, University of Wisconsin, Madison. Elsevier Science Publishing Co., pp. 303-310

Bonanno, A.R., and H.J. Mack. 1983. Yield components and pod quality of snap beans growth under differential irrigation. J. Amer. Soc. Hort. Sci. 105:869-873

Boyer J.S. and H.G. Mc.Pherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23

Elizondo-Barron, J. 1987. Characteristics related to yield of dry bean (*Phaseolus vulgaris* L.) under water stress conditions. M.S. Thesis Michigan State University, East Lansing p. 73

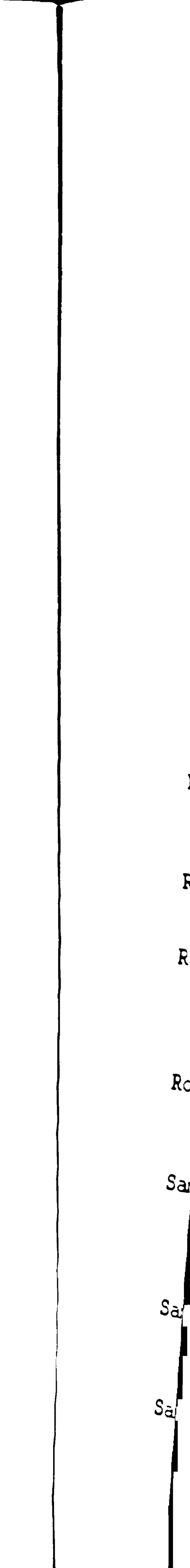
Felix, J.F., Obaton, M., Messiaen, C.M. and L. Salsac. 1981. Nitrate reductase and nitrogenase activities of common beans (*Phaseolus vulgaris* L.) from different geographic locations. Plant and Soil 63:427-438

Fischer, R.A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:277-317

Graham, P.H., and J.C. Rosas. 1977. Growth and development of indeterminate bush and climbing cultivars of *Phaseolus vulgaris* L. inoculated with *Rhizobium*. J. Agric. Sci. Camb. 88:503-508

Hsiao, T.C. and E. Acevedo. 1974. Plant responses to water deficits, water use efficiency, and drought resistance. Agr. Meteorol. 14:59-84

Karamanos, A.J. 1978. Water stress and leaf growth of field beans (*Vicia faba* L.) in the field: leaf number and total leaf area. Ann. Bot. 42:1393-1402


R
R
Ro
Sa
Sa
Sa

McFerson, J. 1983. Genetic and breeding studies of dinitrogen fixation in common bean, (Phaseolus vulgaris L.). Ph. D. Thesis, University of Wisconsin, Madison p. 147

Myers, O. Jr. Yopp, J.H., and M.R.S. Krishnamani. 1986. Breeding soybeans for drought resistance. In: J. Janick (Ed.), Plant Breeding Reviews Volume 4. Avi Publishing Co. Inc. pp. 203-243

Nutman, P.S. 1981. Hereditary host factors affecting nodulation and nitrogen fixation. In: A.H. Gibson and W.E. Neaton (Eds.), Current Perspectives in Nitrogen Fixation, Elsevier / North Holland Biomedical Press, Amsterdam. pp. 194-204

Pacowsky,R.S., Bayne, H.G., and G.J. Bethlenfalvay. 1984. Symbiotic interactions between strains of Rhizobium phaseoli and cultivars of Phaseolus vulgaris L. Crop Sci. 24:101-105

Piha, M.I., and D.N. Munns. 1987. Nitrogen fixation potential of beans (Phaseolus vulgaris L.) compared with other grain legumes under controlled conditions. Plant and Soil 98:169-182

Rennie, R.J., and G.A. Kemp. 1981a. Selection for dinitrogen-fixing ability in Phaseolus vulgaris L. at two low-temperature regimes. Euphytica 30:87-95

Rennie, R.J., and G.A. Kemp. 1981b. Dinitrogen fixation in pea beans (Phaseolus vulgaris) as affected by growth stage and temperature regime. Can. J. Bot. 59:1181-1188

Robins, J.R., and C.E. Domingo. 1956. Moisture deficits in relation to the growth and development of dry beans. Agron. J. 48:67-70

Rosas, J. 1983. Partitioning of dry matter, nitrogen fixation, and seed yield of common bean (Phaseolus vulgaris L.) influenced by plant genotype and nitrogen fertilization. Ph. D. Thesis, University of Wisconsin, Madison p. 127

Rosas, J.C. and F.A. Bliss. 1986. Host plant traits associated with estimates of nodulation and nitrogen fixation in common bean. Hortscience 21:287-289

Samper, C. 1984. Effects of water stress imposed at mid-pod filling upon yield and dry matter partitioning in dry beans (Phaseolus vulgaris L.). M.S. Thesis, Michigan State University, East Lansing p. 131

Samper, C., Adams, M.W., Hanson, A.D., and E. Watt. 1984. Contribution of stored assimilates to the seed following a drought stress in dry beans. Agronomy Abstracts 76:87

Samper, C. and M.W. Adams. 1985. Geometric mean of stress and control yield as a selection criterion for drought tolerance. Ann. Rept. Bean Improv. Coop. 28:53-54

Schubert, K.R., and H.J. Evans. 1976. Hydrogen evolution: A major factor affecting the efficiency of nitrogen fixation in nodulated symbionts. Proc. Natl. Acad. Sci. (USA) 73:1207-1211

Sprent, J.I. 1981. Nitrogen fixation. In: L.G. Paleg and D. Aspinall (Eds.), Physiology and Biochemistry of Drought Resistance in Plants. Academic Press Australia pp.131-143

Stansell, J.R., and D.A. Smittle. 1980. Effects of irrigationregimes on yield and water use of snap bean (*Phaseolus vulgaris* L.). J. Amer. Soc. Hort. Sci. 105:869-873

St. Clair, D.A. 1986. Segregation, selection, and population improvement for ^{15}N-determined dinitrogen fixation ability in common beans (*Phaseolus vulgaris*L.). Ph. D. Thesis, University of Wisconsin, Madison p. 90

Stoker, R. 1974. Effect on dwarf beans of water stress at different phases of growth. N. Z. J. Exp. Agric. 2:13-15

Westerman, D.T., and J.J. Kolar. 1978. Symbiotic N_2 (C_2H_2) fixation by bean. Crop Sci. 18:986-990

Zablotowick, R.M., Focht, D.D. and G.H. Cannell. 1981. Nodulation and nitrogen fixation of field grown cowpeas as influenced by well irrigated and droughted conditions. Agron. J. 73:9-12

CHAPTER 2

SELECTION IN SEGREGATING BEAN POPULATIONS FOR DROUGHT TOLERANCE IN THE FIELD.

INTRODUCTION

There has been comparatively little breeding for drought tolerance in pulse crops. This is probably due to the complexity of the problem and the difficulty of measuring traits identifying drought tolerant genotypes. With the exception of soybeans, most pulse crops are not important in developed nations where much of the work on drought tolerance is conducted.

During the last decade, research has been conducted with the aim of identifying the physiological and/or morphological plant attributes related to drought tolerance, attributes which could be readily used as selection criteria for breeding for drought tolerance in crops. So far, the more reliable approach to select for drought tolerance is the assessment of total biomass or economic yield produced under stress in the field (Hurd, 1976; Parsons, 1979; Quisenberry, 1982; Singh and White, 1988).

Simmonds (1979) indicated that drought tolerance of well adapted varieties seems certain but he pointed out that it is difficult to give clear-cut examples, largely because such adaptation usually results from selection for average performance over seasons rather than for specific selection for drought tolerance *per se*. A clear example of the above statement is the reported performance of recently released soybean cultivars in Illinois (Boyer et al., 1980), which display a degree of drought tolerance without having been specifically bred for tolerance, but rather they were selected on the basis of their performance in multilocational trials.

A variety of approaches have been developed to identify drought resistance in crops (Clarke and Townley-Smith, 1984). Some of the most popular include the use of the pressure bomb and diffusive resistance porometers. An excellent review on methods to determine plant water status and its applicability to physiological studies was presented by Turner (1981). However, most of these approaches involve tedious procedures and/or sophisticated instrumentation that may have limited applicability for field comparisons involving numerous genotypes. In addition to leaf water potential and osmotic potential, leaf water status can be evaluated by indices calculated from the difference between turgid and fresh weight of leaves (Turner, 1981; Clarke and Townley-Smith, 1984).

Water loss from excised leaves is another method which has been used to assess genotypic differences in water retention capacity of plant crops. In wheat, Dedio (1975) suggested that water retention capacity is simply inherited and that the ability to retain water is controlled by dominant gene action.

In cowpea, Walker and Miller (1986) found that the leaf water retention technique, used either in the greenhouse or in the field, was able to differentiate drought tolerant from drought sensitive genotypes even in the absence of water stress. Working with common bean, Mkandawire (1987) combined data from one maize-bean intercropping and one Water Use Efficiency (WUE) experiment but did not find a significant relationship between total biological yield and leaf water retention capacity. However, cultivar differences in capacity to retain water were noticed.

Yield under drought stress (and under non-stress) is a complex terminal outcome of growth to which there are probably diverse and interrelated paths. Two genotypes of similar yield may achieve their final yield by different routes. Plant breeding affects yield through the adjustment of biomass, or partitioning, or both; however, it is surprising how poor is our information on the relative importance of these two major components of yield (Simmonds, 1979). White (1987) has demonstrated that under tropical conditions at CIAT, the bean crop always seems to show strong limitations on assimilate availability while sink demand is usually adequate.

In the current research, it is hypothesized that high yielding bean cultivars under water stress are capable of remobilizing reserve assimilates from storage organs. It was previously demonstrated, with the use of an iodine-potassium iodide starch indicator (IKI), that genotypic differences for levels of stored starch in different plant parts exists in common bean (Adams et al., 1978). Later, Sebasigari (1981) demonstrated that some legume crops with high seed growth rates were correlated with a decrease in the level of non-structural carbohydrates in storage organs. More recently, Samper et al., (1984) have shown evidence of differential remobilization in two bean genotypes under water stress. The higher yielding genotype under stress displayed greater ability to remobilize stored assimilates.

Therefore, a simple, non-destructive technique to evaluate bean genotypes under stress could make use of an IKI solution applied to reserve organs like the root and/or the stem at physiological maturity.

This technique is considered here under the assumption that genotypes showing the smallest or no starch remaining in those organs are good remobilizers under water stress. A possible weak point of this technique is that genotypes which produce more assimilates than those demanded by the sink, and still produce acceptable yields, could be misclassified as inferior remobilizers.

The study reported here was intended to evaluate during 1985 a group of 248 F4 families for drought tolerance and to select promising genotypes. The number of families was then further reduced in 1986 and a group of 113 F6 families was tested following the same objective. The F4 families were originally obtained from selection conducted in the greenhouse on the basis of a visual nodule score, a trait related to BNF ability (Rosas, 1983).

MATERIALS AND METHODS

Plant material. In order to obtain the F4 families, a group of 13 genotypes was selected based on previous performance as either drought tolerant or demonstrating improved nitrogen fixation. These were crossed in specific combinations in the summer of 1983 at the International Center for Tropical Agriculture (CIAT), Cali, Colombia (Table 1). Eleven F1 hybrids were space planted in an unreplicated plot nursery in Sinaloa, Mexico during the winter of 1983-84. A population of 200 F2 seeds per cross and the genotype UW 21-58, considered as a check, were grown in the greenhouse facility of Michigan State University, East Lansing, MI., during the fall of 1984. Forty F2 and 10 UW 21-58 seeds were each planted in flat aluminum containers filled with pure silica sand as growth medium. Seeds were inoculated by using a commercial

Table 1. List of bean genotypes used as parents and crosses made at CIAT* in 1983. East Lansing, MI. 1984

No.	Genotype	Source*	Seed type	Growth habit**
1	N81017	MSU	navy	II
2	N81064	MSU	navy	II
3	B76001	MSU	black	II
4	Dgo.222	INIFAP	white	III
5	Bayo Madero	INIFAP	bayo	III
6	II900-5-M-45	INIFAP	striped	III
7	Mex.1213-2	INIFAP	pinto	III
8	Lef-2-RB	INIFAP	striped	III***
9	UW 23-61	UW	navy	II
10	UW 21-54	UW	black	II
11	UW 21-58	UW	black	II
12	A 411	CIAT	brown	II
13	BAT336	CIAT	cream	II

Cross code	Parents		
8	N81017	x	Lef-2-RB
9	N81017	x	II900-5-M-45
25	N81064	x	Dgo-222
31	UW 21-54	x	Dgo-222
34	B76001	x	UW 21-54
38	UW 21-58	x	Mex.1213-2
39	UW 21-58	x	II900-5-M-45
41	UW 21-58	x	A 411
44	BAT 336	x	UW 21-58
48	UW 23-61	x	Bayo Madero
51	UW 23-61	x	Mex.1213-2

* CIAT = International Center for Tropical Agriculture, Columbia
MSU = Michigan State University
INIFAP = National Institute for Forest and Agriculture Research, Mexico
UW = University of Wisconsin

** Type II = indeterminate-bush, erect stem and branches
Type III = indeterminate-bush, prostrate main stem and branches

*** Type II in Mexico

inoculant and irrigated with a nitrogen free nutrient solution and/or tap water as needed.

A visual mild selection was practiced at 20 DAP by taking one seedling at a time and comparing it to the check genotype for nodule mass (nodule number and nodule size). Those plants that had at least a similar amount of nodule tissue as the check were saved and transplanted, each in a 20 x 30 cm clay pot. For comparison, a small number of plants which showed poor nodulation were also saved. Approximately 50 plants/cross were kept and their seeds were planted as an F3 family during the winter of 1984-85. In this generation, selection was practiced between families and individual plants within selected families were scored following the procedure previously outlined. Again, approximately 50 plants per cross were saved and transplanted as before. At the R3 stage, after the plants were considered to be well established, water was withheld for a 5 day period. Plants showing severe wilting symptoms were discarded. The retained plants were allowed to recover and set seed.

Different numbers of plants per cross were kept for further evaluation and from this stage forward, they were handled as families. In total, 300 families were retained. Here, it is convenient to clarify that some of the crosses were poorly represented, not because they were poor in nodulation but because they were highly photoperiod sensitive.

Experiment 1985. 246 F4 families and 10 parents were planted on a Capac fine loamy soil (mixed mesic, Glossoboric Hapludolfs) (USAD, Soil Conservation Service) in June 1985. Planting was done under the rain-out shelter of the bean program at the Crop Science Research facility of Michigan State University (MSU), East Lansing, MI. Planting followed rain when the soil moisture was considered adequate to allow crop establishment. No fertilizer was used and a commercial inoculant was applied to the seeds. From 25 DAP onward, the rain-out shelter was used to avoid rains during the remainder of the growing season.

Entries were distributed in the field by using a Simple Lattice Design (16 x 16) in small row plots of 50 x 50 cm. Soil moisture was regularly monitored at two different soil depths, 0-15 and 16-30 cm. Soil samples were collected, weighed, and immediately placed in an oven at 110 °C for two days. Soil moisture content was expressed as a percent on a dry weight basis (Table 1, Appendix B). Climate data during the growing season are presented in Table 4 of Appendix A.

Recorded data and procedures are outlined in table 2.

Experiment 1986. The F5 selections from the preceding experiment were grown at Iguala, Mexico, during the winter of 1985-86. No selections were made in this generation.

One hundred twenty one entries, consisting of 113 F6 families and eight parents, were planted at the Crop Research facility of MSU in small row plots (62 x 50 cm) in 1986. A simple Lattice Design (11 x 11) was used to randomize entries under the rain-out shelter. In this year, a similar planting was made adjacent to but outside the rain-out shelter which was sprinkler irrigated as needed. Planting of these two plots was done on June 16 and 17, 1986, respectively. With the exception of leaf nitrogen concentration, recorded data were the same as in the 1985 experiment, and additional data on the number of seeds per pod and 100 seed weight was collected. Soil moisture was again monitored and data are presented in Table 2 (Appendix B). Climatological data during the growing season are reported in Table 4 of Appendix B.

Table 2. Recorded data and procedure. East Lansing, MI. 1985

FLOW : No. of days from planting to flowering, recorded when 50 % of the plants in a plot had at least one flower open.

PHYMA : No. of days from planting to physiological maturity, recorded when pods lose their pigmentation and begin to dry.

TDM : Total dry matter/m^2, calculated after harvested plants were oven dried.

PODS : No. of pods/m^2, calculated by counting the total No.of pods with at least one normal seed per pod.

SEEDS : No. of seeds per pod, calculated from 50 pods per plot at physiological maturity.

SEWT : 100 seed weight in grams.

YIELD : Seed yield g/m^2.

HI : Harvest index, calculated by dividing seed yield by total dry matter.

LENIT : Leaf nitrogen concentration, determined by micro-Kjeldhal analysis on two leaves per plot at R4 stage.

LWC : Leaf water content, determined at R4 stage by excising two full expanded leaves and recording the difference between their fresh and oven dry weights.

LWRC : Leaf water retention capacity, determined at R4 stage by excising two leaves per plot and immediately weighing and placing them at normal room temperature, and weighing them at 24 hours after excision and after drying for 72 hours.

IKI : IKI visual score, determined at physiological maturity by cutting the base of stem and using two or three drops of an IKI solution prepared as described by Adams et al. (1978). Scale from 1-5, 1= no starch, 5= abundant starch.

Analyses of variance for all recorded data were performed with the aid of MSTAT, a microcomputer statistical package for agricultural sciences.

RESULTS

The rainout shelter used to conduct this research was built on a Capac soil. This class of soil characteristically has the soil water table close to the surface during part of the year. In this case, the soil water table level rose at the beginning of the fall. This rise of the water table was associated with the frequency and amount of rainfall in the surrounding area at that time of the year. During both years, 1985 and 1986, the bean genotypes tested were considered to be under at least a mild drought stress at the R3 and R4 stages of development (Tables 1 and 2, Appendix B).

Experiment 1985. The genotypes were significantly different for all the recorded variables, but relatively high coefficients of variation were obtained for most of the variables (Table 3, Appendix B). With the exception of LWC, average values for all variables showed a wide range in variation (Table 7, Appendix B). The range for seed yield extended from genotypes showing values as low as 20 g/m^2 to genotypes with yields higher than 250 g/m^2. It is important to indicate that a few of the low-yielding genotypes performed poorly because of photoperiod sensitivity not because of drought treatment. These genotypes started flowering late in the season and were not killed by freezing temperatures because they were protected by the rainout shelter. At this late time in development, photoperiod sensitive cultivars had been already released from the drought stress by the rising of the soil water table in the adjacent soil profiles.

A frequency distribution for seed yield and biomass under stress is presented in Figure 1. This figure shows again the wide range in response to the effects of drought stress and other nondefined factors of the environment. Similar response was observed for seed yield and biomass. In Figure 1, the relative position of the parents N81064 and UW 21-54 is indicated (by position of *); among the parents, these two were the lowest and highest yielder, respectively. It was also noticed that some of the segregating families produced higher yields than the top yielding parent. Briefly, 22 F4 families were superior to the general mean value by more than one standard deviation, and 16 of them displayed values two standard deviations above the mean. Thus, clearly, experimental genotypes showed variation for seed yield under drought stress and some of them showed an ability to produce relatively well under the drought stress imposed in this experiment.

The matrix of simple correlation values between pairs of variables is presented in Table 3. Seed yield, showed a significant association with TDM, and also with number of pods/m^2 and HI; this was expected since all of these traits partially contribute to the same end product. TDM was significantly and positively correlated to the IKI score and number of days to flowering and physiological maturity, whereas HI showed a significant and negative association with the same traits. With the exception of a relatively important negative association between LWC and HI, in general, LWC, LWRC and leaf nitrogen concentration (LNC) did not show a relationship among themselves nor with the rest of the variables.

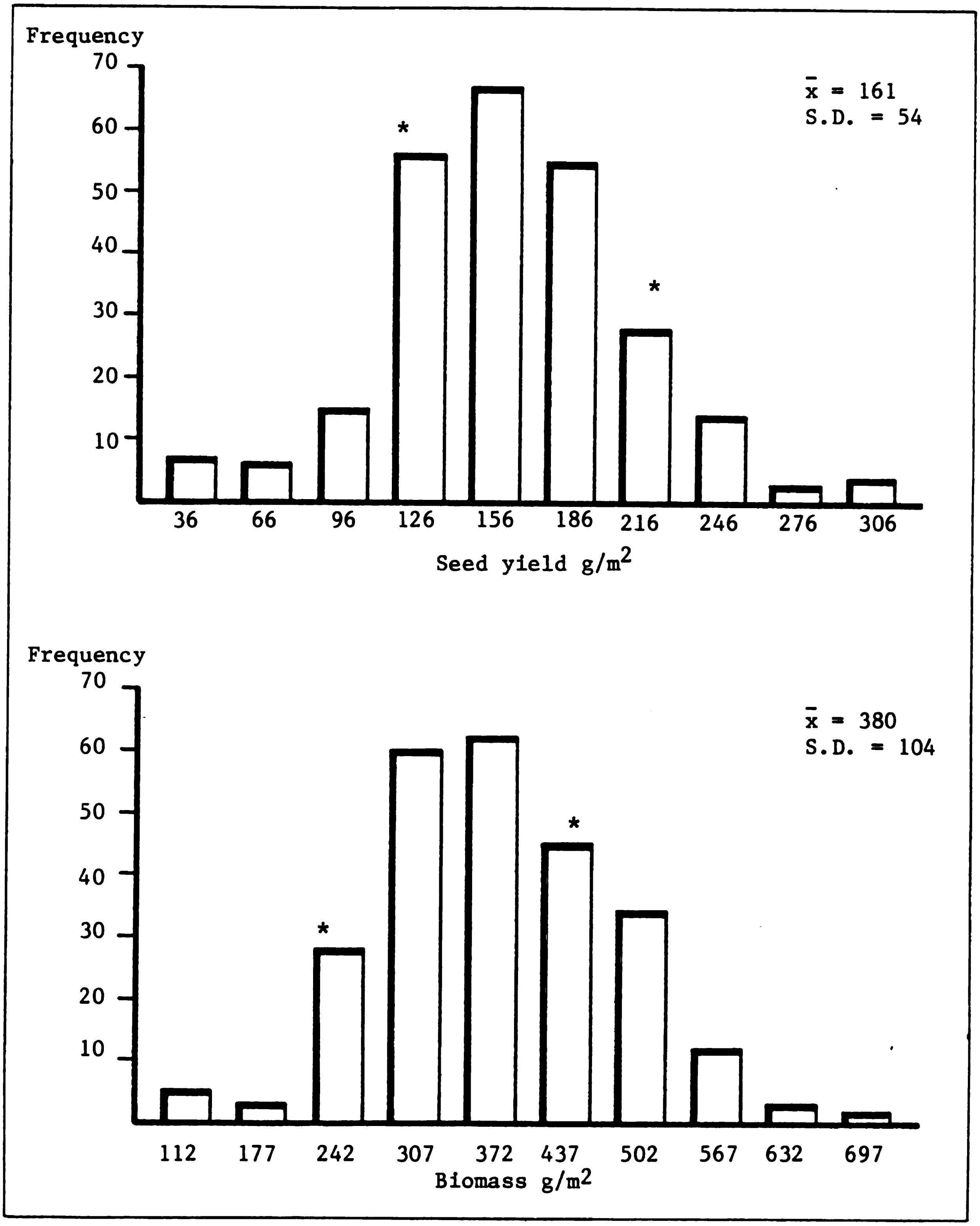


Figure 1. Frequency distribution for seed and biomass yield of 256 bean genotypes grown under water stress (* indicates position of lowest and highest yielding parental genotypes). East Lansing, MI. 1985.

Table 3. Matrix of correlations among seed yield and some plant characteristics of 256 bean genotypes grown under drought stress in a rainout shelter. East Lansing, MI. 1985

	YIELD	PODS	TDM	HI	LWC	LWRC	LNC	IKI	FLOW
PODS	.77**								
TDM	.82**	.64**							
HI	.46**	.34**	-.09						
LWC	-.12	-.17**	-.02	-.18**					
LWRC	.02	.02	.02	.09	.15*				
LNC	-.03	-.04	.02	-.07	.03	-.01			
IKI	.00	-.09	.20**	-.26**	.11	.17	.01		
FLOW	-.11	-.24**	.19**	-.50**	-.07	-.17*	.05	.08	
PHYMA	.02	-.08	.36**	-.54**	.09*	-.15*	.04	.31**	.65**

*,** Significant at P<0.05 and 0.01, respectively.

The average values for seed yield and other variables are presented for some of the promising F4 families and parents in Table 4. It can be seen that for each trait there are at least a few families which show higher values than the top parent. The grand mean for the experiment was slightly larger than the mean of the parents. With the exception of N81064, all genotypes showed a number of days to physiological maturity longer than desirable in agronomic terms. It seems that the release of the drought stress period at seed filling stage extended the length of growth cycle in most of the genotypes. Under normal field conditions terminal drought stress usually tends to accelerate maturity in beans.

Experiment 1986. The 1986 season in Michigan was characterized by fall rainfall considerably above the average (Table 4, Appendix B). An extremely heavy rainfall at the beginning of fall terminated the drought stress sooner than had been expected. In fact, the rainout shelter was always kept in place covering the experimental plots from the rains, but the rising of the soil water table in adjacent soil profiles was unavoidable. In addition, a September storm of more than five inches of rain in a short time period caused run-off from adjacent fields into the rainout shelter. This high soil moisture together with warm temperatures ended the stress period and caused a lengthening of the growth cycle. In the irrigation part of the experiment, the wet conditions resulted in the germination of seeds in the pods of standing plants of early maturing genotypes and a lengthening of the growth cycle of mid and full season genotypes.

Due to the above mentioned factors, high CV's were associated with most of the recorded variables. CV's from the irrigation part of the experiment were essentially of the same magnitude as those from the

Table 4. Mean seed yield and some agronomic characteristics of promising F4 families and two parental genotypes grown under drought stress in a rainout shelter. East Lansing, MI. 1985

Pedigree	Yield g/m^2	Pods $/m^2$	TDM g/m^2	HI	IKI	Days to FLOW	Days to PHYMA
38-18-2	312	208	732	.42	1.8	60	110
48-32	302	272	708	.43	1.8	66	125
48-22	300	224	666	.44	2.3	61	125
48-94	278	268	604	.45	3.3	53	110
51-32-1	276	216	602	.46	3.0	44	110
48-10	264	176	542	.48	2.8	47	110
9-10	258	220	552	.45	3.5	52	110
38-16-2	250	172	556	.44	3.0	56	110
Mean *	156						
UW 21-54	224	224	454	.49	2.5	51	110
N81064	100	116	232	.42	3.5	42	88
Grand mean	161	167	380	.43	2.8	50	103
Std. dev.	54	45	104	.10	0.8	7	13

* Parents' mean, it does not includes Dgo-222 and Mex.1213-2

stressed part of the experiment. In spite of all constraints, highly significant $(P<0.01)$ differences were found among genotypes for all variables except for LWRC under irrigation (Tables 5 and 6, Appendix B). The grand means for seed yield of both drought stressed and irrigated conditions were used to calculate the drought intensity index (DII) of Fischer and Maurer (1978) which gave an average value of 0.28. This value indicates that a mild drought stress period was imposed upon those genotypes grown under the rainout shelter.

Drought condition. A wide range was observed for most of the quantified variables; average values for those variables are presented in Appendix B (Table 8). In Table 5, average values for seed yield and certain agronomic traits of a select group of promising families are presented, in addition to the top and bottom yielding parents. Differences in morpho-physiological characteristics can readily be observed in this table. For example, the top yielding genotype (41-39) shows a large biomass and a relatively acceptable HI, the following three genotypes (41-18-1, 41-48-1 and 8-30) show a better than average biomass and relatively high HI values, and finally, genotype 8-4 shows a large biomass and a smaller than average HI. Thus, it can be noticed that top yielders display different physio-morphological characteristics.

As previously pointed out, it was shown that some genotypes started flowering early enough to reach physiological maturity at around 90 days after planting (DAP), however, their reproductive period was lengthened by the prevalent environmental conditions at the seed filling stage. A further observation is that most of the promising genotypes presented in this table belong to the crosses coded 8 and 41, crosses which include a Michigan and a Wisconsin adapted parent crossed to a Mexican unadapted

Table 5. Mean seed yield and some agronomic variables of promising F6 families and two parental genotypes grown under drought stress in a rainout shelter. East Lansing, MI. 1986

								Days to	
Pedigree	Yield g/m^2	Pods /m^2	Seeds /pod	Seed wt.	TDM g/m^2	HI	IKI	FLOW	PHYMA
41-39	398	319	6.3	24.3	893	.45	3.8	51	105
41-18-1	304	282	6.4	23.1	552	.55	2.5	43	108
41-48-1	288	281	5.7	21.8	570	.51	2.3	42	100
8-30	266	263	6.1	23.7	534	.50	3.0	51	102
8-4	260	281	7.0	18.5	761	.34	2.3	61	120
8-25-2	259	240	6.3	20.7	587	.44	2.8	41	98
8-21-2	257	203	6.7	22.9	560	.46	2.8	63	120
48-109	250	184	6.4	24.6	478	.52	3.5	35	100
Mean *	144								
Lef-2-RB	278	210	5.8	21.4	645	.42	3.5	42	98
II-900-5-M-45 (1)	54	90	2.8	15.2	233	.24	2.8	63	125
Grand mean	149	166	5.9	20.4	397	.37	3.0	51	110
Std. dev.	66	56	0.7	3.5	129	.10	0.6	11	12

* Parents' mean, it does not include Dgo-222 and Mex.1213-2

(1) Photoperiod sensitive.

parent.

Figure 2 is a frequency distribution for seed yield and biomass. This figure shows a wide range in variation with genotypes clustering around the mean value and exhibiting low and high yielders at the left and right ends of the distribution. The relative position of the top and bottom yielding parents is also shown (by position of *). In summary, in this distribution 18 genotypes achieved seed yield values one standard deviation above the mean and three of them showed values larger than two standard deviations above the mean.

As expected for quantitative traits, environmental year to year variation did interact with genotypes influencing the response in seed yield and related agronomic traits. This year- to-year environmental-genotype interaction effect was responsible for an observed low correlation when comparing the yields of the genotypes in 1986 with the yields obtained in 1985 ($r = 0.172$).

Simple correlation between pairs of variables are shown in Table 6. Seed yield was highly and positively associated with the number of pods/m^2, TDM and HI. Seed yield and HI showed a relatively important negative correlation with LWC, IKI score, number of days to flowering and days to physiological maturity. The results obtained with simple correlation in this experiment are essentially the same as those obtained from the previous year's experiment.

Irrigated condition. Beans under irrigation significantly outyielded those under mild drought stress. There were significant differences ($P<0.01$) among the genotypes for every recorded variable except LWRC (Table 6, Appendix B). As in previous experiments, wide variation was observed for most of the variables (Table 9, Appendix B). In the

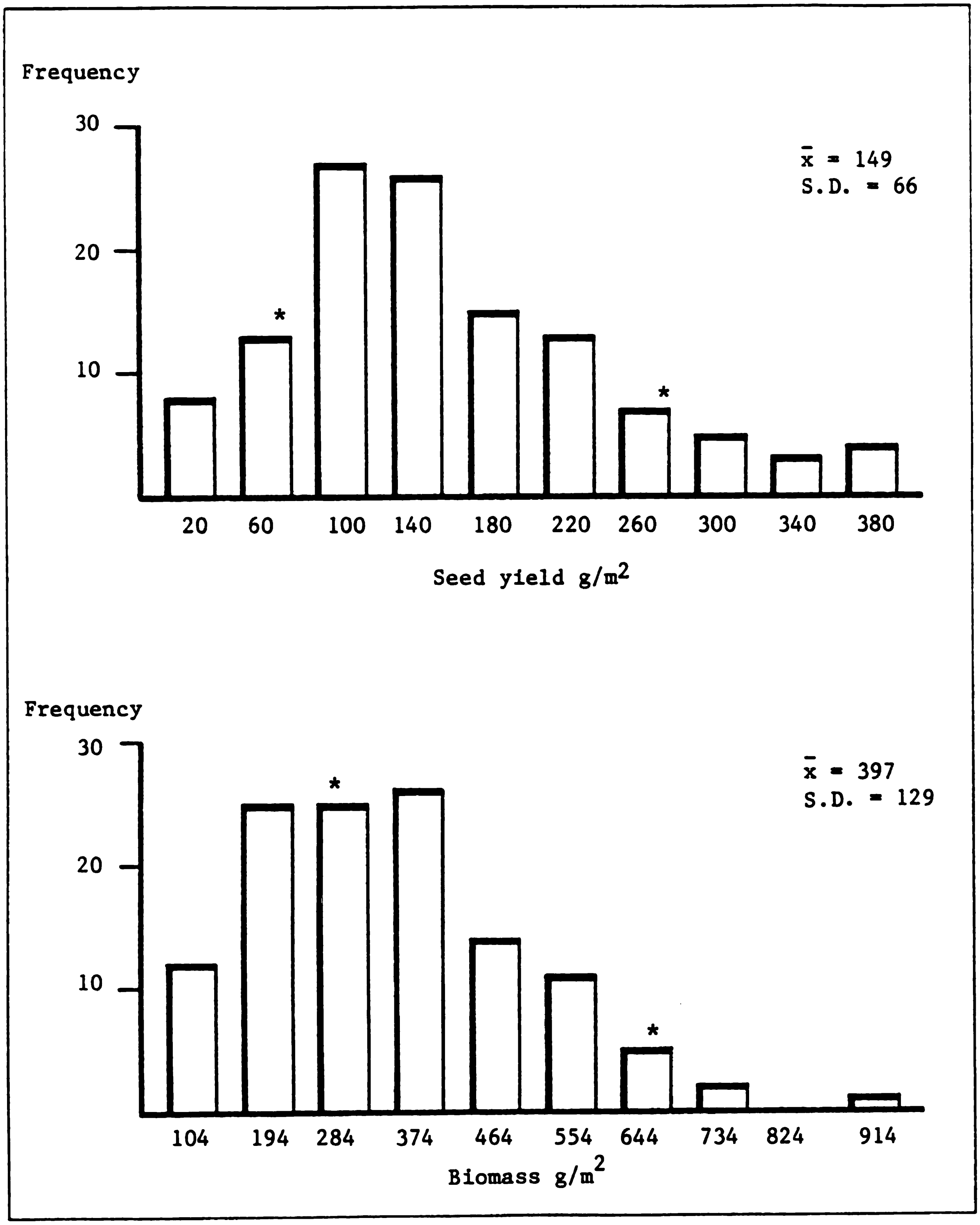


Figure 2. Frequency distribution for seed and biomass yield of 121 bean genotypes grown under water stress (* indicates position of lowest and highest yielding parental genotypes). East Lansing, MI. 1986.

Table 6. Matrix of correlations among average seed yield and some plant characteristics of 121 bean genotypes grown under drought stress conditions in a rainout shelter. East Lansing, MI. 1986

	YIELD	PODS	SEEDS	SEWT	TDM	HI	LWC	LWRC	IKI	FLOW
PODS	.89**									
SEEDS	.27**	.25**								
SEWT	.30**	.15	-.16							
TDM	.79**	.77**	.24**	.06						
HI	.54**	.41**	.04	.43**	.01					
LWC	-.30**	-.32**	.05	-.11	-.07	-.42**				
LWRC	.21*	.27**	.20*	-.11	.23**	-.02	-.05			
IKI	-.21*	-.20*	-.25**	.13	-.05	-.21*	.04	-.09		
FLOW	-.36**	-.31**	.09	-.56**	.00	-.56**	.30**	.01	.05	
PHYMA	-.30**	-.18*	.24**	-.38**	.01	-.45**	.30**	.02	.01	.66**

*,** Significant at P<0.05 and 0.01, respectively.

frequency distribution for seed yield of Figure 3, a drift toward the right side of the distribution is observed. Under this condition, 20 of the genotypes showed seed yields higher than one standard deviation above the mean and eight of them were superior to the mean value by more than two standard deviations. In this case, two of the parental genotypes (UW 21-54 and N81017) were among the top yielders. This result was expected since we were selecting for drought tolerance under mild stress, therefore we had not expected many of the selected families to be superior to the adapted parents under irrigation. However, it is worth noting that the parent N81017, which had already been classified as drought tolerant, also seems to be a good yielding genotype under favorable conditions (Table 7). The same observation is valid for the family 8-4 which is included among the promising families under both stress and non-stress conditions. This family in particular, and the cross code 8 in general, seems to have produced superior recombinants.

Results presented in Table 8 indicate that high yields are associated with a high biomass accumulation and/or a high partitioning ratio (HI). In this particular highly humid environment it was obvious that the type II families derived from adapted parents possessing erect architectural traits were clearly superior to those families possessing a prostrate type III growth habit.

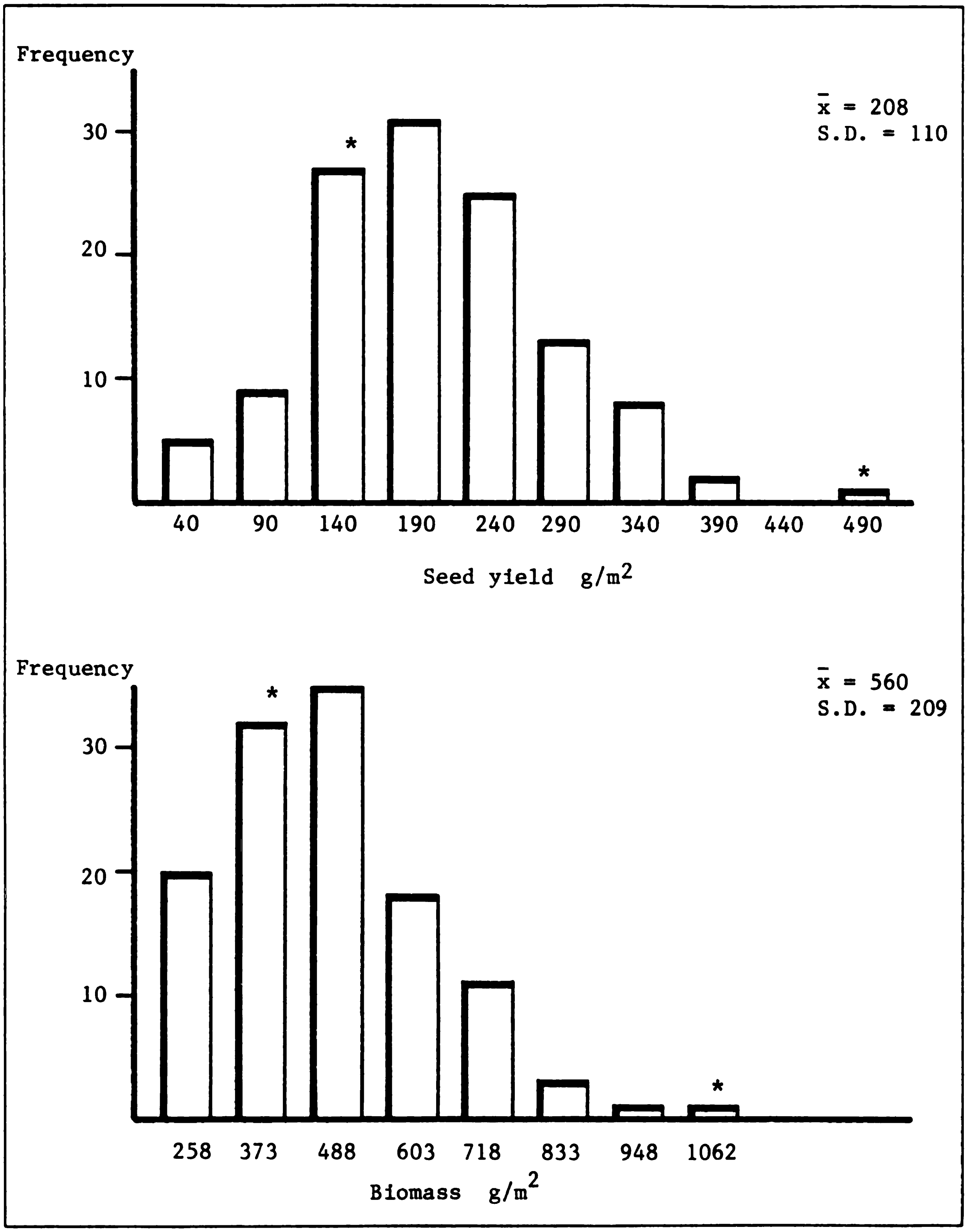


Figure 3. Frequency distribution for seed and biomass yield of 121 bean genotypes grown under irrigation (* indicates position of lowest and highest yielding parental genotypes). East Lansing, MI. 1986.

Table 7. Mean seed yield and some agronomic variables of promising F6 families and two parental genotypes grown under irrigation. East Lansing, MI. 1986

Pedigree	Yield g/m^2	Pods $/m^2$	Seeds /pod	Seed wt.	TDM g/m^2	HI	IKI	Days to	
								FLOW	PHYMA
41-49	502	508	7.0	19.1	1315	.38	4.0	50	115
39-11-1	501	416	7.5	22.8	1114	.45	3.8	56	118
8-42	498	436	6.8	24.3	975	.51	3.0	43	102
8-47	465	486	7.0	18.5	767	.67	3.3	47	105
8-17	455	497	7.0	19.0	995	.46	3.3	54	125
N81017	433	452	6.5	16.9	873	.49	2.5	47	95
8-4	412	423	6.8	16.3	879	.47	2.0	52	112
8-26	412	387	6.9	21.3	804	.51	2.0	43	103
8-6-1	398	448	6.7	18.5	916	.44	3.8	52	112
Mean *	286								
UW 21-54	505	527	7.5	16.9	1036	.49	2.8	56	112
Bayo Madero	150	155	5.0	29.5	441	.34	4.0	52	120
Grand mean	208	256	6.5	17.6	560	.37	3.2	52	115
Std. dev.	110	98	0.5	3.7	209	.14	0.6	9	10

* Parents' means, it does not include Dgo-222, Mex1213-2 and II900-5-M-45.

Table 8. Matrix of correlations among average seed yield and some plant characteristics of 121 bean genotypes grown under irrigation. East Lansing, MI. 1986

	YIELD	PODS	SEEDS	SEWT	TDM	HI	LWC	LWRC	IKI	FLOW
PODS	.92**									
SEEDS	.46**	.49**								
SEWT	.35**	.11	-.25**							
TDM	.81**	.85**	.49**	.08						
HI	.61**	.49**	.13	.47**	.14					
LWC	-.14	-.10	.08	-.14	.02	-.07				
LWRC	.09	.21*	-.09	-.06	.13	.05	-.27**			
IKI	-.34**	-.28**	-.14	-.15	-.12	-.40**	.12	-.03		
FLOW	-.17	-.04	.12	-.43**	.24**	-.45**	.23*	.09	.22*	
PHYMA	-.15	.01	.33**	-.45**	.19*	-.42**	.25**	-.02	.21	.61**

*,** Significant at P<0.05 and 0.01, respectively._

DISCUSSION

This research illustrates in part why breeding for drought tolerance is sometimes elusive. This is particularly true when we have only limited control over the environment and when the evaluation of genotypes is based on the final plant product, biomass or seed yield. After all, the final product is the accumulated output of genetic, environmental and interaction factors all controlling different plant responses in the field during the whole crop cycle. In spite of some constraints in getting reliable drought stress under Michigan conditions, the results obtained with the aid of the rainout shelter indicated that the tested genotypes were under mild drought stress during the most critical portion of the reproductive phase (Tables 1 and 2, Appendix B).

From past experience, we know that a crop can be severely damaged in terms of seed yield if the drought stress coincides with a critical phase of development. Thus, for the comparison of many genotypes a single stress period at the beginning of the reproductive period or in seed filling allowed us to detect differences in response to the mild stress encountered by the plants. However, for future evaluations, it seems sound to separate the different genotypes in groups according to their growth habit and phenology. Large differences in those traits increase the degree of difficulty in interpreting results.

Although selection in more favorable conditions is largely inefficient in identifying the best genotypes for unfavorable conditions (Lewis and Christiansen, 1981; Boyer, 1982; Cecarrelli, 1987), the evaluations of early generation materials at more sites, or at the same site on different planting dates or under differential moisture supply is advised. It can be valuable for two purposes; one, to expose the genotypes to a variety of stresses, in terms of timing and/or intensity, and two, it allows for selection for either arithmetic or geometric mean yield and the use of the drought susceptibility index of Fischer and Maurer (1978). Those data should give an opportunity to identify those drought tolerant genotypes which are likely to occur at a very low frequency, able to perform well under stress, and with sufficient plasticity to respond to improved conditions (Ceccarelli, 1987).

If a population has a sufficiently broad genetic background, as we assume is our case, developmental plasticity will be displayed when an environmental stress is applied to that population.

Results from part one of this research indicated that seed yield under stress is primarily dependent on or associated with pre-existing biomass and secondly with ability to partition (and/or remobilize) photoassimilates to the reproductive organs of the plant. Results obtained here confirmed the high association of biomass with seed yield; in this case, biomass at physiological maturity was important under both stress and nonstress conditions. Similar findings were reported in common bean by Elizondo (1987) and with lima bean by Ziska et al. (1985). However, other traits must be taken into consideration when selecting for drought tolerance, in addition to biomass, since larger biomass in beans is often associated with a delay in maturity (Rodriguez et al., 1987; White, 1987).

Partitioning as indicated by the HI was also highly associated with seed yield, as indicated by the correlation values between these two traits. However, since HI is a calculated ratio rather than a directly measured trait, and one cannot discern between partitioning of current or stored assimilates, we believe it would not be a useful trait to select for under stress conditions. In this study some genotypes showed similar mean yields and different values for the HI. Thus genotypes possessing a greater biomass did produce relatively well under the conditions of these experiments without displaying a high HI value. Genotypes which produced high yields without much biomass, possess a high HI, and can be considered efficient in terms of partitioning, that is in terms of yield/unit area/day. However, in those genotypes, there is little room for genetic improvement as compared with genotypes producing a large biomass. High partitioning without high initial biomass will not lead to high yields unless photo-assimilation is extraordinarily high (Adams and Kelly, 1987).

In any environment, the capacity for high biological yield sets the stage for manipulating plant photosynthate allocation (and reallocation) in such a way that the economically useful part could be increased only after obtaining a vigorous and healthy plant. Stunted bean plants are a common response under drought stress, therefore genotypes that grow more normally than others under stress are the primary target in a selection program. A primary concern in a breeding program for drought tolerance should be the selection of a field that has a stress factor at a level that will discriminate between less tolerant and more tolerant genotypes. As Lewis and Christiansen (1981) pointed out, there is no value to a test if it is located in an environment that is stress-free or if the stress is so severe that nothing survives.

It can be argued that the primary objective in any agricultural situation is the economic yield, however, when crops depend on an unreliable rainy season, stability of yield can be as important as potential yield. In some particular cases biomass is almost as important as the economic product; such is the case of the bean crop in North-Central Mexico, where the crop is grown for seed and hay (Acosta and Kohashi, 1988). A similar situation was described for cowpeas in the semiarid Sahel of Africa (Hall and Patel, 1985) and for beans in Eastern Africa (Adams et al., 1985), where fresh leaves of both crops are eaten as a vegetable. Thus, as indicated by Quisenberry (1982), the ability of the plant to accumulate biomass under stress should be the first criterion in selecting for drought tolerance. A second criterion should be yield _per se_, which ultimately embraces the ability to accumulate biomass and its subsequent allocation into the seeds.

The ranking of the families selected on the basis of seed yield and biomass was inconsistent from year to year. However, progress can be expected if segregating populations are handled as families and evaluated in more than one site. In those cases where seed is short, multiple sites would be prefered rather than replicates in a single site.

Mean seed and biomass yields of the 1986 (F6 families) drought trial were compared with those obtained in 1985 (F4 families). An inconsistent response of the genotypes from one year to the other was observed due to the genotype x environment interaction. However, some good responders were also observed and one should expect that some progress could be made if those genotypes could be consistently identified in a selection program. It seems that in breeding for drought tolerance in beans a more consistent response could be obtained if selections are made based on biomass rather than on seed yield _per se_. This is partially supported by the relatively greater correlation of the genotypes when biomass was used to illustrate the response of the genotypes in both years (r = 0.326 *).

The use of an IKI solution as an aid to select for ability in remobilization under stress is unclear in this research due to the poor relationship observed between IKI scores and seed yields. However, we have noted a consistent negative relationship between the IKI score and the HI. This may indicate the inability of some genotypes to remobilize stored starch or the presence of a larger source as compared to the sink. After the plants have been released from the stress, a small sink during pod filling could be due to a high pod drop during early flowering. It may be this circumstance which sometimes enhances size of the seed under stress as compared to non-stress. Nonetheless, beans in general possess an acceptable sink size and a small source as indicated by flower and pod dropping and intra-pod competition under stress and non-stress conditions (Acosta and Kohashi, 1988).

Drought tolerance from an agronomic and plant breeding point of view means the ability for higher or at least more stable yield of the economic part of the plant grown under stress. We know that yield is the total sum of many biochemical and physiological processes and environmental factors and has low heritability. Therefore, yield should not be the sole criterion when selecting for drought tolerance; other traits can be considered, i.e. earliness, growth habit, grain filling length, etc.

In beans, the chain of biochemical and physiological events between genes and final phenotypic expression under drought stress is not known but, if a key step in the chain is known to be highly correlated with drought tolerance, selection could be practiced for it rather than for the final phenotype. Unfortunately, such key steps still remain to be discovered and much has to be learned with respect to the response of _Phaseolus vulgaris_ to drought stress.

Based on the observed response of the cultivars to the mild drought stress imposed in both years in Michigan, and on preliminary observations from plots planted in Mexico during the summer of 1986, a final group of 19 families was selected for further testing in 1987.

CONCLUSIONS

1. No relationship was found between the IKI scores and seed yield, however, a significant negative correlation between IKI scores and HI may indicate the inability of some genotypes to remobilize. In spite of differences observed among genotypes, the use of the IKI solution has to be further tested because the photoperiod sensitivity of many of the genotypes in these experiments seems to affect the pattern of assimilate partitioning and remobilization.

2. Seed yield and biomass seemed to be affected in the same way by water stress. Since biomass showed a higher correlation value than other traits when comparing results from 1985 and 1986, it is suggested that more progress could be achieved by using biomass as a criterion for selection. Selection for increased biomass without modifying the HI may lead to increased seed yield under both stress and non-stress conditions.

3. For reasons inherent to their morphology, genotypes belonging to the type II growth habit proved to be superior to type III's under the moist environment caused by the heavy rains during fall of 1986.

REFERENCES

Acosta Gallegos, J.A. and J. Kohashi Shibata. 1988. Effect of water stress on growth and yield of indeterminate dry bean (Phaseolus vulgaris L.) cultivars. Submitted : Field Crops Research. Netherlands

Adams, M.W., Wiersma, J.W., and J. Salazar. 1978. Differences in starch accumulation among dry bean cultivars. Crop Sci. 18:155-157

Adams, M.W. and J.D. Kelly. 1987. The role of architecture, crop physiology and recurrent selection in ideotype breeding for yield in dry beans. In: Symposium on Breeding for Higher Yields in Common Beans. XXXIII meeting of the PCCMCA, Guatemala, C.A. CIAT-B/C CRSP-ICTA p. 16

Boyer, J.S., Johnson, R.R., and S.G. Saupe. 1980. Afternoon water deficits and grain yields in old and new soybean cultivars. Agron. J. 72:981-986

Boyer, J.S. 1982. Plant productivity and environment. Science 218:443-448

Ceccarelli, S. 1987. Yield potential and drought tolerance of segregating populations of barley in contrasting environments. Euphytica 36:265-273

Clarke, J.M. and T.F. Townley-Smith. 1984. Screening and selection techniques for improving drought resistance. In: P.B. Vose and S.G. Blixt (Eds.), Crop Breeding, a Comtemporary Basis. Pergamon Press pp.137-162

Dedio, W. 1975. Water relations in bean leaves as screening tests for drought resistance. Can. J. Plant Sci. 55:369-378

Elizondo-Barron, J. 1987. Characteristics related to yield of dry beans (Phaseolus vulgaris L.) under water stress conditions. M.S. Thesis Michigan State University, East Lansing p. 73

Fischer, R.A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I.Grain yield responses. Aust. J. Agric. Res. 29:277-317

Hall, A.E. and P.N. Patel. 1985. Breeding for resistance to drought and heat. In: S.R. Singh and K.O. Rachie (Eds.), Cowpea: Research, Production and Utilization. John Wiley & Sons pp 137-151

Hurd, E.A. 1976. Plant breeding for drought resistance. In: T.T Kozlowski (Ed.), Soil Water Measurements, Plant Responses and Breeding for Drought Resistance. Academic Press pp.317-353

Lewis, C.F. and M.N. Christiansen. 1981. Breeding plants for stress environments. In: K.J. Frey (Ed.), Plant Breeding II. Iowa State University, Ames, Iowa pp 151-164

Mkandawire, A.B.C. 1987. Productivity of Malawian landrace dry beans under intercropping and drought conditions. Ph.D. Thesis, Michigan State university, East Lansing p.127

Parsons, L.R. 1979. Breeding for drought resistance: what plant characteristics impart resistance? Hort. Sci. 14:590-593

Quisenberry, J.E. 1982. Breeding for drought resistance and plant water use efficiency. In: J.W. Christiansen and C.F. Lewis, (Eds.), Breeding Plants for Less Favorable Environments. John Wiley and Sons, Inc. pp. 193-212

Rodriguez, R.R, Miranda, C.S. and S.E. Beebe. 1987. Morpho-physiological characterization of early genotypes in common beans (Phaseolus vulgaris L.). In: Symposium on Breeding for Higher Yields in Common Beans. XXXIII meeting of the PCCMCA, Guatemala, C.A. CIAT-B/C CRSP-ICTA p.30

Rosas, J.C. 1983. Partitioning of dry matter, nitrogen fixation, and seed yield of common bean (Phaseolus vulgaris L.) influenced by plant genotype and nitrogen fertilization. Ph.D. Thesis, University of Wisconsin, Madison p.127

Samper, C., Adams, M.W., Hanson, A.D., and E. Watt. 1984. Contribution of stored assimilates to the seed following a drought stress in dry beans. Agron. Abst. 76:87

Sebasigari, K. 1981. Patterns of partitioning and remobilization of non-structural carbohydrates in common bean and other selected grain legumes. M.S. Thesis, Michigan State University, East Lansing p.152

Simmonds, N.W. 1979. Principles of Crop Improvement. Longman Inc. New York. pp. 40-65

Singh, S.P. and J.W. White. 1988. Breeding common beans for adaptation to drought conditions. In: G. Hoogenboom, F. Ibarra, S.P. Singh, J.W. White and S. Zuluaga (Eds.), Research on Drought Tolerance in Common Beans. CIAT, Cali, Colombia. In press

Turner, J.C. 1981. Techniques and experimental approaches for the measurement of plant water status. Plant and Soil 58:339-366

Walker, D.W. and J,C, Miller. 1986. Rate of water loss from detached leaves of drought resistant and susceptible genotypes of cowpea. Hort. Sci. 21:131-132

White, J.W. 1987. Strategies at CIAT for increasing yield potential of common beans -- finishing the domestication process. In: Symposium on Breeding for Higher Yields in Common Beans. XXXIII meeting of the PCCMCA, Guatemala, C.A. CIAT-B/C CRSP-ICTA p. 34

Ziska, L.H., Hall, A.E., and R.M. Hoover. 1985. Irrigation management methods of reducing water use of cowpea (*Vigna unguiculata* [L.] Walp.) and lima bean (*Phaseolus lunatus* L.) while maintaining seed yield at maximum levels. Irrig. Sci. 6:223-239

CHAPTER 3

EVALUATION OF BEAN (*Phaseolus vulgaris* L.) GENOTYPES GROWN IN A NITROGEN-FREE MEDIUM FOR BIOLOGICAL NITROGEN FIXATION.

INTRODUCTION

Variability in field responses to nodulation in beans has been ascribed to unsatisfactory host-microsymbiont interactions (Graham, 1981), competition between introduced and native rhizobia and, in temperate climates, to the environment (Sprent, 1981) including soil water deficits. In spite of inconsistent results with inoculation trials in the field, evidence is accumulating that the quantitative variation in nodulation and nitrogen fixation in beans is sufficient to attempt to increase nitrogen fixation through breeding and selection (Rennie and Kemp, 1981a,b; McFerson et al., 1982; McFerson, 1983; Rosas, 1983; Bliss, 1985; Rosas and Bliss, 1986; St.Clair, 1986). McFerson et al. (1982) and Bliss (1985) have recently demonstrated transgressive segregation for nitrogen fixation. Among backcross derivatives some families showed higher rates of nitrogen fixation than the recurrent parent.

In selecting better genotypes for nitrogen fixation from large segregating populations in the field, indirect selection utilizing easy-to-measure correlated traits may allow the screening of numerous genotypes. Rennie and Kemp (1981a) found that the amount of nitrogen fixed in a phytotron trial with eleven bean cultivars was correlated with leaf area and leaf and shoot weight. They suggested that those characteristics may help bean breeders in selecting bean plants with superior dinitrogen fixing abilities. The use of shoot nitrogen content has also been suggested as a criterion of ability for BNF (St.Clair, 1986).

As we previously postulated, high ability to fix nitrogen might contribute positively to the final response of the bean plant under drought stress at the seed filling stage. Chapman and Muchow (1985) found marked differences in total nitrogen accumulated among six pulse crop species as well as a significant water regime x species interaction. Nitrogen accumulation and nitrogen accumulation rate decreased in response to prolonged water deficits and also the proportion of nitrogen partitioned to the seeds tended to decrease. In an irrigation experiment, Ziska et al. (1985), working with cowpea and lima bean, found a low biomass production for treatments having longest irrigation intervals and lowest level of soil nitrogen. They indicated that these results may have been due to drought-induced reduction in nitrogen fixation during flowering and pod filling. Higher levels of soil nitrogen caused small increases in biomass, with the greatest increase occurring with the longest irrigation interval.

In the introductory part of this report, we stated the hypothesis that bean genotypes can partially avoid drought effects during pod filling by remobilizing previously stored nitrogen and carbohydrate compounds. It is also clear that in beans the vegetative nitrogen fixation period of early maturing beans is shorter than for late maturing genotypes (Rennie and Kemp, 1981b). In addition, the peak of fixation is around flowering time (Graham and Rosas, 1977; Rennie and Kemp, 1981a) followed by a decrease in fixation due to the strong sink for assimilates of the developing pods. Thus, to assess the ability for nitrogen fixation of the bean families selected for drought tolerance in previously described field experiments, this part of the research reports a comparative study on the ability of a group of 26 bean genotypes for biological nitrogen fixation (BNF) measured as response in biomass, seed yield and total nitrogen content under greenhouse conditions.

MATERIALS AND METHODS

The experiment was conducted at the greenhouse facility of Michigan State University (MSU), East Lansing, MI., during the spring of 1987. Nineteen F7 families, six parental genotypes and a check cultivar (Table 1) were used in this experiment. The F7 families had been previously selected on the basis of their adaptation to moisture stress. The genotypes were grown in 20 cm diam. x 15 cm deep pots containing sterile silica sand:perlite (4:1). Three seeds were planted per pot and fifteen days after planting, seedlings were thinned to one per pot. After emergence, seedlings were inoculated several times with a commercial inoculant specific for dry beans (Nitragin Co. Milwaukee, Wis.). Plants were fertilized three days per week with a nitrogen-free solution as described by Pacowsky et al. (1984), and tap water was used the rest of the days. Ten pots were used per genotype and a Complete Randomized Design was used to distribute the pots on the greenhouse benches.

MEASUREMENTS AND ANALYSES.

When most of the families reached physiological maturity (80 % of the pods had lost their chlorophyll), the plants were cut at the sand level in the pot and separated into seeds, roots and shoots. Fallen

Table 1. Origin and pedigree of the evaluated bean genotypes. East Lansing, MI. 1987

Entry no.	Genotype	Pedigree	Origin
6	8-3	N81017 X LEF-2-RB	INIFAP-MSU
13	8-4	N81017 X LEF-2-RB	INIFAP-MSU
19	8-17	N81017 X LEF-2-RB	INIFAP-MSU
7	8-15-1	N81017 X LEF-2-RB	INIFAP-MSU
3	8-25-2	N81017 X LEF-2-RB	INIFAP-MSU
9	8-42-1	N81017 X LEF-2-RB	INIFAP-MSU
10	8-42-2	N81017 X LEF-2-RB	INIFAP-MSU
15	8-47	N81017 X LEF-2-RB	INIFAP-MSU
5	9-39-1	N81017 X LEF-2-RB	INIFAP-MSU
8	39-17-1	UW 21-58 X II900-5-M-45	INIFAP-MSU
11	41-18-1	UW 21-58 X A411	INIFAP-MSU
12	41-39	UW 21-58 X A411	INIFAP-MSU
14	41-48-1	UW 21-58 X A411	INIFAP-MSU
1	48-10	UW 23-61 X BAYO MADERO	INIFAP-MSU
2	48-66	UW 23-61 X BAYO MADERO	INIFAP-MSU
4	48-94B-1	UW 23-61 X BAYO MADERO	INIFAP-MSU
16	48-109	UW 23-61 X BAYO MADERO	INIFAP-MSU
18	51-5-3	UW 23-61 X MEX1213-2	INIFAP-MSU
17	51-29-3	UW 23-61 X MEX1213-2	INIFAP-MSU
* 20	N81017	KENT/N2//PIJAO/BUNSI	MSU
* 21	LEF-2-RB	VER10/CHIS143//PUE144	INIFAP
* 22	UW 21-58	PORRILLO SIN/PUE152	UW
* 23	UW 23-61	EX-RICO/PUE152	UW
* 24	BAYO MADERO	BAYO RGZ/C-102	INIFAP
* 25	II900-5-M-45	PINTO AM/C-14	INIFAP
(1)26	PUE-152	LOCAL PUEBLA, MEXICO	UW

* Entries 20-25 are the parental genotypes

(1) cultivar check

INIFAP = National Institute for Forestry and Agriculture Research, Mexico.

MSU = Michigan State University, USA.

UW = University of Wisconsin, USA.

leaves were included. Roots were washed and together with shoots were oven dried at 60 ^{o}C for 72 hours. Daylength sensitive genotypes were harvested at 90 days after planting regardless of their phenological stage. The dry weight of different plant parts were recorded and micro-kjeldahl analyses were performed for seeds and a representative sample of the total dry matter per plant. Seed protein content (SPC), total nitrogen and nitrogen harvest index (NHI) were calculated for each genotype except Bayo Madero which never set pods. Other recorded and calculated data included : number of days to flowering and physiological maturity, seed yield per plant, yield components, HI, total dry matter and nitrogen accumulated per plant per day (TDM/p/d and N/p/d). Analyses of variance were performed on all variables following a Complete Randomized Design and simple correlations were performed among the variables with the aid of MSTAT, a microcomputer statistical package for agricultural research.

RESULTS AND DISCUSSION

The tested bean genotypes received no nitrogen fertilizer, therefore, we assume that all plant nitrogen was derived from the planted seed and the N_2 gas from the atmosphere through BNF. Even though the actual amount of nitrogen fixed per genotype was unknown, the accumulated nitrogen in the dry matter (including abscised parts) was used here to compare the relative ability of the different genotypes for BNF. If the average seed N content is substracted from the total nitrogen content, the result gives a conservative estimate of nitrogen fixation (Pacowsky et al., 1984).

Evidence of significant variation ($P<0.01$) among the genotypes was found for all recorded and calculated variables (Table 2). Some of the

Table 2. Analyses of variance for N assimilation and related variables in 26 inoculated bean genotypes grown in a N-free medium in the greenhouse. East Lansing, MI. 1987

Variable	Mean square	C.V. %
Days to flowering	207.5 ***	9.34
Days to maturity	12.1 ***	4.31
Seed yield g/plant	9.76 ***	36.2
No. of pods/plant	9.69 ***	31.4
No. of seeds/pod	0.57 ***	16.0
Seed weight mg	1367.1 ***	19.7
Total dry matter g/plant	1078.3 ***	27.3
Harvest Index	0.034 ***	25.9
N assimilated mg/plant	532028 ***	28.4
Seed protein %	41.64 ***	17.6
Nitrogen Harvest Index	0.079 ***	22.7
TDM g/plant/day	0.113 ***	26.7
N assimilated mg/plant/day	55.78 ***	27.8
Root/shoot ratio	0.082 ***	47.2

*** = significant at a $P < 0.001$

genotypes were daylength sensitive and did not set pods or the partitioning of assimilates to their reproductive parts was low; however, a comparison of all genotypes was possible using the traits total dry matter and nitrogen assimilated per plant.

The seed yield of some families was superior to the yield obtained by the check, variety PUE 152. PUE 152 was chosen as a check for its superior expression in nitrogen fixation (Graham, 1981). Few families were equivalent or superior to the parental line UW 21-58, which was the higher yielding genotype among the parents. This was not unexpected, since UW 21-58 was bred for BNF ability (Bliss, 1985). The family 48-66 was the top yielder in the test and the families 8-3, 48-94B-1, and 51-29-3, which were included as poor responders, were indeed among the low yielders (particularly 51-29-3)(Table 3). Family 9-39-1, which was daylength sensitive, showed an outstanding 30% protein content in the seed whereas the parental genotype Lef-2-RB showed the lowest value for this variable (Table 3).

The genotypes UW 21-58, Bayo Madero, and II900-5-M-45 showed the highest dry matter yields among the parents. The Mexican parents which were previously selected as drought tolerant probably had been indirectly selected for BNF ability since they are from the Mexican Plateau where the agricultural soils are low in N content. The families, 39-17-1, 48-66, and 8-4 achieved maximum values for total dry matter (TDM). With respect to the total amount of nitrogen accumulated per plant, the parental genotype Bayo Madero and the previously mentioned families, 48-66, 39-17-1 and 8-4, showed maximum values (Table 4). It seems that the families with better ability for nitrogen assimilation (BNF) were also able to transform it into biomass (primary

Table 3. Values of seed yield per plant, yield components, HI, seed protein content, and nitrogen harvest index (NHI) of 25 bean genotypes* grown in a N-free medium in the greenhouse. East Lansing, MI. 1987

Ent. No.	Pedigree	Seed yield /plant	Pods/ plant	Seeds /pod	Seed weight	HI@	Seed protein	NHI
		-- g --			-- mg --		-- % --	
1	48-10	7.9	8	4.34	235	0.26	24.0	0.39
2	48-66	16.5	14	4.96	237	0.37	23.0	0.59
3	8-25-2	9.6	12	5.19	165	0.34	21.8	0.53
4	48-94B-1	8.4	14	3.99	288	0.31	23.7	0.51
5	9-39-1	8.8	11	4.94	142	0.21	30.0	0.41
6	8-3	7.6	10	4.75	169	0.31	25.3	0.54
7	8-15-1	6.7	8	4.91	162	0.34	22.5	0.50
8	39-17-1	8.8	11	3.34	238	0.18	24.2	0.32
9	8-42-1	8.8	9	4.45	223	0.32	22.9	0.50
10	8-42-2	10.0	8	5.07	251	0.35	22.9	0.55
11	41-18-1	9.2	10	4.95	176	0.33	24.6	0.52
12	41-39	7.8	9	3.92	232	0.21	24.3	0.35
13	8-4	12.7	15	6.06	144	0.28	23.4	0.46
14	41-48-1	6.4	8	4.97	157	0.34	26.8	0.52
15	8-47	9.6	10	5.22	185	0.31	23.8	0.51
16	48-109	8.4	9	4.80	186	0.33	22.0	0.50
17	51-29-3	6.2	9	4.12	156	0.28	23.9	0.45
18	51-5-3	7.4	11	4.51	155	0.32	22.9	0.51
19	8-17	9.5	11	4.47	200	0.33	21.8	0.53
20	N81017	7.5	10	4.84	165	0.30	23.5	0.52
21	Lef-2-RB	8.4	8	4.84	209	0.36	18.4	0.52
22	UW 21-58	10.1	11	5.84	156	0.30	23.4	0.54
23	UW 23-61	4.8	7	4.72	139	0.28	23.6	0.44
25	II900-5-M-45	6.4	6	4.70	204	0.14	24.8	0.23
26	PUE 152(1)	8.1	8	3.88	267	0.22	22.4	0.30
LSD (0.05)		2.7	2.7	0.67	33	0.07	3.7	0.09

* Bayo Madero was not included.

@ Roots and senesced leaves were included in the denominator.

(1) Check genotype.

Table 4. Values of plant phenology, plant dry matter, total N per plant, biomass/plant/day (b/p/d), nitrogen accumulation g/plant/day (N/p/d) and root/shoot ratio of 26 bean genotypes grown in a N-free medium in the greenhouse. East Lansing, MI. 1987

Ent. No.	Pedigree	Days to FLOW	Days to MAT	TDM	Assimilated N/plant	b/p/d	N/p/d	Root/ shoot
				-- g --	-- mg --	-- g --	-- mg --	
1	48-10	43	80	33.17	724.8	0.41	9.09	0.31
2	48-66	49	85	44.60	1007.9	0.52	11.91	0.20
3	8-25-2	44	80	28.18	636.8	0.35	8.11	0.19
4	48-94B-1	40	79	29.00	636.3	0.37	8.09	0.21
5	9-39-1	54	87	39.60	880.4	0.46	10.41	0.43
6	8-3	43	77	25.59	571.3	0.33	7.34	0.28
7	8-15-1	48	80	19.64	467.9	0.25	5.91	0.24
8	39-17-1	46	88	50.98	1071.3	0.58	12.24	0.34
9	8-42-1	45	82	24.85	546.8	0.31	6.56	0.20
10	8-42-2	47	79	30.22	682.7	0.38	8.66	0.17
11	41-18-1	38	78	27.98	645.0	0.36	8.34	0.21
12	41-39	47	83	38.57	817.3	0.46	10.03	0.29
13	8-4	51	87	45.08	953.3	0.52	11.01	0.25
14	41-48-1	38	76	18.86	438.0	0.25	5.80	0.35
15	8-47	48	80	30.98	680.5	0.39	8.59	0.17
16	48-109	42	77	25.68	550.8	0.33	7.12	0.25
17	51-29-3	38	77	22.45	565.3	0.29	7.42	0.23
18	51-5-3	37	75	23.87	506.5	0.32	6.83	0.27
19	8-17	45	78	29.57	616.9	0.38	7.99	0.23
20	N81017	44	78	25.49	560.2	0.33	7.24	0.23
21	Lef-2-RB	42	78	23.14	415.9	0.30	5.46	0.18
22	UW 21-58	47	83	34.04	709.3	0.41	8.50	0.24
23	UW 23-61	38	75	17.34	385.0	0.23	5.17	0.35
24	BAYO MAD.	--	90	53.59	1343.8*	0.60	14.92	0.50
25	II900-5-M-45	51	85	49.83	984.2	0.58	11.70	0.46
26	PUE 152(1)	42	85	41.14	882.1	0.48	10.22	0.32
LSD (0.05)		3.6	3.1	7.76	178.0	0.09	2.13	0.11

* Not corrected by N seed content, thus total N per plant.

(1) Check genotype.

productivity); however, one cannot say that BNF is the direct cause of the increase in biomass but rather that there is a marked relationship between BNF and productivity.

This high relationship between BNF and productivity has been repeatedly shown in the common bean and other legume crops. Rennie and Kemp (1981a) compared the N fixation ability of eleven dry bean cultivars at 56 days after planting and found that weight and area of leaves, plant dry matter and N yields were significantly correlated with N_2 fixed. In a second study, to assess the amount of fixation of four cultivars under two temperature regimes, they found that the amount of N fixed was highly correlated with plant dry matter and N yield but not with acetylene reduction over the entire season (Rennie and Kemp, 1981b). Pacowsky et al. (1984) evaluated several bean-Rhizobium strain combinations for N_2 fixation, N assimilation and biomass production. They indicated that assimilated nitrogen is a better, more direct measure of efficiency in the bean-rhizobia symbiosis than the estimate of nitrogen fixation by acetylene reduction and hydrogen production.

Cultivars which came into flowering later were more productive in terms of seed yield, biomass and N accumulated than the early flowering genotypes. Thus, the best responders in this test were those genotypes with a relatively longer vegetative period than the low responders. It seems that the genetic system governing daylength sensitivity, which sets the developmental stage for assimilate partitioning in beans (Wallace et al. 1987), is affecting BNF. This suggests that it may be advantageous to select beans that have a longer vegetative period to prolong the time of active N_2 fixation within the limits of acceptable season length to ensure normal maturity (Rennie and Kemp, 1981b).

Since there were genotypes in this experiment with different plant types (i.e. types II and III) and phenology, two efficiency indexes were calculated to further evaluate the differences among genotypes, namely, biomass/plant/day and N assimilation /plant/day (Table 4). In general, the use of these indexes indicated the same results as using biomass and N assimilation per plant. In previous experiments in the greenhouse and in the field (Part 1, this research), the Mexican genotype Bayo Madero had shown an average ability to fix atmospheric nitrogen and a high response to the addition of nitrogen fertilizer; in this particular test, Bayo Madero showed the highest value for total nitrogen per plant. This result was due probably to its extended vegetative phase which is equivalent to a lengthened fixation period directly producing a larger biomass.

In Table 5 some important correlation coefficients between N assimilation with biomass and other agronomic variables are presented. A marked relationship is observed between N- assimilation with the number of days to maturity, the weight of the root system and biomass (TDM). HI and NHI were highly associated, as was expected, since probably both variables depend on the same mechanism(s). With the exception of a non- significant positive correlation of HI and NHI with seed yield, these two indexes (HI and NHI) were negatively and significantly associated with all the other recorded traits. This result confirms the multiple-site competition for photoassimilates between the root nodules and the developing fruits in the pulse-rhizobia association where the seeds are the strong N and C sinks. Therefore, as indicated by Graham (1981) and Pate and Minchin (1979), N_2 fixation is

Table 5. Correlation coefficients among nitrogen assimilation, plant biomass (TDM), seed yield, and related variables in a group group of 26 inoculated bean genotypes grown in a N-free medium in the in the greenhouse. East Lansing, MI. 1987

	Nitrogen assimilation	TDM	Seed yield	NHI
Days to flowering	0.65***	0.66***	0.44*	-0.24
Days to maturity	0.91***	0.91***	0.47*	-0.52**
Root weight	0.91***	0.90***	0.11	-0.81***
Root/Shoot ratio	0.53**	0.51**	-0.42*	-0.74***
Harvest Index (HI)	-0.61***	-0.64***	0.32	0.94***
TDM	0.97***	1.00	0.49*	-0.58**
Seed yield	0.54**	0.49*	1.00	0.38
Nitrogen Harvest Index (NHI)	-0.53**	-0.58**	0.38	1.00

*,**,*** = P<0.05, 0.01, 0.001, respectively

influenced by N source-sink relationships among plant organs. A positive non-significant correlation between seed yield and seed protein content was observed.

The seeds of grain legumes are strong sinks for nitrogen due to their high protein content (Sinclair and de Wit, 1975) and part of their requirement is partially met by remobilization of N from other plant parts. Later in development, senescing leaves can supply large quantities of the nitrogen needed by protein rich seeds (Pate and Minchin, 1979; Izquierdo, 1981). Thus, as pointed out by Summerfield (1981), the death of leaves during reproductive growth cannot be divorced from their photosynthetic activity and interrelationships with symbiotic dinitrogen fixation during the pre-flowering period.

CONCLUSIONS

The evaluated families showed variation for traits related to BNF and some promising genotypes were identified. In addition, a high association between total dry matter and total nitrogen assimilated per plant may suggest that selection for BNF can be done by selecting vigorous plants from segregating populations. Since BNF is a quantitative trait, a portion of the segregating population, say the best 5 or 10 percent, could be taken to be parents of the next generation in which selection can continue. A reduction in the number of crosses by careful selection of parents will allow the handling of relatively large segregating populations. Rennie and Kemp (1981b) suggested selection on the basis of leaf area, assuming that a plant with a larger leaf area may have greater photosynthetic capability and should support greater amounts of nitrogen fixation. Growing bean plants in a N-free medium forces total dependence on seed and atmospheric N_2 thus providing a convenient screening procedure for BNF ability before field experimentation (Graham, 1981). The inherent ability of the beans to support nitrogen fixation should not be altered under field conditions although the efficiency of using fertilizer or soil nitrogen, or both, may alter the absolute amount of nitrogen fixed (Rennie, 1979). Recently, St. Clair (1986) pointed out that shoot N can be used as an effective selection criterion for measuring nitrogen fixation in plants with similar plant type and maturity grown on a low-N soil.

Thus, as stated by Graham (1981) and Bliss (1985), the selection and breeding of high N_2 fixing bean genotypes is an important step toward increasing seed yields in both optimal and suboptimal conditions. A bean genotype displaying a quick vigorous seedling establishment with ability for high BNF may have more chance of success in a stressed environment. The experiments conducted so far in this research partially support this hypothesis, however, a further critical study in the greenhouse and in the field involving a few good and poor N fixer genotypes is needed to test the hypothesis.

REFERENCES

Bliss, F.A. 1985. Breeding for enhanced dinitrogen fixation potential of common bean (*Phaseolus vulgaris* L.). In: P.W. Ludden and J.E. Burris (Eds.). Nitrogen Fixation and CO_2 metabolism. Proc. 14th Steenbock Symposium, 17-22 June 1984, University of Wisconsin, Madison. Elsevier Science Publishing Co., pp. 303-310

Chapman, A.L. and R.C. Muchow. 1985. Nitrogen accumulated and partitioned at maturity by grain legumes grown under different water regimes in a semi-arid tropical environment. Field Crops Research 11:69-79

Graham, P.H., and J.C. Rosas. 1977. Growth and development of indeterminate bush and climbing cultivars of *Phaseolus vulgaris* L. inoculated with *Rhizobium*. J. Agric. Sci. Camb. 88:503-508

Graham, P.H. 1981. Some problems of nodulation and symbiotic nitrogen fixation in *Phaseolus vulgaris* L. : a review. Field Crops Res. 4:93-112

Izquierdo, F.J.A. 1981. The effect of accumulation and remobilization of carbon assimilate and nitrogen on abscission, seed development, and yield of common bean (*Phaseolus vulgaris* L.) with differing architectural forms. Ph.D. Thesis, Michigan State university, East Lansing p. 188

McFerson, J., Bliss, F.A., and J.C. Rosas. 1982. Selection for enhanced nitrogen fixation in common beans (*Phaseolus vulgaris*). In: P.H. Graham and S. Harris (Eds.), Biological Nitrogen Fixation Technology for Tropical Agriculture, CIAT Series No. 03E-5 (82) pp. 39-44

McFerson, J. 1983. Genetic and breeding studies of dinitrogen fixation in common bean, (*Phaseolus vulgaris* L.). Ph. D. Thesis, University of Wisconsin, Madison p. 147

Pacowsky,R.S., Bayne, H.G., and G.J. Bethlenfalvay. 1984. Symbiotic interactions between strains of *Rhizobium phaseoli* and cultivars of *Phaseolus vulgaris* L. Crop Sci. 24:101-105

Pate, J.S. and F.R. Minchin. 1979. Comparative studies of carbon and nitrogen nutrition of selected grain legumes. In: R.J. Summerfield and A.H. Bunting (Eds.), Advances in Legume Science, London HMSO pp. 105-114

Rennie, R.J. 1979. Comparison of ^{15}N-aided methods for determining symbiotic dinitrogen fixation. Rev. Ecol. Biol. Sol. 16:455-463

Rennie, R.J., and G.A. Kemp. 1981a. Selection for dinitrogen-fixing ability in *Phaseolus vulgaris* L. at two low-temperature regimes. Euphytica 30:87-95

Rennie, R.J., and G.A. Kemp. 1981b. Dinitrogen fixation in pea beans (*Phaseolus vulgaris*) as affected by growth stage and temperature regime. Can. J. Bot. 59:1181-1188

Rosas, J. 1983. Partitioning of dry matter, nitrogen fixation, and seed yield of common bean (*Phaseolus vulgaris* L.) influenced by plant genotype and nitrogen fertilization. Ph. D. Thesis, University of Wisconsin, Madison p. 127

Rosas, J.C. and F.A. Bliss. 1986. Host plant traots associated with estimates of nodulation and nitrogen fixation in common bean. Hortscience 21:287-289

Sinclair, T.R. and C.T. de Wit. 1975. Photosynthate and nitrogen requirements for seed production by various crops. Science 189:565-567

Sprent, J.I. 1981. Nitrogen fixation. In: L.G.Paleg and D. Aspinall (Eds.), Physiology and Biochemistry of Drought Resistance in Plants. Academic Press, Australia pp.131-143

St. Clair, D.A. 1986. Segregation, selection, and population improvement for ^{15}N-determined dinitrogen fixation ability in common beans (*Phaseolus vulgaris*L.). Ph. D. Thesis, University of Wisconsin, Madison p. 90

Summerfield, R.J. 1981. Adaptation to environments. In: C. Webb and G. Hawtin (Eds.). Lentils. ICARDA, Page Bross (Norwich) Ltd. pp 91-110

Wallace, D.H., K.S. Yourstone and P.N. Massaya. 1987. Daylength modulation of partitioning to yield and its control by a single photoperiod gene of bean (*Phaseolus vulgaris* L.). Agron. Abst. 79:102

Ziska, L.H., Hall, A.E., and R.M. Hoover. 1985. Irrigation management methods of reducing water use of cowpea (*Vigna unguiculata* [L.] Walp.) and lima bean (*Phaseolus lunatus* L.) while maintaining seed yield at maximum levels. Irrig. Sci. 6:223-239

CHAPTER 4

PLANT TRAITS RELATED TO PRODUCTIVITY IN BEANS (*Phaseolus vulgaris* L.) UNDER STRESS AND NON-STRESS CONDITIONS.

INTRODUCTION

The Mexican Plateau is the largest bean producing area in Mexico. In this area, the bean crop depends on unreliable natural rainfall to meet the moisture requirements of the crop. Drought is a severe problem during the early flowering and pod filling stages of the bean crop. Usually, farmers plant beans following the onset of the rainy season during June or early July. In most years, the crop meets its moisture requirements during the vegetative phase but the frequency of occurrence of drought increases later during the reproductive stage.

The breeding of crop plants for drought tolerance has been the goal of breeders for a long time, although progress in this area of research has been slow. In fact, breeding for drought resistance has been considered elusive and frustrating. For example, Arnon (1980) pointed out that breeding for drought resistance was probably the greatest source of wasted breeding effort in the whole field of plant breeding.

Drought occurs in many different ways and one of the difficulties in improving the yield of bean plants exposed to drought under uncertain rainfall patterns, as is the case in the Mexican Plateau. The difference in timing and intensity of drought stress can influence the final crop yield in various ways. In other words, drought is multifaceted, varying greatly over different production regions and often interacting with other detrimental factors such as high temperatures, pathogenic soil fungi and the use of marginal soils to grow beans (Singh and White, 1988).

Hanson (1980), has listed the various types of drought adaptive mechanisms found in sorghum; mechanisms which probably are also important in most crop plants: phenological, morphological, physiological and biochemical. However, these adaptations should not be considered singly since they are largely interrelated; for example, many biochemical and physiological responses to drought stress influence crop growth and the final yield through changes in phenology and morphology. Although progress has been achieved in the understanding of basic physiological and biochemical responses of plants subjected to drought stress, much more remains to be learned. At the present time, in the improvement of any species for drought tolerance, breeders have to rely on two of the adaptive mechanisms indicated by Hanson (1980), namely, phenological and morphological attributes.

During the evolution of higher plants, successful colonization of terrestrial environments was largely due to a wide array of phenological and morphological adaptations, whereas the basic biochemical apparatus remained essentially unchanged (Begg, 1980). Modifications of plant form and structure and changes in the number of plant parts may affect reproductive fitness. Thus, it can be argued that progress might be made in breeding for drought tolerance with the aid of phenological and morphological traits that are related to drought response in crop plants.

In cowpeas, some of the advances made toward increased productivity in moisture stress environments are through a decrease in the length of time for a crop to reach maturity (Hall and Patel, 1985). However, earliness as a trait is not favored among breeders because in many crops it has consistently been shown that a negative correlation exists between yield and early maturity. Beans grown in rainfed areas in Latin America are expected to be under moisture deficits during their reproductive phase (Laing et al., 1983). Therefore, it seems that indeterminate, mid-season cultivars with developmental plasticity are the most appropriate to develop for the sporadic rainfall patterns of the semi-arid Mexican Plateau. It is assumed that mid-season cultivars may be able to produce high yields in those years when above normal moisture is available and may also be able to accelerate their cycle and produce relatively well in the face of terminal drought.

In this study, research is concentrated, among other traits, on those adaptative features which are intermediary in character, i.e. leaf area, (quantified at a particular time, not the integral of leaf area duration over time), or which have an overall integrative effect such as shoot biomass and seed yield per se. The objectives of the research reported herein were : 1) To determine growth and yield responses to drought stress in 26 bean genotypes grown in two different locations, and 2) To evaluate the responses in order to determine whether any traits other than yield per se are amenable for use by plant breeders during selection for drought tolerance.

MATERIALS AND METHODS

Two experiments were conducted during summer of 1987, one at the Centro de Investigaciones Forestales y Agropecuarias (CIFAP) field station in F.I. Madero, Durango, Mexico, and the other at the Kellogg

Biological Station (KBS) of Michigan State University near Battle Creek, MI. The Durango site is located at 24° 20' North and 104° 20' West, at an altitude of 1932 masl, and the soil is a Luvic chernozem (Typic Argiudoll, FAO classification) from volcanic ash with overlaying fragmented rock and low organic matter content. The KBS site is located at 42° 25' North and 85° 30' West, at an altitude of 250 masl, and the soil is a Kalamazoo sandy loam (Fine-loamy, mixed mesic, typic Hapludolf, FAO classification).

A separate randomized complete block design experiment with three replications was used with 26 genotypes (Table 1, previous Chapter, except PUE 152) at two moisture levels in each location, with differential drought stress induced by use of a rain-shelter and natural rainfall plus irrigation. Experimental plots consisted of a single row 4-6 m in length per genotype, depending on space under rain-out shelters in both locations. Planting dates in Michigan were June 6th and 10th, for stressed and irrigated portions of the experiment, respectively. In Durango, both parts of the experiment were planted on July 4th, however, at this site water for irrigation was not available and thus it was a stressed and a rainfed experiment. Plant stand in Michigan was approximately 20 plants/m^2 and was 10 plants/m^2 in Durango. At both locations, plant stands used were similar to those used by the farmers in commercial fields. In the stressed part of the experiment at both sites, plots were protected against rains from the beginning of flowering (most of the genotypes) to physiological maturity. This protection was achieved with the aid of an automated rain-out shelter at KBS and with a set of minishelters consisting of polyethylene sheets over gabled metal frames (1.5 m height at the mid point) at Durango.

PLANT SAMPLING AND MEASUREMENTS

Plant samples were taken at three times during the growth cycle as follows : 40 days after emergence (40 DAE), 57 or 60 DAE and at physiological maturity (PM). For the first two sampling dates, the plants of a 0.5 m section of row were cut at the soil level and dissected to determine leaf area index (LAI) with the use of a leaf area meter (LI-3000, LICOR instruments, Lincoln NB.) and the leaves, stems and branches oven dried and weighed. Abscissed and yellow leaves in the sample were not included, however, during the second sampling date, their weights were recorded to quantify the amount of abscission in response to moisture treatments. At the second sampling date, the weight of developing pods was also included. Five days after drought treatment was established, leaf expansion rate (LER) was estimated daily for two weeks from the product of leaflet length and width measurements using a linear regression equation. The equation was determined with the use of the actual area of leaves measured directly with the leaf area meter and regressed against the length times the width of the same leaflets. A regression equation was calculated for each genotype. In the Durango experiment, during the second sampling time, three fully expanded leaves, uniform in size, were cut from different plants in a plot and used to determine the leaf water content (LWC) and leaf water retention capacity (LWRC) at 24 and 48 hours after excision.

At physiological maturity, a 2 m section of row per genotype was harvested to quantify the amount of total dry matter (TDM) excluding the leaves, which were removed in late maturing genotypes for uniformity of comparisons. Weights of remaining aerial parts are highly correlated with the actual total biomass (Wallace et al., 1987). In the same sample, the seed yield, yield components, harvest index, percent of seed protein and total amount of protein produced in seeds/m^2 were determined.

In the Durango experiment, three plants exhibiting a uniform degree of maturity were used to estimate visually the amount of carbohydrates in the stem with the use of an iodine-potassium iodide (IKI) indicator as described by Adams et al. (1978) and Izquierdo (1981).

PLANT TRAITS

From plant sampling and measurements, a total of 33 trait-variables were calculated. Different numbers of traits per location and water regime are presented in detail because they (i) were recorded after stress treatment was imposed, and/or exhibited (ii) significant variation among genotypes and/or (iii) significant correlation with seed yield or TDM at maturity. The traits were grouped in sets according to the method of measurement and/or agronomic basis of the trait (Table 1).

Statistical analyses

Data for each trait were analyzed within moisture treatment for each location, and a combined analysis of variance including both locations was performed following McIntosh (1983). A stability analysis was performed by considering each moisture treatment-location as a distinct environment. For each moisture level per location, phenotypic correlations using means of three replications were estimated and used to study the association of seed yield and total dry matter (excluding leaves) at maturity with the rest of the variables. Although simple correlations are not indicative of cause and effect, they show the degree and direction of associations between two traits.

Table 1. List of plant traits measured in 26 bean genotypes grown under two moisture regimes at two locations. 1987

Variable	Abbreviation
Phenological	
No. of days from sowing to 50 % flowering.	Flow
No. of days from sowing to physiological maturity.	PhyMa
Length of reproductive phase (days)	RePha
Biomass*	
Dry weight of leaf lamina at 40 DAE** (g/m^2)	LeWt1
Dry weight of stems at 40 DAE (g/m^2)	SmWt1
Shoot dry weight at 40 DAE (g/m^2)	TDM1
Dry weight of leaf lamina at 57 and 61 DAE*** (g/m^2)	LeWt2
Dry weight of stems at 57 and 61 DAE (gm^2)	SmWT2
Dry weight of developing pods (g/m^2)	PodWt
Shoot dry weight at 57 and 61 DAE (g/m^2)	TDM2
Shoot dry weight at physiological maturity (g/m^2)	TDM
Dry weight of senesced leaves (g/m^2)	WtSeLe
Physiological	
Leaf area index at 40 DAE	LAI1
Crop growth rate at 40 DAE $(g/m^2/d)$	CGR1
Net assimilation rate at 40 DAE $(g/m^2/d)$	NAR1
Leaf weight ratio at 40 DAE	LWR1
Leaf area index at 57 and 61 DAE	LAI2
Crop growth rate at 57 and 61 DAE $(g/m^2/d)$	CGR2
Leaf weight ratio at 57 and 61 DAE	LWR2
Net assimilation rate at 57 and 61 DAE $(g/m^2/d)$	NAR2
Leaf expansion rate $(cm^2/leaflet/d)$	LER
Leaf water content (% dry wt. basis)(1)	LWC
Leaf water retention capacity (% dry wt. basis)(1)	LWRC
Crop Growth Rate average	CGRAV
Chemical composition	
Seed protein in per cent	SePro
N seed yield (g/m^2)	Nitro
IKI visual score (1)	IKI
Yield and components	
Seed yield (g/m^2)	Yield
Number of pods/m^2	Pods
Number of seeds per pod	Seeds
100 seeds weight (g)	SeWt
Harvest Index	HI

---

* Above-ground plant parts.

** Days after emergence.

*** At 57 and 61 DAE in Durango and Michigan, respectively.

(1) Traits only recorded in Durango.

Principal Component Analysis (PCA) was used to identify the characteristics representing the components accounting for most of the variation associated with each set of data. Varimax rotation was employed to accentuate the traits with larger loadings and facilitate the biological interpretation in each component. Two sets of data were formed with average values of 28 and 25 characteristics measured on the twenty six genotypes under both water regimes at Durango and Michigan, respectively. All traits, except those recorded at maturity, were subjected to Multiple Regression Techniques to determine which trait(s) could account for the largest proportion of the variation among the genotypes for seed yield and biomass at maturity. Variables resulting in the highest R^2 as single traits or in combination with other traits were then selected to be used in the development of the best model for seed yield and biomass at maturity in each location and water regime. Plant traits were used as independent variables and seed yield and biomass as dependent variables.

RESULTS AND DISCUSSION

Significant variation was found for moisture treatments and among bean genotypes per location and averaged over locations (Tables 1, 2, and 3, Appendix C). In the analyses per location, more variables showed a highly significant genotype X water regime interaction at KBS (Table 2, Appendix C) than at Durango (Table 3, Appendix C). It seems that the genotype X environment interactions at the KBS-site were due largely to highly contrasted environments encountered by the genotypes between the irrigated and stressed plots. At this site, the genotypes were able to express more completely their genetic potential for yield under the irrigated regime. The calculated drought intensity index (DII) at KBS was equal to 0.58, while at Durango it was 0.38. In this case, however the lower DII does not mean that the stress imposed at this site was less than the one imposed at KBS. Instead, it means that in Durango the difference between the stressed and non-stressed plots was smaller than at KBS due to the lack of irrigation and the inability of the genotypes to express their maximum genetic potential.

In Table 2, the mean yield per water treatment and site indicates that the stressed environment in KBS can be considered moderate, and equivalent, in terms of moisture stress, to the rainfed environment of Durango. From this table, it can also be seen that the range for seed yield under severe stress is limited in comparison to the range observed at KBS under irrigation. It is important to point out that the top yielders under stress include parental as well as recombinant genotypes, whereas under irrigation the top yielders are only recombinant progeny. This situation indicates that the level of drought tolerance of the parents was incorporated among some of the progenies, however, it seemed difficult to obtain superior transgressive segregants for drought tolerance. As indicated by the irrigation experiment at KBS, segregants with superior yield potential were also obtained, even though the evaluated genotypes were previously selected under mild drought stress conditions.

The above results imply that selection for drought tolerance at higher yield potentials may be difficult. In addition, the fact that the genotype 8-47 was among the top yielders under stress and non-stress in Michigan and one of the low yielders in Durango indicates that the association between yield potential and drought tolerance becomes weaker as the stress level increases. A further complication is that some other

Table 2. Seed yield of 26 bean genotypes grown under two moisture regimes at two locations. 1987

	Durango		Michigan (KBS)	
Genotype	stressed	rainfed	stressed	irrigated
	g/m²			
48-10	78.9	110.1	119.9	219.5
48-66	78.7	106.1	134.0	251.8
8-25-2	75.1	103.5	80.2	186.9
48-94B-1	70.8	109.4	127.3	293.1
9-39-1	64.9	86.6	85.0	184.7
8-3	53.5	117.8	77.9	187.5
8-15-1	62.0	120.0	86.9	318.5
39-17-1	78.7	131.4	83.3	189.7
8-42-M-1	69.6	133.1	118.4	299.7
8-42-M-2	69.6	141.7	125.8	301.0
48-18-1	61.4	104.8	111.4	268.5
41-39	50.3	95.8	101.0	363.1
8-4	59.6	81.4	102.2	213.9
41-48-1	64.6	98.7	123.4	238.0
8-47	41.8	69.1	136.7	371.5
48-109	50.0	115.4	130.5	258.5
51-29-3	45.3	122.8	105.8	251.7
51-5-3	57.0	111.2	88.6	282.8
8-17	62.3	128.9	102.7	326.0
N81017	65.8	111.2	109.8	231.2
Lef-2-RB	65.2	104.2	106.5	295.1
UW 21-58	52.3	93.4	95.2	270.9
UW 23-61	67.8	125.0	136.9	259.2
Bayo Madero	79.2	158.3	83.4	236.3
II-900-5-M-45	73.1	114.7	139.7	293.6
Katolika	85.1	113.6	123.9	291.0
Site mean	64.7	111.8	109.1	264.8
Range	45.3-85.1	69.1-158.3	80.2-139.7	184.7-371.5
LSD (0.05)	23.8	34.2	24.3	47.3
C.V. %	22.6	18.6	18.5	13.8

environmental factors and interactions become apparent when evaluating genotypes in different environments. Furthermore, it is only under severe water stress that the drought tolerance mechanisms are totally expressed and yield maintained in the most tolerant types.

In general, the rank of the genotypes in the different test environments was markedly different; the exception was the family 9-39-1 which was among the poor responders, and the parental genotypes N81017 and II900-5-M-45 which were among the better performers (Table 2). The genotypic mean yield and some stability parameters were calculated to further assess the adaptability of the genotypes (Table 3). A range of responses in adaptation was obtained as indicated by the regression slope values of the genotypes. The majority of the genotypes displayed slopes stastistically equal to 1.0, even though many of them are arithmetically different; this occurs because the associated error is relatively large. The five top yielders include four of the F7 families and one of the parental genotypes. Some genotypes such as 8-42-M-2, 8-42-M-1, 48-18-1, II900-5-M-45 and check cultivar Katolika, seem to respond relatively well to the test environments. Families 8-47 and 41-39 showed a high response to favorable moisture conditions. Results shown by genotypes like 8-47, which exhibited a large Sd^2 value, should be viewed with caution. Since the climatic conditions in Michigan were more favorable than those in the Mexican Plateau (Tables 4 and 5, Appendix C), this evaluation for wide adaptation may imply the risk of selecting for mediocrity for the Michigan environment. This statement is reinforced by an observed highly significant positive relationship among the regression slopes of the individual cultivars and yield under irrigation in Michigan (R^2 = 0.96 ***).

Table 3. Mean seed yield and stability parameters of 26 bean genotypes grown under stress and non-stress conditions in Durango (Mexico) and Michigan (USA). 1987

Genotype	Mean yield		b(1)	Sd^2(2)	R^2(3)
	g/m^2				
8-42-M-2	159.5	|@	1.13	95.4	0.994
II-900-5-M-45	155.2	|	1.09	201.9	0.985
8-42-M-1	155.2	|	1.14	38.9	0.997
8-17	155.0	|	1.34*	147.1	0.993
8-47	154.8	|	1.68	1394.0	0.959
Katolika	153.4	|	1.06	122.5	0.991
41-39	152.6	|	1.62*	262.1	0.991
48-94B-1	150.1	||	1.12	114.8	0.992
UW 23-61	147.2	||	0.91	215.3	0.978
8-15-1	146.8	||	1.32	346.3	0.983
Lef-2-RB	142.7	|||	1.12	75.2	0.995
48-66	142.6	|||	0.86	229.5	0.974
Bayo Madero	139.3	||||	0.78	1339.9	0.838
48-109	138.6	||||	0.98	357.0	0.969
48-18-1	136.5	|||||	1.04	22.4	0.998
51-5-3	134.9	|||||	1.15	128.2	0.992
48-10	132.1	|||||	0.69*	40.7	0.993
51-29-3	131.4	|||||	0.98	258.0	0.997
41-48-1	131.2	|||||	0.85	203.3	0.976
N81017	129.5	|||||	0.81*	20.8	0.997
UW 21-58	128.0	|||||	1.11	33.9	0.998
39-17-1	120.7	||||	0.55	545.5	0.864
8-4	114.3	|||	0.78	136.7	0.981
8-25-2	111.4	|||	0.58*	152.6	0.962
8-3	109.2	||	0.64	444.4	0.914
9-39-1	105.3	|	0.61**	18.5	0.996

@ Duncan's Multiple Range Test (0.05).
* b is different from 1 at a $P<0.05$
(1) Regression coefficient.
(2) Sum of squares from deviations.
(3) Coefficient of Determination.

Evidently, the bean crop in Michigan encounters different environmental conditions than those in the Mexican highlands, not just with regard to the drought stress, but other factors determined by the physical environment and/or by cultural practices. The varieties better adapted and widely grown in these two distinct places display strong differences in morphology (Kelly et al., 1987; Acosta and Khohashi, 1988) and they probably possess different attributes with which to cope with drought. In addition, as Singh and White (1988) pointed out, much research has been conducted for unspecified drought conditions, implicitly assuming that drought is a single, well defined condition. This is most assuredly not the case. Therefore, before starting a breeding program for drought tolerance in any region, the soil and climatic conditions should be characterized to determine the level and kind of tolerance that is needed.

Given the difference in drought situation between Durango (Mexico) and Michigan, in the rest of this report results from each location will be presented and discussed separately.

Experiment in Michigan (KBS)

With the exception of the weight of the leaves at 61 DAE, there was a significant detrimental effect of the water stress treatment for all the recorded traits and calculated variables (Table 4). The stress slightly reduced the length of the reproductive phase and therefore the whole cycle was reduced as indicated by the number of days needed to reach maturity.

Those traits most affected by drought were those related to growth, the dry weight of the developing pods at 61 DAE and TDM at maturity. Since there was no difference between treatments in the time at which

Table 4. Effect of two moisture regimes on plant traits of 26 bean genotypes. Kellogg Biological Station, Battle Creek, MI. 1987

	Variable	Rainfed	Stressed	Reduction in %
Phenological				
	PhyMa	91.2**	87.3	4.3
	RePha	47.3**	43.5	8.0
Biomass@				
	LeWt2	103.5 NS	102.7	0.8
	SmWt2	175.0 *	157.0	10.3
	PodWt	115.0 **	72.5	37.0
	TDM2	357.8 *	313.3	12.4
	TDM (1)	520.9 **	315.8	39.4
Physiological				
	LAI2	3.38 *	2.98	11.8
	CGR2	5.87 *	5.14	12.4
	LWR2	0.30 *	0.33	-9.1
	LER	2.87 **	1.03	64.1
	CGRAV(2)	6.02 *	3.45	42.7
Chemical composition				
	SePro	21.9 **	29.4	-35.5
	Nitro	8.87 **	4.87	45.1
Yield and components				
	Yield	264.8 **	109.1	58.8
	Pods	265.2 **	178.3	32.8
	Seeds	4.61 **	3.00	34.9
	SeWt	21.7 *	21.0	3.2
	HI	0.51 *	0.35	31.4

*,** Significant at $P<0.05$ and 0.01, respectively.

@ Above-ground plant parts.

(1) Leaves not included.

(2) Average of 21 days after stress was established.

the genotypes commenced flowering, the weight of developing pods can be considered as a gross estimate of partitioning to the economic plant parts. Although translocation is considered one of the less sensitive physiological traits affected by water stress (Hsiao, 1973) and since partitioning depends on translocation, its reduction is important and very similar to the calculated index for partitioning at maturity i.e. HI. TDM at maturity, as measured in this study, was reduced in the same proportion as the developing fruits (Table 4).

Water deficit affects many aspects of crop growth, development and yield. Hsiao (1973) stated that almost any trait of crop growth is affected by water stress, provided that the stress is severe and lasts long enough. Of the physiologically related traits, the LER and the average CGR were the most affected by water stress. The large decrease in LER indicated the marked sensitivity of leaf expansive growth to water deficits (Figure 1). From Figure 1, it is apparent that the stress was building up slowly as indicated by the slight reduction in leaf expansion at 8 days after it was imposed. As a consequence of the reduced expansion in leaf growth, the CGR, measured as a daily average of 21 days during the stress build up, was also markedly reduced (Table 6).

Under both stress and non-stress, LER was positively and significantly associated with all the phenological variables while negatively associated with dry weight of the developing pods. Since LER and the weight of the developing fruits were measured at the same growth stage, this negative association between them at the beginning of pod filling suggests competition for assimilates between these plant organs.

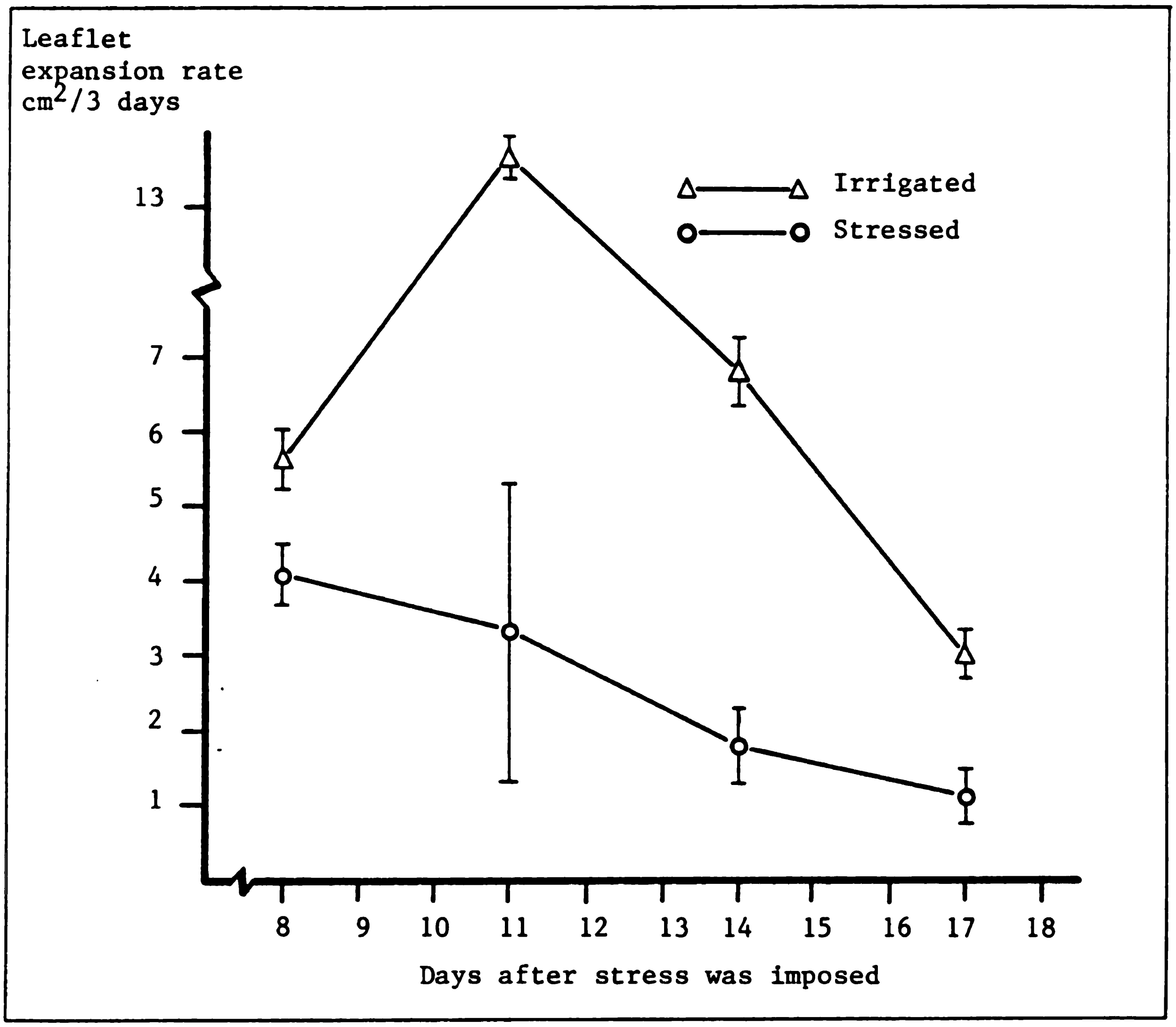


Figure 1. Average leaf expansion rate of 26 bean genotypes grown under irrigated and water stressed conditions. Kellogg Biological Station, Battle Creek, MI. 1987.

Since expansive growth can be viewed as an integrator of the metabolic and environmental events that influence over-all plant productivity (Braford and Hsiao, 1982), it may be justifiable to determine the amount of genetic variation for LER available to the breeders and its usefulness as a selection criterion. LER was previously suggested as a negative index of drought sensitivity in several crops (Boyer, 1970; Hsiao and Acevedo, 1974; Boyer and McPherson, 1975; Sammons et al., 1978). Vidal and Arnoux (1981) found in soybeans a high correlation between the reduction in leaf expansion and petiole growth on the one hand, and the reduction in biomass and seed yield under stress, on the other.

The percentage of protein in seeds was highly reduced under irrigation, demonstrating the negative association between seed protein content and yield. However, the total amount of protein harvested in the seeds per unit area was severely reduced by the stress since yield was also significantly reduced.

In the case of seed yield, an average reduction of 58.8 % under stress showed the accumulated effect of drought stress upon the economic product. Using the individual yield per genotype under both stress and non-stress, different drought susceptibility indices were calculated (Table 5). Genotypes 8-47, 8-42-M-2, 48-94B-1 and 41-39 showed a good yield response under both drought stress and non-stress conditions as indicated by their geometric mean values, while genotypes 8-3, 8-25-2, 9-39-1 and 39-17-1 obtained the lowest values with the use of this index. In general, the percent reduction of seed yield under stress did not agree with the ranking obtained with the use of the geometric mean; the best genotypes as identified by the geometric mean showed higher

Table 5. Drought tolerance indices of 26 bean genotypes grown under two moisture regimes. Kellogg Biological Station, Battle Creek MI. 1987

Genotype	Arith. mean		Geom. mean	Yield reduct. %	Drought suscep. index(1)
	------------ g/m^2		-------------		
8-47	254.1	|@	225.3	63.2	1.1
41-39	232.0	||	191.5	72.2	1.2
48-94B-1	220.2	|||	193.2	56.6	1.0
II-900-5-M-4	216.6	||||	202.5	52.4	0.9
8-17	214.3	||||	183.0	68.5	1.2
8-42-M-2	213.4	||||	194.6	58.2	1.0
8-42-M-1	209.0	||||	188.3	60.5	1.0
Katolika	207.4	||||	189.9	57.4	1.0
8-15-1	202.7	||||	166.3	72.7	1.2
Lef-2-RB	200.8	||||	177.3	63.9	1.1
UW 23-61	198.0	||||	188.4	47.2	0.8
48-109	194.5	||||	183.7	49.5	0.8
48-66	192.9	||||	183.7	46.8	0.8
48-18-1	189.9	||||	172.9	58.5	1.0
51-5-3	185.7	||||	158.3	68.7	1.2
UW 21-58	183.0	||||	160.6	64.9	1.1
41-48-1	180.7	|||||	171.4	48.2	0.8
51-29-3	178.7	||||||	163.2	58.0	1.0
N81017	170.5	|||||	159.3	52.5	0.9
48-10	169.7	|||||	162.2	45.4	0.8
Bayo Madero	159.8	||||	140.4	64.7	1.1
8-4	158.0	||||	147.9	52.2	0.9
39-17-1	136.5	|||	125.7	56.1	1.0
8-25-2	135.5	||	122.4	57.1	1.0
9-39-1	134.8	||	125.3	54.0	0.9
8-3	132.7	|	120.9	58.5	1.0
Average	187.0		169.2	58.8	1.0

(1) Fischer and Maurer (1978), Appendix A.

@ Duncans' Multiple Range Test (0.05).

than average yield reductions under stress. Nevertheless, the percent reduction agreed with the drought susceptibility index of Fischer and Maurer (1978) (r=0.98 ***). Therefore, these latter two indices should be used to separate genotypes which display yields above the average of the test, particularly if the degree of the stress in the target region is not severe. Some genotypes, e.g. 48-66, seem to display true drought tolerance as indicated by the values obtained with all the calculated indices.

The relationship between seed yield under stress and irrigated conditions indicated the presence of genotypes which displayed both drought tolerance and good response under irrigation (r=0.43 **).

The number of pods/m^2 and the number of seeds/pod were markedly and equally affected by the stress, while the weight of 100 seeds remained almost unchanged (Tables 6 and 7). In spite of the relative mildness of the stress, it was enough to diminish the setting of pods at the beginning of the reproductive phase and continued with the same intensity during the rest of the cycle, creating a strong intra-ovary competition, leading to reduction in the number of seeds/pod. Stress markedly decreased HI values (Tables 6 and 7); although some genotypes did not show a significant decrease, e.g. 48-94B-1 and N81017. Thus, it appears that differences in partitioning under stress exist among genotypes. The data confirm work reported that N81017 is a good remobilizer of stored assimilates towards the economic product under drought stress (Samper et al, 1984).

Simple correlation values of seed yield and TDM at maturity with other traits are presented in Table 8. Under stress and non-stress, yield was essentially associated with TDM, HI and two of the primary

Table 6. Yield components, TDM and HI of 26 bean genotypes grown under irrigation. Kellogg Biological Station, Battle Creek, MI. 1987

Genotype	Pods /m^2	Seeds /pod	100 Seed weight	TDM	HI
			------- g -------		
48-10	209.7	4.4	25.2	410.0	0.54
48-66	251.0	4.7	22.1	517.7	0.49
8-25-2	277.3	4.1	17.4	368.7	0.50
48-94B-1	300.7	4.2	19.6	496.7	0.59
9-39-1	220.0	4.9	18.1	404.7	0.46
8-3	252.3	4.8	15.9	424.4	0.44
8-15-1	276.7	4.5	20.7	584.0	0.54
39-17-1	301.7	3.7	23.4	437.9	0.44
8-42-M-1	229.7	4.8	24.7	585.3	0.51
8-42-M-2	222.7	5.3	27.4	588.1	0.51
48-18-1	295.0	4.3	21.8	532.1	0.50
41-39	311.7	3.8	23.3	680.1	0.55
8-4	222.0	5.2	17.4	519.6	0.41
41-48-1	283.7	4.6	19.3	441.9	0.54
8-47	289.3	5.5	19.0	800.3	0.46
48-109	278.0	4.6	21.3	467.0	0.55
51-29-3	296.0	3.9	23.1	436.0	0.58
51-5-3	332.0	3.8	22.4	425.4	0.68
8-17	278.7	5.0	20.8	610.3	0.53
N81017	305.0	4.3	18.8	524.6	0.44
Lef-2-RB	261.3	4.7	25.7	516.4	0.57
UW 21-58	239.3	6.4	18.7	579.0	0.47
UW 23-61	334.7	4.6	18.7	488.6	0.53
Bayo Madero	172.7	3.3	32.7	552.4	0.43
II900-5-M-45	231.7	4.6	23.4	531.5	0.56
Katolika	223.0	5.5	23.1	621.9	0.48
Average	265.2	4.6	21.7	520.9	0.51

Table 7. Yield components, TDM and HI of 26 bean genotypes grown under stress. Kellogg Biological Station, Battle Creek, MI. 1987

Genotype	Pods /m^2	Seeds /pod	100 Seed weight	TDM	HI
			-------- g --------		
48-10	177.3	3.0	22.5	325.4	0.37
48-66	189.3	2.9	26.5	414.1	0.32
8-25-2	174.0	2.0	19.6	374.1	0.21
48-94B-1	240.3	3.1	18.0	253.9	0.51
9-39-1	82.0	4.1	19.8	237.8	0.36
8-3	154.7	3.1	16.9	239.9	0.32
8-15-1	145.3	2.8	20.7	295.5	0.30
39-17-1	140.0	2.6	25.2	359.8	0.23
8-42-M-1	192.7	2.8	24.1	355.7	0.33
8-42-M-2	137.0	3.5	27.7	341.7	0.37
48-18-1	205.3	2.8	20.2	337.6	0.34
41-39	148.3	2.6	22.7	304.4	0.33
8-4	164.3	3.1	19.7	363.2	0.29
41-48-1	212.3	3.5	15.8	272.6	0.45
8-47	197.3	3.3	20.3	348.2	0.39
48-109	180.7	3.5	19.9	318.1	0.41
51-29-3	196.0	2.8	18.3	240.5	0.43
51-5-3	219.7	2.3	16.6	267.5	0.33
8-17	199.7	2.7	20.5	300.7	0.34
N81017	201.0	2.9	18.5	266.8	0.41
Lef-2-RB	189.0	2.5	22.2	274.4	0.39
UW 21-58	144.0	3.4	19.6	279.1	0.34
UW 23-61	284.0	3.1	15.1	301.4	0.45
Bayo Madero	100.3	2.8	31.0	342.0	0.24
II900-5-M-45	168.3	3.9	21.2	387.5	0.36
Katolika	192.3	3.0	24.3	410.3	0.31
Average	178.3	3.0	21.0	315.8	0.35

Table 8. Correlation coefficients of seed yield and TDM at maturity with some characteristics of phenology, plant growth and primary yield components of 26 bean genotypes grown under two moisture regimes. Kellogg Biological Station, Battle Creek MI. 1987

	Seed yield		TDM	
Variable	Stressed	Irrigated@	Stressed	Irrigated@
TDM at 40 DAE	-.13	.54**	-.05	.48**
LAI at 40 DAE	.14	.52**	.03	.45*
LAI at 61 DAE	.25	.36	.61**	.39
CGR at 40 DAE	.13	.54**	.05	.48*
Leaf exp. rate	.18	.27	.41*	.16
Days to flowering	.00	.22	.49*	.47*
Days to maturity	.02	.03	.53**	.11
Length rep. phase	.03	.24	.50**	-.23
No. pods/m^2	.56**	.47	.05	-.04
No. seeds/pod	.43*	.21	-.08	.40*
100 seed weight	.02	.23	.59***	.17
N in seeds (g/m^2)	.94***	.95***	.30	.80***
Seed yield (g/m^2)	----	----	.38	.83***
Harvest Index	.63***	.41*	-.51**	.16

*,**,*** significant at P<0.05, 0.01, and 0.001, respectively.

@ Rainfed and sprinkle irrigated.

yield components i.e. pods/m^2 and seeds/pod. In addition, yield under irrigation was also associated with those growth traits recorded during the first sampling date, TDM1, LAI1 and CGR1, which indicates the importance of a good initial establishment of the crop to obtain high yields under favorable conditions.

Significant correlation values of TDM with phenological traits were also observed (Table 8). Under stress, a significant and positive correlation between TDM and LAI2 and LER, both of which were measured after stress was established, point out the importance of the photosynthetic apparatus in the total accumulation of dry matter under mild stress conditions.

The level of drought tolerance exhibited by some of the recombinant families appears to be enough to cope with the occasional water stress encountered in Michigan. The addition of further tolerance, especially that conferred by survival mechanisms, may not be useful because it may lead to reduced mean yields in non-stress environments.

Experiment in Durango, Mexico

Rainfall data recorded during the growing season in this location (Table 5, Appendix C) revealed the occurrence of several drought periods during the season. Consequently, the potential yield of the genotypes grown under rainfall, which represented the non-stress environment, was not expressed. However, the severity of the stressed environment was large enough to significantly decrease yield along with almost all other recorded variables in this experiment (Table 9).

Results obtained with phenological traits were similar to those observed in Michigan; the length of the reproductive phase was reduced and thus the number of days to reach maturity. All the traits related

Table 9. Effect of two moisture regimes on plant traits of 26 bean genotypes. Durango, Mexico. 1987

	Variable	Rainfed	Stressed	Reduction in %
Phenological				
	PhyMa	90.5**	85.8	5.2
	RePha	46.2**	41.8	9.5
Biomass@				
	LeWt2	98.9 **	49.4	50.1
	SmWt2	76.3 **	46.7	38.8
	PodWt	60.5 **	39.2	35.2
	TDM2	235.7 **	135.2	42.6
	TDM (1)	194.2 **	119.2	38.6
Physiological				
	LAI2	2.72 **	1.36	50.0
	CGR2	4.13 **	2.37	42.6
	LWR2	0.43 **	0.37	14.0
	CGR (2)	8.58 **	2.70	68.5
	LER	1.84 **	0.55	70.1
	LWC	79.3 NS	81.5	-2.7
	LWRC	9.7 **	49.4	-80.4
Chemical composition				
	SePro	28.6 NS	29.1	-1.7
	Nitro	4.92 **	2.88	41.5
	IKI	2.86 *	2.62	8.4
Yield and components				
	Yield	111.8 **	64.7	42.1
	Pods	139.5 **	86.4	38.1
	Seeds	4.30 **	3.93	8.6
	SeWt	19.2 NS	19.4	-1.0
	HI	0.57 *	0.54	5.3

*,** Significant at $P<0.05$ and 0.01, respectively.
@ Above-ground plant parts.
(1) Leaves not included.
(2) Average of 17 days after stress was established.

to biomass which were measured after the stress was established were severely affected by the stress as indicated by their percent reduction (Table 9). At this site, the LER and the LAI at 57 DAE were markedly reduced. Acosta and Kohashi (1988) previously reported a positive association between LAI at this stage in development and final seed yield; in their research (Acosta and Kohashi, 1988) the cultivars were released from stress at the beginning of pod filling. In the present study, the cultivars were not released from the stress for the rest of the season and thus senescence was further hastened. The early onset of severe stress in this location was demonstrated by the decrease in LER measured one week after the stress was imposed (Figure 2). Under stress, a significant and positive correlation between LER and dry weight of senesced leaves was observed. An important consequence of reduction in leaf area and early senescence is a reduction in the rate of water use and a delay in the onset of more severe stress.

Leaf water content was essentially the same under stress and non-stress (Table 9). However, in the case of leaf water retention capacity (LWRC) of detached leaves, leaves of genotypes under non-stress lost 80 % more water in 24 hours than leaves from stressed plants (Table 10). Detached leaves were kept at room temperature (24+2° C day, 17+2 °C night, and 50+5 % relative humidity) during LWRC determination. Under stress, significant differences were found among the genotypes at 24 and 48 hours after leaves were detached ($P<0.1$ and 0.05, respectively). As expected, LWC and LWRC were positively associated with LER.

It appears that the genotypes under stress were pre-conditioned to retain their moisture, while, if grown under a more favorable soil water status they were not. Currently, the mechanism(s) the leaves used to

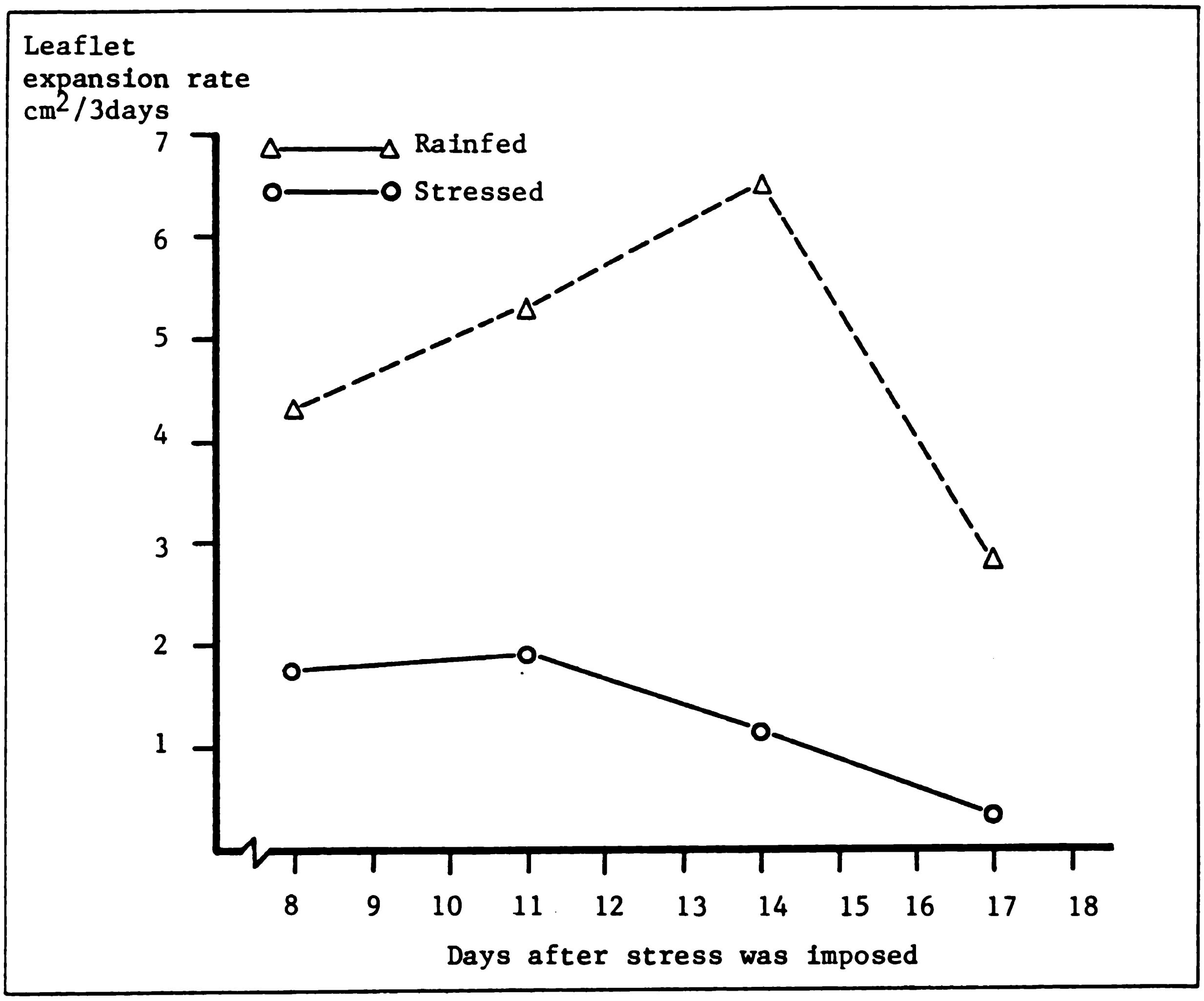


Figure 2. Average leaflet expansion rate of 26 bean genotypes grown under rainfed and water stressed conditions. Durango, Mexico. 1987.

Table 10. Leaf water content of detached leaves of 26 bean genotypes grown under drought stress and rainfed conditions at 50 DAE. Durango, Mexico. 1987

Genotype	Stressed			Rainfed	
	0 hs	24 hs	48 hs	0 hs	24 hs
			%*		
48-10	80.9	53.9	36.0	81.0	13.7
48-66	80.5	51.3	34.5	79.2	12.0
8-25-2	79.3	35.2	15.9	79.0	7.4
48-94B-1	81.4	50.9	33.0	79.9	11.2
9-39-1	82.1	46.0	26.8	81.4	20.6
8-3	77.4	43.3	23.0	76.9	10.6
8-15-1	80.2	50.3	26.1	79.5	8.0
39-17-1	79.3	46.1	26.3	79.6	13.0
8-42-M-1	80.1	47.6	28.2	80.5	9.9
8-42-M-2	80.4	49.3	26.5	78.1	7.2
48-18-1	83.2	57.1	37.5	78.4	8.1
41-39	84.3	54.6	37.7	78.0	6.5
8-4	83.5	45.0	23.1	79.5	8.5
41-48-1	80.6	51.0	29.7	79.7	7.3
8-47	79.9	41.0	20.6	81.0	7.4
48-109	80.9	49.4	32.3	79.0	9.1
51-29-3	83.0	53.4	37.8	78.2	5.4
51-5-3	82.6	54.0	33.3	79.0	7.4
8-17	83.7	54.6	33.1	79.0	11.1
N81017	79.8	44.5	22.9	80.0	7.4
Lef-2-RB	82.8	52.0	34.7	79.2	9.5
UW 21-58	78.9	45.8	26.5	81.1	14.1
UW 23-61	82.0	46.1	28.4	78.3	11.2
Bayo Madero	82.9	50.6	33.1	78.9	8.6
II900-5-M-45	86.2	58.2	41.0	80.7	12.7
Katolika	83.9	54.2	29.3	77.6	4.6
Average	81.5	49.4	29.9	79.3	9.7
LSD (0.05)	4.1	10.0	11.7	4.1	10.0

* Water percent on weight basis.

keep their moisture is not known. However, work conducted by Ibarra (personal communication, 1988) which included some of the same genotypes used in this study and the same water regimes, demonstrated that those genotypes under stress showed a reduction in stomatal conductance. Generally, stomatal closure has been reported to occur when a critical leaf water potential is reached, thus preventing a further decrease in potential. In addition, it has been suggested that increases in specific leaf weight in snap beans subjected to drought stress may be due, among other factors, to an increase in epicuticular wax (Bonnano and Mack, 1983), which could enhance cuticular resistance to water loss.

Under stress and non-stress, LWRC showed a consistent, nonsignificant negative correlation with seed yield and TDM at maturity. Assessment of water loss from excised leaves has shown some promise for differentiating between drought resistance of wheat cultivars (Dedio, 1975; Clarke and McCaig, 1982; Clarke and Townley-Smith, 1984). In this study, the low values for LWRC of genotypes under stress may indirectly indicate the ability of the genotype to extract soil water more efficiently. This is supported by negative association between LWRC with TDM and seed yield. High LWRC appears to be related to survival mechanisms.

The use of the IKI solution to visually assess the amount of starch left in the stem at maturity indicated that starch amount was slightly reduced under stress ($P<0.05$); a significant difference was detected among the genotypes for this variable under both stress and non-stress conditions and for the interaction between water regime x genotype ($P<0.01$). This variable showed a negative non-significant correlation ($r=-0.33$) with seed yield under stress. Since LER, LWRC and the IKI score showed differences among genotypes, it may be worth further work to assess their usefulness as a screening technique for drought tolerance in beans.

The calculated drought tolerance indices (Table 11) showed that local genotypes, e.g. Bayo Madero, Mex 1213-2 and Dgo-222, were the most adapted to the stress conditions of this experiment in terms of seed yield. The data from Mex 1213-2 and Dgo-222 are not shown because they were excluded from the test in Michigan due to their daylength sensitivity. Within the tested families, 39-17-1 was among the top yielders under both stress and rainfed conditions exhibiting the largest geometric mean value. The results behaved in a similar fashion to those obtained in Michigan, the ranking of the genotypes by the geometric mean was markedly different than that shown using either the yield reduction (%) or the drought susceptibility index (DSI). The later two scales both essentially gave the same result as indicated by a high correlation (r=0.99 ***) found between the ranking of the genotypes by these two indices.

Genotypes with average susceptibility or tolerance to drought have DSI values of 1.0. Values of DSI less than 1.0 indicate less susceptibility and greater adaptation to drought, with a value of DSI = 0.0 indicating maximum possible adaptation to drought (Hall and Patel, 1985). It seems that the use of either the yield reduction or the drought susceptibility index identifies those genotypes with true drought tolerance. Therefore, these indeces do not identify those genotypes which possess the ability to produce high yields under favorable conditions. In both locations, a positive relationship was observed between seed yield under <u>non-stress condition</u> and the DSI. In

Table 11. Drought tolerance indices of 26 bean genotypes grown under two moisture conditions. Durango, Mexico. 1987

Genotype	Arith. mean		Geom. mean	Yield reduct. (%)	Drought suscep. index(1)
	------g/m^2------				
Bayo Madero	118.7	|[@]	112.0	50.0	1.2
8-42-M-2	105.6	||	99.3	50.9	1.2
39-17-1	105.0	||	101.6	40.1	1.0
8-42-M-1	101.3	|||	96.2	47.6	1.1
Katolika	99.3	|||	98.3	25.1	0.6
UW 23-61	96.4	||	92.1	45.8	1.1
8-17	95.6	|||	89.6	51.7	1.2
48-10	94.5	|||	93.2	28.3	0.7
II-900-5-M-45	93.9	|||	91.6	36.3	0.9
48-66	92.4	||||	91.4	25.8	0.6
8-15-1	91.0	||||	86.2	48.3	1.1
48-94B-1	90.1	|||||	88.0	35.3	0.8
8-25-2	89.3	|||||	88.2	27.4	0.7
N81017	88.5	|||||	85.5	40.8	1.0
8-3	85.6	|||||	79.4	54.6	1.3
Lef-2-RB	84.7	||||	82.4	37.4	0.9
51-5-3	84.1	||||	79.6	48.7	1.2
51-29-3	84.0	||||	74.6	63.1	1.5
48-18-1	83.1	||||	80.2	41.4	1.0
48-109	82.7	||||	75.9	56.7	1.3
41-48-1	81.6	||||	79.9	34.6	0.8
9-39-1	75.7	||||	75.0	25.1	0.6
41-39	73.0	|||	69.4	47.5	1.1
UW 21-58	72.8	|||	69.9	44.0	1.0
8-4	70.5	||	69.7	26.8	0.6
8-47	55.4	|	53.7	39.5	0.9
Average	88.2		84.7	42.1	1.0

(1) Fischer and Maurer (1978), Appendix A.

[@] Duncans' Multiple Range Test (0.05)

general, those genotypes with small DSI were the less productive. Likewise Fischer and Wood (1979) found that in cereals drought susceptibility increased with increased non-drought yield.

However, Sojka et al. (1981) indicated that in wheat the given traits of any one cultivar which result in a high yield potential are likely to be expressed over a large range of environments and thus produce a high baseline yield under drought. This baseline must not be confused with drought resistance; drought resistance is better defined as the ability to minimize yield loss in the absence of optimal soil water availability. The challenge of applying these findings lies in transfering the ability to maintain percent yield under stress to cultivars with higher absolute yield levels. Nevertheless, with our present knowledge of the adaptation of crop plants to drought stress, it seems impractical to separate drought tolerance from agronomic performance or yielding ability.

The relationship between yield under stress and non-stress showed a positive association indicating the presence of some genotypes which respond in a similar fashion to the different applied water regimes (r =0.43 *).

Stress caused a severe reduction in pod number and a mild reduction in the number of seeds per pod, while seed weight remained unaltered (Tables 12 and 13). The number of pods/m^2 or pods/plant has consistently been the component most affected by water stress in all the experiments conducted in this research. Since the number of pods set is largely determined in the first few days of flowering, in order to evaluate a group of genotypes for adaptation to drought using the criterion of seed yield, the genotypes must be sub-divided on the basis

Table 12. Yield components, TDM and HI of 26 bean genotypes grown under water stress. Durango, Mexico. 1987

Genotype	Pods /m^2	Seeds /pod	100 Seed weight	TDM	HI
			------- g --------		
48-10	76.6	4.3	23.7	133.9	0.59
48-66	98.8	3.8	20.7	139.8	0.56
8-25-2	116.4	3.7	17.9	131.6	0.57
48-94B-1	101.2	4.1	16.9	119.6	0.59
9-39-1	88.0	4.7	15.9	119.3	0.54
8-3	82.2	4.3	14.9	101.5	0.52
8-15-1	92.1	4.3	15.8	136.3	0.45
39-17-1	94.4	2.9	27.8	129.8	0.59
8-42-M-1	94.4	3.6	20.4	128.7	0.54
8-42-M-2	87.4	3.3	24.1	139.5	0.50
48-18-1	82.7	3.8	19.3	112.6	0.54
41-39	67.0	3.6	20.5	103.2	0.48
8-4	87.7	4.3	15.2	116.4	0.50
41-48-1	79.8	4.7	17.2	117.0	0.55
8-47	72.5	3.4	17.1	98.5	0.43
48-109	71.3	4.1	17.0	94.7	0.53
51-29-3	71.3	3.6	17.9	82.7	0.54
51-5-3	88.9	3.9	16.3	102.0	0.56
8-17	98.8	3.4	18.7	120.8	0.51
N81017	89.5	4.1	17.7	118.7	0.55
Lef-2-RB	87.1	3.5	20.8	119.0	0.54
UW 21-58	80.1	3.6	18.4	102.3	0.51
UW 23-61	103.5	4.3	14.9	124.0	0.54
Bayo Madero	79.8	3.0	33.8	135.7	0.58
II900-5-M-45	80.7	4.1	22.2	131.0	0.56
Katolika	73.4	5.6	21.5	142.1	0.61
Average	86.4	3.9	19.4	119.2	0.54

Table 13. Yield components, TDM and HI of 26 bean genotypes grown under rainfed conditions. Durango, Mexico. 1987

Genotype	Pods /m^2	Seeds /pod	100 Seed weight	TDM	HI
			-------- g --------		
48-10	124.3	4.3	21.1	194.7	0.57
48-66	154.6	3.5	20.0	195.8	0.54
8-25-2	133.3	4.2	18.1	177.9	0.58
48-94B-1	143.9	4.6	16.3	180.5	0.61
9-39-1	121.3	4.4	16.4	167.5	0.52
8-3	184.2	4.5	14.6	209.2	0.56
8-15-1	154.4	4.3	17.9	220.2	0.54
39-17-1	141.0	3.9	24.6	209.9	0.63
8-42-M-1	134.0	4.7	20.7	216.9	0.61
8-42-M-2	162.5	4.2	20.8	248.2	0.57
48-18-1	134.6	4.0	19.5	177.4	0.59
41-39	139.5	3.2	20.9	188.2	0.50
8-4	113.2	3.7	19.3	152.6	0.53
41-48-1	135.7	4.4	16.7	175.4	0.56
8-47	118.0	3.7	15.8	155.9	0.44
48-109	144.1	4.4	18.7	198.0	0.58
51-29-3	110.5	6.3	19.4	191.9	0.64
51-5-3	161.2	4.9	14.2	190.1	0.58
8-17	151.3	4.1	20.8	230.9	0.56
N81017	142.8	4.5	17.4	203.7	0.54
Lef-2-RB	139.0	3.7	19.9	182.7	0.56
UW 21-58	135.3	4.2	17.2	161.6	0.58
UW 23-61	182.5	4.5	15.3	205.9	0.61
Bayo Madero	118.0	4.1	34.6	223.9	0.71
II900-5-M-45	124.6	4.5	20.6	205.9	0.56
Katolika	123.0	4.9	18.9	183.8	0.62
Average	139.5	4.3	19.2	194.2	0.57

of phenological characteristics in order to stress them evenly.

The plants were under severe stress in Durango from the beginning of flowering and the number of pods/m^2 was determined early during the reproductive phase (Figure 1, Appendix C). Therefore, since the plants retained few pods per plant, the number of seeds /pod was not affected by the stress in the same magnitude as the number of pods (Tables 12 and 13). At the Michigan site, the stress was less severe and it built up more slowly than in Durango. In Michigan, a continuous dropping of pods was observed throughout the reproductive phase and, at maturity, almost half of the pods had just one or two seeds each. In addition, in this site, some pods did not have a single normal seed. Thus, it is clear that each of those yield components was affected separately by the stress due to their sequential development and the timing, intensity and duration of the applied stress (Figure 3).

Harvest Index was only slightly reduced by the stress in the Durango experiment. Indeed, some genotypes, e.g. 48-10, 48-66 and N81017, displayed equivalent or slightly larger HI values under stress (Tables 12 and 13). Similar correlation coefficients were found between seed yield and HI under stress and non-stress (Table 14). With respect to the use of the IKI solution, a significant negative association was found between it and HI under stress (r=-0.53 **), which may indicate the inability of the poor yielders to carry out starch remobilization. If yield under severe stress at the pod filling stage depends to some significant extent upon stored assimilates, then cultivars with an early, vigorous establishment, and a relatively large biomass accumulated at the beginning of seed filling, may be the better adapted genotypes in this stressed environment. An important aspect of

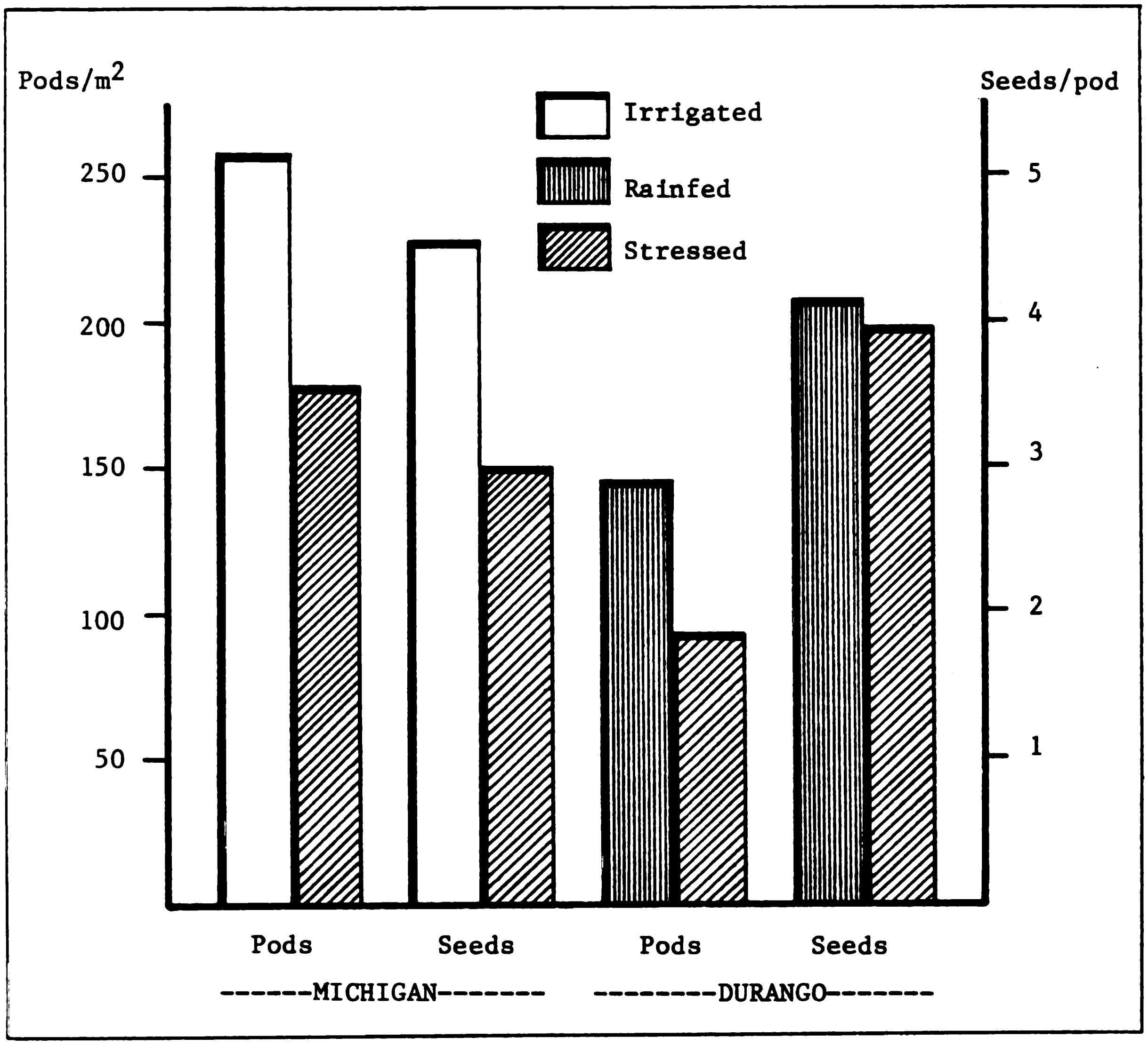


Figure 3. Effect of water stress during the reproductive phase on the yield components of 26 bean genotypes grown in Michigan (USA) and Durango (Mexico). 1987.

Table 14. Correlation coefficients of seed yield and TDM at maturity with some characteristics of phenology, plant growth and primary yield components of 26 bean genotypes grown under two moisture regimes. Durango, Mexico. 1987

	Seed yield		TDM	
Variable	Stressed	Rainfed	Stressed	Rainfed
Days to flowering	-.33	-.54**	.00	-.28
No. pods/m^2	.43*	.30	.45*	.47*
No. seeds/pod	.15	.30	.11	.12
100 seed weight	.55**	.59**	-.48*	.41*
Seed protein (%)	-.59***	-.07	.61***	-.03
N in seeds (g/m^2)	.98***	.98***	.88***	.87***
TDM at maturity (g/m^2)	.90***	.88***	----	----
Harvest Index	.73***	.77***	.37	.39

*,**,*** significant at $P<0.05$, 0.01, and 0.001, respectively.

developmental plasticity is the ability of plants to transfer assimilate accumulated prior to seed filling to the seed during the seed filling stage.

Type III varieties are the most adapted to the semiarid Mexican highlands (Acosta and Kohashi, 1988). The type III genotypes used in this study were selected after the evalution of hundreds of local landraces and bred cultivars. Therefore, is not a surprise that they were the most productive in the Durango environment.

Principal Components and multiple regression analyses

Michigan experiment. The PCA was used here to reduce the dimensions of multivariate data and to identify important variables to be used for prediction in multiple regression models.

The first five principal components accounted for different cumulative amounts of variation under stress and irrigated conditions and different traits accounted for that variation in each condition (Tables 7 and 8, Appendix C). Under stress, the first PC accounted for 30% of the variation and was characterized by phenological traits, the second PC accounted for 17% of the variation and was characterized by early growth and weight traits at the beginning of flowering. Yield and yield related traits showed maximum loading in the third PC and explained 12% of the variation; the fourth PC accounted for 13% of the variation and was characterized by growth traits measured at the reproductive stage, and in the fifth PC the amount of senesced leaves showed maximum loading and accounted for 7% of the variation. On the other hand, under irrigation variables related to growth measured at different phenological stages were prominent in the first three PC's, primary productivity traits (seed yield and biomass) displayed maximum loading values in the fourth PC, and the primary yield components in the fifth. Under irrigation the first five PC's accounted for 22, 17, 10, 12, and 7% of the total variation associated with the data, respectively.

With a representative trait from each component and traits which have shown a significant association with seed yield and/or biomass, multiple regression models were chosen to estimate the combination of traits which could account for the largest amount of variation for seed yield and biomass among the genotypes in each location and water regime. Traits measured at maturity were not included in order to avoid unrealistic estimation of R^2, since, for example, biomass, seed yield, HI and the primary yield components are all part of the same end product. In addition, the presented models are not unique; better models might be generated by using other criteria and other statistical procedures.

Data from both water regimes were used to construct separate models. The traits selected for the models were subjected to a stepwise multiple regression procedure after which traits were removed or added until the best models, based on the magnitude of R^2, were identified. Predictor variables that were intercorrelated were removed from the models based on their tolerance values; tolerance values near zero indicate high intercorrelation among predictor variables (Wilkinson, 1986).

Different combinations of plant traits resulted in the highest R^2 values with seed yield or biomass in each water regime (Table 15). The best multiple regression models for seed yield under stress and non-stress included two traits each and accounted for 29 and 35 % of the

Table 15. Combination of plant traits resulting in the best multiple regression model for seed yield and biomass at maturity for a group of 26 bean genotypes grown under drought stress and irrigation. Kellogg Biological Station, Battle Creek MI. 1987

Variable		Regression coefficient	Partial R^2	Probability R^2	
Dependent	Independent			partial*	cumulative@
Irrigated					
Seed yield					
	constant	36.824		0.583	
	TDM1	0.784	0.289	0.004	
	LER	182.641	0.058	0.169	
R^2			0.346		0.008
Biomass					
	constant	-115.347		0.426	
	SmWt2	1.497	0.430	0.003	
	WtSeLe	-3.361	0.090	0.004	
	Flow	9.193	0.089	0.043	
	LeWt1	1.294	0.042	0.077	
R^2			0.665		0.000
Stressed					
Seed yield					
	constant	184.607		0.000	
	NAR1	-43.632	0.192	0.037	
	CGRAV	3.243	0.146	0.080	
R^2			0.295		0.042
Biomass					
	constant	128.898		0.010	
	LWR2	299.443	0.366	0.028	
	SmWt2	0.584	0.326	0.065	
R^2			0.455		0.001

* T test (Two tail).

@ F test for regression

genotypic variability associated with seed yield, respectively. The best models for biomass under irrigated and stressed condition included four and two traits and accounted for 66 and 45 % of the variability in biomass, respectively. It appears that better models can be generated for biomass than for seed yield as indicated by the R^2 values.

Forty three percent of the variability associated with biomass under irrigation was explained by a single trait, namely, the weight of the stems (StWt2) at 61 DAE. This indicates that genotypes with strong thick stems seem to be better adapted to favorable conditions in Michigan. The bean genotypes which display that morphological characteristic are the type II growth habit with the modified ideotype or architype as described by Adams (1982). It was previously indicated that type II architype cultivars are well adapted and exhibit high yield potential under the Michigan conditions (Kelly et al., 1987). Kelly and Adams (1987) and Acquaah (1987) found that the transfer of architectural traits, e.g. strength of main stem, is relatively easy within the same gene pool. Davis and Evans (1977) studied the importance of a set of phenological and morphological traits in the construction of selection indices for seed yield in navy beans. They indicated that the best indices included the thickness of the stem (hypocotyl) which also showed a relatively high heritability.

In this study, the evaluated families, which were derived from crosses involving type II and III parents from diverse origin, were not selected based on architectural traits (see Chapter 2), but on the basis of seed and biomass productivity. Consequently, since it seems that the type II's are more adapted to the environment in Michigan, the Mexican genotypes, Bayo Madero, Lef-2-RB and I1900-5-M-45, together with

Katolika, which display the type III growth habit, were excluded, and principal component and multiple regression analyses were recomputed for the type II's only.

Results of PC analysis excluding type III cultivars under stress showed that the first five components accounted for approximately the same amount of variation as in the previous analysis (80 %). The variables with the maximum loading coefficients were essentially the same in the first two components, but with opposite signs; while the variables with maximum loadings in the remaining components were different (Table 9, Appendix C). Under irrigation, the variables showing maximum loadings were different than those in the previous analysis in all the PC's (Table 10, Appendix C). Even though the loading of the variables into the components were somewhat different than in previous analyses, most of the important variables remained the same, thus PCA was useful in reducing the number of variables to be used for prediction or description with or without all bean genotypes.

With the elimination of the data from type III cultivars, the magnitude of the R^2 estimates for the models to explain the variation in seed yield under irrigation and drought stress was increased (Table 16). Those R^2 values were 46 and 48%, respectively. The R^2 value for the models with biomass at maturity as the dependent variable was slightly reduced under irrigation, but in the new model just two predictor variables were included versus four in the previous model. Under stress, the new calculated model kept the same variables, but its R^2 decreased. It seems that under stress type III cultivars were more associated with the observed variation in biomass.

Table 16. Combination of plant traits resulting in the best multiple regression model for seed yield and biomass at maturity for a group of 22 bean genotypes grown under drought stress and irrigation. KBS, Battle Creek MI. 1987

Variable				Probability R^2	
Dependent	Independent	Regression coefficient	Partial R^2	partial*	cumulative@
		Irrigated			
Seed yield					
	constant	-279.588		0.122	
	CGR1	15.743	0.274	0.221	
	CGR2	36.217	0.257	0.035	
	Flow	5.468	0.088	0.121	
R^2			0.458		0.010
Biomass					
	constant	264.450		0.002	
	SmWt2	2.265	0.434	0.000	
	WtSeLe	-3.233	0.128	0.008	
R^2			0.614		0.000
		Stressed			
Seed yield					
	constant	279.374		0.000	
	NAR1	-46.492	0.138	0.048	
	CGRAV	4.339	0.171	0.015	
	RePha	-2.287	0.116	0.019	
R^2			0.479		0.007
Biomass					
	constant	243.907		0.016	
	SmWt2	0.837	0.226	0.170	
	LWR2	0.272	0.223	0.180	
R^2			0.298		0.060

* T test (Two tail).
@ F test for regression

In the case of seed yield, different variables related to early growth and phenology were included in all proposed models under both stress and non-stress, while for biomass, the weight of the stem at 61 DAE was important in all the calculated models (Tables 15 and 16). The importance of a closely related trait, namely, hypocotyl diameter, as an important component of plant architecture in beans was indicated by Acquaah (1987).

<u>Durango Experiment</u>. At this location the first five PC's accounted for similar amounts of the variance under rainfall and stress, 68.5 and 67.5%, respectively (Tables 12 and 13, Appendix C). In the first PC, traits related to early growth showed maximum loadings under both conditions. This response was expected, since at the time those variables were recorded, the stress treatment had not yet been imposed. The loadings on PC2 and subsequent PC's varied in sign and magnitude under rainfall as compared to those observed under stress. Under rainfall, PC2 was characterized by growth traits measured at 57 DAE (beginning of pod filling); in PC3 yield <u>per se</u> and related traits showed the highest loadings. Days to physiological maturity was the most important trait in PC4 and leaf weight ratio at 57 DAE (LWR2) in PC5 (Table 11, Appendix C). Under stress, heavily loaded traits in PC's 2 to 4 were essentially the same traits as under rainfed conditions, but with opposite signs; and in the fifth PC, leaf water content (LWC) and leaf water retention capacity (LWRC) showed maximum loadings (Table 12, Appendix C).

The observed differences for trait loadings under rainfall and stress indicates a different contribution to variability from the same traits. Thus, the bean genotypes expressed different traits to adapt to the different environments.

Data from both water regimes were used to construct separate models (Table 17). When seed yield under rainfall was the dependent variable, the number of days to start flowering (Flow) was the only important trait by itself (R^2=0.29 ***), and with the addition of two more variables to the model (WtSeLe and TDM1), it accounted for 48.6% of the variation associated with seed yield. The best model for biomass included four independent variables and accounted for only 37.1% of the variation.

Under drought stress, the best models included different variables than under irrigation and the R^2 estimates for seed yield and biomass were 35.0 and 27.2%, respectively; these were lower than those obtained under rainfed conditions. The weight of the stem was again an important trait for both dependent variables studied. This result was probably due to the fact that 85% of the evaluated cultivars belong to the type II growth habit, in which most genotypes display heavier main stems than type III cultivars. Since in this site type III cultivars were the most productive and are the best adapted to this environment, it was considered impractical to remove all type II cultivars and recompute the models on the basis of only four cultivars.

The IKI score was a trait measured at maturity and since it was considered as not being interrelated to seed yield or biomass, it was included as a predictor variable in the models. IKI score became an important predictor trait for seed yield under stress.

The weight of the senesced leaves (WtSeLe) was used here as a measure of the rate of leaf senescence under stress. However, it was only included in the models for seed yield and/or biomass under

Table 17. Combination of plant traits resulting in the best multiple regression model for seed yield and biomass at maturity for a group of 26 bean genotypes grown under drought stress and rainfall. Durango, Mexico. 1987

Variable				Probability R^2	
Dependent	Independent	Regression coefficient	Total R^2	partial*	cumulative@
		Rainfed			
Seed yield					
	constant	370.840		0.000	
	Flow	-5.695	0.294	0.001	
	WtSeLe	1.189	0.081	0.022	
	TDM1	-0.364	0.002	0.019	
R^2			0.486		0.002
Biomass					
	constant	677.291		0.023	
	LWC	-8.133	0.111	0.030	
	RePha	3.667	0.096	0.096	
	WtSeLe	-0.403	0.040	0.051	
	TDM1	1.339	0.034	0.058	
R^2			0.371		0.038
		Stressed			
Seed yield					
	constant	122.976		0.000	
	WtSt2	-0.486	0.142	0.043	
	IKI	-8.163	0.113	0.024	
	NAR2	-13.305	0.059	0.142	
R^2			0.350		0.022
Biomass					
	constant	122.976		0.010	
	SmWt2	-1.527	0.134	0.028	
	LeWt2	1.165	0.029	0.115	
	LER	112.785	0.071	0.200	
R^2			0.272		0.067

* T test (Two tail).

** F test for regression

favorable conditions, and its coefficient of regression was always negative. This suggest that under favorable conditions, leaf area duration (LAD) might be a key trait to manipulate in order to increase productivity. Laing et al. (1983) have pointed out the importance of LAD upon seed yield of several legume crops. The amount of senesced leaves as measured in this research may be of more practical use than determining the integral of LAI during the ontogeny of the crop.

In designing an optimum model to predict yield or biomass under stress and/or non-stress, many aspects should be considered. From the present results, it seems obvious that the evaluation of cultivars belonging to the same growth habit will result in the identification of better models. The grouping of similar-type cultivars might diminish the complexity of the data by removing some of the multiple interactions that can be obtained with the use of phenologically and morphologically diverse genotypes.

In general, when different models were compared, it was clear that the best independent variables varied between location and, to a lesser extent within locations. The plant traits act together in different ways in different genetic backgrounds and in different environments. It seems reasonable to assume that genotypes developed from different genetic backgrounds might use different physiological strategies in achieving their final productivity. The variation of traits included in the best models in the same location indicates that adaptation to drought stress and high productivity in this group of genotypes is conferred by different plant attributes.

CONCLUSIONS

1. A wide range in variation among the genotypes was observad for all evaluated characteristics, except for leaf water content.

2. A high and positive correlation between the drought susceptibility index and seed yield at the most favorable environment indicates that some adaptations are mutually exclusive. Therefore, the best genotypes under stress were different from those under non-stress conditions.

3. Genotypic drought response in two different locations, namely Durango (Mexico) and Michigan (USA), were not consistent. This suggests that other factors in addition to stress are important in adaptation.

4. In Durango (Mexico) reduction in yield was due mainly to a smaller number of pods per m^2, while in Michigan (USA) both the number of pods per m^2 and the number of seeds per pod were decreased by the stress. At both locations, individual seed weight was little affected by water stress.

5. It appears that no single variable investigated in this study can alone be reliably utilized to assess performance for seed or biomass productivity under stress and non-stress conditions.

REFERENCES

Acosta Gallegos, J.A. and J. Kohashi Shibata. 1988. Effect of water stress on growth and yield of indeterminate dry bean (*Phaseolus vulgaris* L.) cultivars. Submitted : Field Crops Research. The Netherlands

Acquaah, G. 1987. Genetic and multivariate statistical evaluation of a phenotypic recurrent selection program for recombining erect architecture and large seed size in *Phaseolus vulgaris* L. Ph.D. Thesis, Michigan State University, East Lansing p.317

Adams, M.W., Wiersma, J.W., and J. Salazar. 1978. Differences in starch accumulation among dry bean cultivars. Crop Sci. 18:155-157

Adams, M.W. 1982. Plant architecture and yield breeding. Iowa State J. Res. 56:225-254

Adams, M.W. and J.D. Kelly. 1987. The role of architecture, crop physiology and recurrent selection in ideotype breeding for yield in dry beans. In: Symposium on Breeding for Higher Yields in Common Beans. XXXIII meeting of the PCCMCA, Guatemala, C.A. CIAT-B/C CRSP-ICTA p. 16

Arnon, I. 1980. Breeding for higher yield. Co-ordinator's report on the 1st session. In: International Potash Institute (Ed.), Physiological Aspects of Crop Productivity. Proceedings of the 15th Colloquium of the International Potash Institute. Wagenningen. The Netherlands pp. 77-81

Begg, J.E. 1980. Morphological adaptation of leaves to water stress. In: N.C. Turner and P.J. Kramer (Eds.), Adaptation of Plants to Water and High Temperature Stress. Wiley, New York pp. 33-42

Bonanno, A.R., and H.J. Mack. 1983. Yield components and pod quality of snap beans growth under differential irrigation. J. Amer. Soc. Hort. Sci. 105:869-873

Boyer, J.S. 1970. Leaf enlargement and metabolic rates in corn, soybean and sunflower at various leaf water potentials. Plant Physiol. 46:233-235

Boyer J.S. and H.G. Mc.Pherson. 1975. Physiology of water deficits in cereal crops. Adv. Agron. 27:1-23

Braford, K.J. and T.C. Hsiao. 1982. Physiological responses to moderate water stress. In: P.S. Nobel, C.B. Osmond, and H. Ziegler (Eds.), Encyclopedia of Plant Physiology, new series, vol. 12B Springer-

Verlag, Berlin, FRG. pp. 264-324

Clarke, J.M. and T.N. McCaig. 1982. Evaluation of techniques for screening for drought resistance in wheat. Crop Sci. 22:503-505

Clarke, J.M. and T.F. Townley-Smith. 1984. Screening and selection techniques for improving drought resistance. In: P.B. Vose and S.G. Blixt (Eds.), Crop Breeding, a Comtemporary Basis. Pergamon Press pp.137-162

Davis, J.H.C. and A.M. Evans. 1977. Selection indices using plant type characteristics in navy beans (Phaseolus vulgaris L.). J. Agric. Sci. Camb. 89:341-348

Dedio, W. 1975. Water relations in wheat leaves as screening test for drought resistance. Can. J. Plant Sci. 55:369-378

Fischer, R.A., and R. Maurer. 1978. Drought resistance in spring wheat cultivars. I. Grain yield responses. Aust. J. Agric. Res. 29:277-317

Fischer, R.A. and J.T. Wood. 1979. Drought resistance in spring wheat cultivars . III. Yield association with morphophysiological traits. Aust. J. Agric. Res. 30:1001-1020

Hall, A.E. and P.N. Patel. 1985. Breeding for resistance to drought and heat. In: S.R. Singh and K.O. Rachie (Eds.), Cowpea: Research, Production and Utilization. John Wiley & Sons pp 137-151

Hanson, A.D. 1980. Interpreting the metabolic responses of plants to stress. Hort Science 15:9-15

Hsiao, T.C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24:519-570

Hsiao, T.C. and E. Acevedo. 1974. Plant responses to water deficits, water use efficiency, and drought resistance. Agr. Meteorol. 14:59-84

Izquierdo, F.J.A. 1981. The effect of accumulation and remobilization of carbon assimilate and nitrogen on abscission, seed development, and yield of common bean (Phaseolus vulgaris L.) with differing architectural forms. Ph.D. Thesis, Michigan State university, East Lansing p. 188

Kelly, J.D. and M.W. Adams. 1987. Phenotypic recurrent selection in ideotype breeding of pinto beans. Euphytica 36:69-80

Kelly, J.D., Adams, M.W. and G.V. Varner. 1987. Yield stability of determinate and indeterminate dry bean cultivars. Theor. Appl. Genet. 74:516-521

Laing, D.R., Kretchmer, P.J., Zuluaga, S. and P.G. Jones. 1983. Field bean. In: W.H. Smith and S.J. Banta (Eds), Symposium on Potential

Productivity of Field Crops Under Different Environments. Los Banos, Philippines, 1980 (Proceedings) IRRI pp 227-248

McIntosh, M.S. 1983. Analysis of combined experiments. Agron. J. 75:153-155

Sammons, D.J., Peters, D.B. and T. Hymowitz. 1978. Screening soybeans for drought resistance. I. Growth chamber procedure. Crop Sci. 18:1050-1054

Samper, C., Adams, M.W., Hanson, A.D., and E. Watt. 1984. Contribution of stored assimilates to the seed following a drought stress in dry beans. Agron. Abst. 76:87

Singh, S.P. and J.W. White. 1988. Breeding common beans for adaptation to drought conditions. In: G. Hoogenboom, F. Ibarra, S.P. Singh, J.W. White and S. Zuluaga (Eds.), Research on Drought Tolerance in Common Beans. CIAT, Cali, Colombia. In press

Sojka, R.E., Stolzy, L.H. and R.A. Fischer. 1981. Seasonal drought response of selected drought cultivars. Agron. J. 73:838-845

Vidal, A. and M. Arnoux. 1981. Drought tolerance processes in soybeans. Biol. Plant. 23:434-441

Wallace, D.H., K.S. Yourstone and P.N. Massaya. 1987. Daylength modulation of partitioning to yield and its control by a single photoperiod gene of bean (Phaseolus vulgaris L.). Agron. Abst. 79:102

Wilkinson, L. SYSTAT. 1986. The system for statistics. Evanston IL. SYSTAT, Inc.

GENERAL DISCUSSION

Before discussing the results of this research, it is pertinent to recall that water is as important to drought adapted plants as to non-adapted ones. It is linked to productivity and is a substrate, a constituent and the medium in which all cellular processes take place. Water is also essential for evaporative cooling of the plant and is crucial for the flow of nutrients, hormones and other substances. Therefore, best yields can only be obtained with adequate water, even in the case of the most resistant plants. Maximum biomass production will be achieved only by supplying sufficient water to realize potential leaf area and meet evaporative demand during growth.

In the present report, a modest breeding effort to improve drought tolerance and biological nitrogen fixation in beans was undertaken. The objective was to determine whether it is possible to select for drought tolerance and nitrogen fixation concurrently in the same population, and whether genotypes superior in both characteristics simultaneously could be produced.

The results obtained during the evaluation of the parental genotypes indicated that nitrogen accumulation (under controlled conditions) in different plant parts was closely related to biomass production and the length of the vegetative phase of growth. In the field, increases in biomass in type III cultivars at the reproductive stage was closely associated with a low partitioning to the developing pods. In type III cultivars, the vegetative and reproductive phases overlap, and a competition for assimilates among new expanding leaves and roots versus developing pods and seeds takes place.

Mexican genotypes displayed a profusely branched root system which on a dry weight basis is lighter than the root system of type II Michigan cultivars. It seems that the root system of Mexican type III genotypes is designed to explore a larger superficial soil volume. The Michigan type II's possess a thick, less branched root system which can go deeply into the soil profile, where a large amount of moisture accumulates during the winter or after prolonged rainy periods in the spring.

All Mexican type III genotypes proved to be highly photoperiod sensitive. In spite of slow partitioning to the developing pods, some type III cultivars were as productive as type II's under stress. The combination of an acceptable ability for nitrogen fixation and drought tolerance seemed to be already present in some of the parental genotypes e.g. Lef-2-RB, II900-5-M-45, and N81017.

A set of segregating populations was produced using Mexican (unadapted) and Michigan and Wisconsin (adapted) genotypes. During the advance of generations and selection (1984-1986), most of the segregant progenies with morphological and/or phenological traits derived from parental Mexican type III cultivars were indirectly eliminated. Two factors contributed most to that elimination: the sensitivity of those progenies to the long day photoperiod, even though some of them exhibited large biomass under stress, and the excesive amount of rainfall during the fall of 1986. Under the wet conditions of 1986, the morphological characteristics of type II genotypes gave them advantage over prostrate type III genotypes. The final yield of type III genotypes was reduced due to a close contact of their branches and pods with the wet soil and an enhanced incidence of white mold (Sclerotinia sclerotiorum). A group of nineteen genotypes (F6 families) was selected for further evaluation based on their response to mild drought stress encountered in Michigan. Field and greenhouse experiments were conducted in Michigan, USA, and Durango, Mexico.

Under controlled conditions, promising genotypes with enhanced BNF were identified. A high association between total dry matter and total nitrogen assimilated (nitrogen fixed) per plant suggested that preliminary selection for BNF can be done by using an estimation of the total dry matter of segregating populations grown in a N-free medium.

The results obtained in 1987 in the field indicated that depending upon the history of the crop during past ontogeny, stress can or cannot affect the proportion of dry matter allocated to the seed. In Durango, the stress treatment had no significant effect on the HI, while in Michigan it was drastically decreased by the stress. The crop in Michigan was under near optimum water supply before the stress, thus, these large plants when exposed to the stress were more affected than the smaller, already hardened, bean plants at Durango.

A positive association observed between leaf expansion rate (LER) and the amount of senesced leaves indicated that under stress new leaves develop more slowly, and old leaves senesce more rapidly. Thus, there is likely to be a reduction in the photosynthetic area of stressed plants and selection could be practiced by evaluating genotypes on the basis of either an increased LER or a reduced senescence under stress. On the other hand, increased senescence under favorable conditions was associated with a larger biomass. Different selection criteria may prove useful in breeding beans for drought adaptation. Leaf expansion rate has been proposed several times as a selection criterion for drought tolerance in soybeans (Boyer, 1970; Hsiao and Acevedo, 1974; Boyer and McPherson, 1975; Sammons et al., 1978). In the case of beans, LER could be used provided that the set of genotypes to be evaluated includes genotypes of similar growth habit. Since type III cultivars may be developing and senescing a larger number of leaves than types II's.

The weight of the stem was a preponderant morphological trait among the genotypes evaluated. Since this trait is related to one of the main features of the architectural cultivars in Michigan, namely hypocotyl strength, it may be suitable for selection in Michigan under stress and non-streess conditions. The diameter of the hypocotyl or main stem at a certain internode could be used as an indicator for this trait.

Morphologically different genotypes may display different attributes by which to cope with drought; and the timing of the stress coupled to different phenological stages may induce differential responses in final yield. In screening for drought tolerance, it is rarely possible to hold all other factors constant while screening for a few specific traits. Therefore, the less interactions the plants go through, the more straight forward the interpretation of data. Grouping the genotypes in a final evaluation for drought tolerance upon the basis of their phenology and growth habit is suggested.

Drought affects many internal plant processes, plant morphology and phenology, therefore, it is not likely that a single plant trait can account for the response in yield or biomass under drought stress. The use of traits other than the end product (seed or biomass yield) may speed the advance during selection in the field, provided that an extra nursery is planted under favorables conditions for seed security and increase.

Breeders have to analyze the type of drought condition in combination with the characteristics of preferred and/or adapted cultivars in the target area. Where unpredictable water deficits occur, maximum productivity should be the goal. Maximum productivity will be achieved where leaf expansion and senescence are relatively insensitive to water deficit, where rate of leaf expansion recovers quickly on relief of water deficits, and where minimum dry matter is partitioned into immobile root reserves.

The semi-arid highlands of Mexico are characterized by extreme annual variations in total rainfall and its seasonal distribution. Especially at the lower range of rainfall, wide annual variation exist in the timing and the magnitude of stress imposed upon the bean plants. The environment of the semi-arid highlands exerts its effects on the genotypes with different intensities and in different directions from generation to generation. It is suggested that two locations at different representative sites in the target area should be used when testing early lines in preliminary yield trials.

Since the natural conditions in the semi-arid highlands of Mexico during most years do not allow for full expression of the genetic potential of bean cultivars, yield and drought adaptation could be handled as separate genetic entities. Stable genotypes should be the goal in this environment. A negative association between potential yield and a drought tolerance trait (such as early maturity) need not exclude that trait, since potential yield is neither realized under the actual conditions nor under severe stress. However, in Michigan, where bean cultivars traditionally encounter a more favorable environment, such negative associations must be considered. In addition, since the drought stress level in these two regions is clearly different, it would not be expected that the cultivars display the same mechanisms of drought adaptation in both regions.

In conclusion, recombinant families were produced which displayed good adaptation to the Michigan environment, with improved ability to fix atmospheric nitrogen and with enhanced drought tolerance. Further enhancement of these two traits in a single genotype is feasible, but since nitrogen fixation is readily depressed by water stress, these two traits must be expressed at different developmental stages, i.e. enhanced nitrogen fixation during the vegetative phase and drought tolerance during the reproductive phase. Many mechanisms relate to drought adaptation in plants. The importance of biochemical and physiological traits in adaptation to semi-arid regions cannot be neglected, however, the present understanding of such complex traits is incomplete and their utilization in the breeding of common bean for drought tolerance is far from reality. It seems inevitable that certain complex traits, such as yield under stress, are better handled as such, rather than by dissecting them into components for analysis or investigation. Nonetheless, a better understanding of the most important traits influencing seed yield and biomass under water deficits could, in the long run, lead to improved production practices and more efficient breeding programs.

APPENDICES

APPENDIX A

Appendix A

THE METHOD OF FISCHER AND MAURER (1978)

With this approach, yields of individual genotypes must be determined under drought stress (Ys) and irrigated conditions (Yi). Data on the average yield of all genotypes under stress (Ys) and non-stress conditions (Yi) are used to calculate the drought intensity index (DII).

$$DII = 1 - Ys / Yi$$

Then the drought susceptibility (DSI) of individual genotypes is calculated as follows:

$$Ys = Yi\ (1 - DSI*DII)$$

$$DSI = [1 - (Ys / Yi)] / DII$$

Varieties with average resistance to drought have a DSI value of 1.0. values less than 1.0 indicate less susceptibility and greater resistance to drought with a value of DSI = 0.0 indicating maximum possible drought resistance (Hall and Patel, 1985).

Table 1, Appendix A. Climatic conditions recorded at the Botany Farm of Michigan State University during the growing season. East Lansing, MI. 1985

	Temperature °C		
Period	maximum	minimum	Rainfall in mm
May			
1 - 10	22.0	6.9	22.1
11 - 20	23.5	10.5	16.2
21 - 31	22.8	7.5	32.0
June			
1 - 10	24.5	9.8	00.0
11 - 20	19.6	9.9	28.7
21 - 30	28.0	12.7	4.3
July			
1 - 10	28.1	15.0	12.9
11 - 20	27.8	15.1	39.1
21 - 31	26.8	14.4	14.0
August			
1 - 10	27.2	13.9	26.7
11 - 20	25.5	13.0	42.9
21 - 31	24.0	14.1	23.6
September			
1 - 10	28.2	18.4	49.0
11 - 20	22.1	8.5	0.5
21 - 30	19.2	7.3	34.3

Table 2, Appendix A. Method to determine visual rating of root system for Biological Nitrogen Fixation from Rosas and Bliss (1986).

Visual rating	Nodulation class	subjective description
1	poor nodulation	< 50 % nodulation of control
2	below average	51-80 % of control
3	average level	81-120 % of control
4	higher than average	121-150 % of control
5	highly superior	> 150 % of control

Table 3, Appendix A. Soil moisture content in percent at four different depths during the growing cycle. East Lansing, MI. 1985

Days After Planting		Soil depth in cm.			
		0-15	16-30	31-45	46-60
-5		2.5	8.0	9.7	10.0
2		20.7	21.0	17.0	17.6
10		13.5	12.5	10.6	11.3
17		17.3	16.2	12.9	13.6
24		9.6	14.2	10.9	11.9
31		11.5	13.3	10.7	9.3
38		10.4	10.2	10.2	10.2
* 48		8.7	8.1	----	----
* 58	Rainfed	9.2	8.2	----	----
	Stressed	6.9	7.3	----	----
* 70	Rainfed	11.1	8.1	----	----
	Stressed	9.1	7.2	----	----

* each value is an average of 48 determinations.

Table 4, Appendix A. Mean squares and significance of F value for nodule fresh weight, plant biomass and acetylene reduction of 11 bean genotypes evaluated under four treatments. East Lansing, MI. 1985

		Mean Squares			
				Acetylene Reduction[1]	
Source of variation	df	Nodule fresh weight	Plant biomass	plant	g nodule/plant
Treatment	3	1.87**	1.54**	0.97	1.14
Genotype	10	0.06**	0.42**	6.48**	2.71**
T X G	30	0.01	0.11**	0.64	0.21
Error	132	0.01	0.04	1.05	0.53

** F is significant at a = 0.01

1- Treatment with nitrogen fertilizer was not included, resulting in different degrees of freedom for sources of varietion.

Table 5, Appendix A. Analyses of variance and significance of F value of different traits of eight bean genotypes under two nitrogen sources at 45 days after planting. East Lansing, MI. 1985

		mean squares				
Source of Variation	df	roots	stems	leaves	shoot	TDM
		g/m^2				
Nitrogen	1	0.067	20.8*	94.1*	203.4*	210.8*
Genotype	7	1.805**	14.7**	34.2	87.4*	68.1
N X G	7	0.253	3.6	11.2	26.5	29.9
Error	30	0.573	3.8	16.2	33.7	39.3
CV %		16	22	21	21	19

Source of Variation	df	LAI	Stomatal conduc. cm/s	LWP	LSW	LAR	Root/ shoot
Nitrogen	1	0.38	2.07	0.02	1992	327	0.006*
Genotype	7	1.13**	3.78*	5.90	6789**	2366**	0.011**
N X G	7	0.35	0.67	4.73	3153	884	0.001
Error	30	0.19	1.42	3.82	2212	751	0.001
CV %		26	46	32	22	22	19

*,** significance of F at a = 0.05 and 0.01, respectively.

* LAI = leaf area index.
LWP = leaf water potential.
LSW = leaf specific weight.
LAR = leaf area ratio.

Table 6, Appendix A. Analyses of variance and significance of F value of different plant traits of eight bean genotypes grown under two moisture regimes and two nitrogen sources at 70 days after planting. East Lansing. MI.1985

Source of variation	df	mean squares Root	Stem	Leaves	Shoot	Pods
Moisture	1	12.2	362*	2533*	7209	242*
Error "a"	2	0.69	194	113	736	7.45
Nitrogen	1	0.92	130	92	1384	262*
M X N	1	0.03	35	80	60	50
Genotype	7	13.2**	155*	678**	581	2601**
M X G	7	3.5	15.4	50	285	84
N X G	7	2.4	58.5	60	353	25
M X N X G	7	0.8	58	55	389	82
Error "B"	60	3.0	62.4	73	387	53
CV %		25	36	27	29	46

Source of Variation	df	Mean squares TDM	Seed yield	Pods /plot	Seed wt.	Harvest Index
Moisture	1	436178	264992*	149696*	9.98	0.009
Error A	2	218994	13161	9245	0.68	0.004
Nitrogen	1	115392	4050	13421	1.33	0.001
M X N	1	1120	12747	2952	1.56	0.003
Genotype	5	44669	41979**	46753**	648.1	0.019**
M X G	5	26970	27474	11509	7.1	0.003
N X G	5	24630	10467	9451	7.0	0.003
M X N X G	5	22192	4997	1457	6.5	0.004
Error B	44	32185	12021	5907	3.5	0.004
CV %		29.5	32.3	19.2	7.7	10.9

*,** F is significant at a = 0.05 and 0.01, respectively.

APPENDIX B

Table 1, Appendix B. Percent soil moisture at two soil depths during the growing cycle. East Lansing, MI. 1985

Days After Planting	Soil depth in cm.			
	0-15	16-30	31-45	46-60
-5	2.5	8.0	9.7	10.0
2	20.7	21.0	17.0	17.6
10	13.5	12.5	10.6	11.3
17	17.3	16.2	12.9	13.6
24	9.6	14.2	10.9	11.9
31	11.5	13.3	10.7	9.3
38	10.4	10.2	10.2	10.2
48	8.7	8.1	----	----
58	6.9	7.3	----	----
70	9.1	7.2	----	----

Table 2, Appendix B. Percent soil moisture at two soil depths during the growing cycle. East Lansing, MI. 1986

Days after Planting	Soil depth in cm.			
	0 - 30		31 - 60	
	Stressed	Irrigated	Stressed	Irrigated
-5	15.2	19.6	18.9	18.6
10	19.1	17.5	20.4	18.7
25	12.2	14.1	19.3	20.2
32	11.0	11.4	15.0	19.7
39	11.0	12.0	15.4	16.1
46	10.2	12.5	17.4	17.0
53	8.7	14.5	11.5	16.4
60	9.5	19.6	12.6	21.2
67	8.3	15.6	13.1	12.4
74	8.1	13.3	11.2	13.2
81	7.2	19.7	12.0	20.0
92	10.0	19.3	16.8	16.2
104	15.0	19.0	17.0	18.5

Table 3, Appendix B. Analyses of variance and significance of F-value of seed yield and some plant characteristics in 256 bean genotypes grown under drought-stress conditions in a rainout shelter. East Lansing, MI. 1985

		Mean Squares						
Source	df	Seed yield	TDM	HI	IKI Score	Pods m^2	LWC	LWRC
Rep.	1	760	3719	0.0	0.47	338	43.2	4327
Treat. Unadj.	255	4759**	21878**	0.01**	1.42**	4138**	5.0**	76**
Treat. Adj.	255	(1)	21725**	0.01**	(1)	(1)	4.9**	77**
Error RCB	255	2340	10022	0.005	0.66	2030	1.5	62
Effec. Error	225	---	9946	0.005	---	---	1.3	61
CV %		30.2	26.2	16.1	29.1	1.4	26.9	26.4

*,** F is significant at a = 0.05 and 0.01, respectively.

(1) No lattice corrections

Table 4, Appendix B. Climatic conditions recorded at the Botany Farm of Michigan State University during the growing season. East Lansing, MI. 1986

	Temperature °C		
Period	maximum	minimum	Rainfall in mm
May			
1 - 10	20.7	5.8	24.2
11 - 20	20.5	9.6	134.0
21 - 31	21.8	11.5	35.0
June			
1 - 10	24.1	10.6	168.2
11 - 20	24.4	12.8	239.7
21 - 30	25.5	13.7	40.0
July			
1 - 10	28.0	15.6	55.5
11 - 20	29.2	18.7	72.0
21 - 31	29.0	16.3	3.2
August			
1 - 10	25.3	14.5	43.2
11 - 20	26.0	12.2	12.7
21 - 31	23.4	9.4	184.7
September			
1 - 10	23.0	7.5	24.2
11 - 20	20.2	8.4	74.7
21 - 30	25.1	15.7	314.2

Table 5, Appendix B. Analyses of variance and significance of F-value of seed yield and some plant characteristics in 121 bean genotypes grown under drought stress conditions in a rainout shelter. East Lansing, MI. 1986

		Mean squares								
Source	df	Seed yield	Pods /m^2	Seeds /pod	Seed wt.	TDM	HI	IKI	LWC	LWRC
Rep.	1	50664	24496	.25	109	246633	.003	.20	15	251
Treat. Unadj.	120	1048262**	6297**	.90	24**	33569**	.023**	.64**	8**	126**
Treat. Adj.	120	982595**	6062**	(1)	(1)	32765**	.022**	(1)	7**	130**
RCB Error	120	474184	2850	.46	6.2	17405	.008	.33	4	63
Effec. Error	100	383193	2721	---	---	16308	.007	---	4	59
CV %		41.4	31.4	11.7	12.2	32.1	23.1	18.9	2.3	12.2

** F is significant at a = 0.01

(1) No lattice corrections

Table 6, Appendix B. Analysis of variance and significance of F-value of seed yield and some plant characteristics in 121 bean genotypes grown under irrigation. East Lansing, MI. 1986

		Mean squares								
Source	df	Seed yield	Pods /m^2	Seeds /pod	Seed wt.	TDM	HI	IKI	LWC	LWRC
Rep.	1	34694	45622	.51	1.8	106004	.001	1.8	134	1298
Treat. Unadj.	120	24180**	19290**	.62**	28**	87586**	.03**	.67**	5**	36
Treat. Adj.	120	22543**	18440**	.62**	(1)	(1)	(1)	.66**	5**	34
RCB error	120	7777	7715	.35	6.4	38094	.02	.23	3	29
Effec.	100	6885	7075	.34	---	---	---	.22	3	27
CV %		39.8	32.9	9.0	14.4	34.8	35.7	14.6	2.1	6.5

** F is significant at a = 0.01

(1) No lattice corrections

Table 7, Appendix B. Average values of some agronomic traits of 256 bean genotypes grown under a rainout shelter. East Lansing, MI. 1985

Family code	Days to Flower.	Days to Mat	Pods /m*	IKI score	Yield g/m*	TDM g/m*	HI
48-13	52	110	156	2.5	172	400	.43
48-20	42	88	208	2.0	142	310	.46
48-7	57	110	144	3.0	166	462	.36
48-22	61	125	224	2.3	300	666	.44
48-4	46	96	200	2.8	158	384	.41
48-21	58	110	188	2.8	242	562	.43
48-12	43	100	200	2.3	202	446	.47
48-10	47	110	176	2.8	264	542	.48
31-95	55	105	106	2.5	122	300	.41
48-16	48	112	174	2.8	180	458	.40
48-17	47	100	184	2.0	140	306	.44
48-19	46	120	220	2.8	198	490	.40
48-15	52	100	252	3.8	256	502	.51
48-14	48	100	126	1.5	94	230	.41
48-8	46	88	172	2.5	160	334	.48
48-11	48	100	148	1.8	146	312	.45
31-50-2	58	110	164	2.0	144	330	.45
31-26-1	56	100	158	2.0	126	286	.44
31-29-2	57	105	164	3.3	144	394	.37
31-33-1	51	93	172	1.8	188	372	.50
31-48-1	57	99	192	2.0	156	410	.39
31-30-1	53	95	108	1.0	94	252	.37
31-52-2	47	88	164	2.5	128	274	.47
31-31-1	48	98	144	3.3	132	308	.42
31-29-1	62	105	138	3.8	126	386	.33
31-54-1	51	98	230	3.3	218	476	.46
31-40-1	53	99	218	2.5	186	400	.48
31-51-3	48	100	180	1.5	158	354	.44
31-48-2	43	110	172	2.5	156	394	.39
31-33-2	56	98	154	2.5	186	378	.49
31-23-1	58	110	114	3.5	114	258	.44
31-24-2	51	120	140	3.0	108	338	.29
48-105	40	100	162	3.0	184	428	.43
48-102	44	88	146	3.5	76	214	.35
48-107	46	92	172	2.3	174	348	.49
48-109	41	90	202	3.0	200	474	.41
48-99	48	110	116	3.8	130	286	.45
48-101	46	95	118	4.3	154	264	.57
48-104	51	112	150	2.8	166	352	.50
48-101	40	105	180	3.0	148	318	.47
48--93	46	85	192	2.5	166	370	.43
48-106	40	85	160	4.3	156	342	.45
48-106	47	88	232	1.3	146	316	.46
48-107	48	95	172	3.3	112	274	.43

Table 7, Appendix B (Cont.)

48-102	58	125	154	3.8	138	398	.35
48-110	46	88	150	1.5	140	262	.53
48-109	53	110	122	1.3	100	222	.45
48-111	41	84	202	2.8	186	360	.52
25-13-1	40	100	132	3.3	134	292	.46
25-23-1	48	100	160	4.3	184	432	.45
25-31-2	47	96	72	2.0	42	120	.35
25-16-1	37	89	154	2.0	188	336	.56
25-14-2	41	84	94	1.3	126	250	.59
25-42-1	44	100	152	3.5	162	374	.48
25-42-2	46	100	146	1.8	120	266	.45
25-1-2	52	94	70	3.5	48	108	.44
25-3-1	43	84	176	2.0	146	322	.45
25-40-2	40	95	150	3.8	132	306	.44
25-33-1	40	102	142	4.0	98	300	.35
25-31-1	54	98	30	1.0	22	80	.24
25-50-1	53	125	138	4.3	160	490	.32
25-40-1	37	88	138	3.8	132	232	.58
25-53-2	36	100	158	4.0	170	318	.53
25-1-1	43	88	140	3.8	150	302	.50
48-72	52	128	296	3.5	218	586	.37
48-99	46	110	162	4.0	140	368	.38
48-76	48	120	254	2.3	176	408	.42
48-75	47	98	218	4.0	190	454	.40
48-86	41	96	290	2.8	242	488	.50
48-71	48	110	166	4.0	234	602	.38
48-91	48	105	158	1.0	144	362	.40
48-74	50	120	138	2.5	170	416	.41
48-79	48	100	182	3.3	172	340	.53
48-100	53	112	108	3.5	114	348	.29
48-87	56	105	186	2.8	172	392	.46
48-94	53	110	268	3.3	278	604	.45
48-78	60	125	210	3.5	208	532	.38
48-90	57	110	212	3.8	186	474	.40
48-84	44	100	184	3.0	176	422	.42
48-98	40	90	200	2.5	202	396	.51
51-14-1	37	80	140	1.5	92	160	.59
51-19-1	37	90	152	3.0	108	252	.43
51-8-1	42	88	232	1.5	192	384	.50
38-18-2	60	110	208	1.8	312	732	.42
51-16-1	80	150	72	3.8	42	220	.19
51-5-3	40	83	236	1.3	180	360	.50
51-8-3	38	84	140	3.3	148	278	.54
51-16-2	57	104	76	2.5	84	190	.46
51-6-1	38	84	196	2.8	220	370	.59
51-8-2	38	84	154	3.3	194	382	.51
38-16-2	56	110	170	3.0	250	566	.44
51-18-1	67	120	214	3.0	202	462	.44
51-1-1	61	100	62	2.5	50	136	.31
51-1-2	41	98	226	3.5	192	478	.41

Table 7, Appendix B (Cont.)

38-18-1	58	110	144	3.0	192	458	.43
38-16-1	60	110	184	1.8	248	588	.43
51-32-1	44	110	280	3.0	276	602	.46
51-40-1	58	120	118	2.8	144	354	.40
51-46-1	40	83	112	2.5	100	234	.42
51-23-3	44	86	144	2.3	122	282	.43
51-47-1	43	120	214	3.0	224	478	.47
51-29-2	43	100	178	4.3	142	386	.37
51-24-2	43	84	168	1.0	170	332	.51
51-22-2	44	88	220	1.8	144	324	.44
51-22-1	42	86	240	3.3	148	414	.35
51-44-1	38	80	236	1.3	114	252	.45
51-26-1	80	150	108	3.3	64	270	.24
51-19-2	64	120	52	2.5	38	116	.24
51-20-1	46	86	194	2.3	138	292	.47
51-29-3	38	110	234	4.0	196	452	.43
51-37-1	45	88	132	2.3	118	238	.50
51-23-1	38	88	204	2.8	124	264	.46
31-58-2	56	110	154	2.8	132	336	.39
31-60-1	54	125	122	4.3	158	444	.35
31-85-2	58	120	112	4.0	132	572	.25
31-94	58	110	72	2.5	78	290	.28
31-87-1	55	120	142	4.3	102	296	.35
31-93	58	110	116	2.8	128	318	.39
31-62-2	42	80	138	2.5	112	288	.38
31-63-1	52	98	118	2.3	114	290	.40
31-65-1	45	98	174	3.5	188	480	.39
31-67-1	46	96	110	4.0	120	294	.41
31-59-1	69	120	94	4.0	70	554	.11
31-56-4	46	100	142	1.3	146	290	.50
31-58-1	58	110	196	2.0	152	368	.41
31-54-2	52	107	200	3.8	166	382	.44
31-61-1	44	98	176	2.3	120	300	.39
31-90	52	90	170	2.0	150	326	.46
31-17-1	48	120	218	4.0	172	512	.34
31-4-1	57	102	162	4.3	160	436	.37
31-5-1	57	102	206	3.0	160	390	.41
51-49-1	38	120	294	2.8	212	586	.38
31-8-1	48	96	140	2.0	118	342	.34
31-11-1	52	96	156	2.3	182	396	.46
31-6-2	47	88	196	3.5	164	344	.48
51-53-1	45	120	124	2.5	96	328	.29
31-7-1	50	96	198	4.0	184	404	.46
31-20-1	43	92	116	2.8	116	286	.38
31-22-1	46	85	174	3.3	134	300	.45
31-13-1	52	100	132	3.5	140	338	.41
31-18-2	52	94	192	1.3	176	404	.44
31-20-3	52	98	128	1.5	106	296	.33
31-7-2	47	91	242	2.3	216	474	.46
31-3-1	52	99	154	3.8	154	388	.40

Table 7, Appendix B (Cont.)

48-48	48	105	164	3.5	168	448	.34
48-64	48	120	136	3.0	130	368	.35
48-55	41	125	136	4.3	142	350	.40
48-63	48	110	136	4.0	140	382	.37
48-66	52	110	202	2.3	222	530	.42
48-60	55	105	170	3.8	146	362	.41
48-65	59	125	186	2.0	162	416	.39
48-61	43	100	194	2.0	168	442	.38
48-56	55	125	138	3.3	142	332	.45
48-70	48	110	162	3.8	168	400	.42
48-62	51	110	142	4.0	136	328	.42
48-53	47	115	168	3.5	132	312	.42
48-58	45	90	214	1.8	210	510	.42
48-49	48	125	150	2.8	140	354	.39
48-57	51	110	180	3.8	162	442	.36
48-52	41	85	190	2.5	164	300	.53
DGO-222	80	150	46	4.3	30	530	.06
8-26	46	85	202	1.8	194	416	.47
UW-23-61	46	80	184	1.8	148	320	.46
8-14	48	92	180	2.8	190	432	.43
8-28	46	92	176	3.3	162	368	.43
1213-2	80	150	84	4.0	58	486	.12
8-25	57	98	260	1.5	242	494	.49
II900-5-M-45	54	110	114	3.3	150	392	.38
UW 21-58	48	94	136	2.0	148	344	.42
UW 21-54	51	110	224	2.5	224	454	.49
LEF-2-RB	44	88	140	3.8	180	376	.48
8-23	48	96	158	3.0	164	344	.47
8-27	50	90	114	3.3	134	310	.44
BAYO MAD	48	100	144	4.3	176	414	.43
N81064	42	88	114	3.5	100	232	.42
N81017	47	88	126	1.8	122	240	.51
9-18	51	110	212	2.8	228	510	.45
9-6	50	100	112	3.8	128	298	.44
9-15	47	90	166	3.5	188	418	.45
9-20	52	100	226	2.8	232	492	.47
9-8	52	110	228	2.3	212	490	.43
9-3	50	112	196	2.5	172	430	.41
9-12	47	96	186	2.0	178	424	.41
9-4	48	100	174	2.5	178	438	.41
48-94	55	110	122	3.5	108	278	.38
9-2	52	120	208	2.5	228	568	.40
9-10	52	110	218	3.5	258	552	.45
9-16	46	92	206	2.5	204	460	.45
9-17	48	110	160	3.8	198	482	.41
9-7	43	98	232	2.0	220	512	.43
9-11	47	105	158	2.0	234	440	.53
9-21	51	101	172	2.5	160	410	.39
48-43	61	125	192	3.0	244	556	.44
48-32	66	125	272	1.8	302	708	.43

Table 7, Appendix B (Cont.)

48-34	39	105	230	4.0	204	484	.42
48-35	63	125	200	2.0	164	366	.46
48-45	45	85	142	2.0	122	266	.43
48-24	52	125	140	3.0	116	322	.36
48-46	36	110	204	2.3	190	406	.47
48-27	58	110	228	2.3	182	454	.40
48-36	47	100	168	2.5	150	416	.35
48-44	46	105	206	2.5	178	398	.44
48-30	41	105	138	2.5	142	288	.46
48-23	51	125	218	3.3	214	486	.44
48-37	48	105	184	4.0	192	476	.40
48-42	52	110	190	2.8	176	338	.53
48-40	48	100	170	3.8	148	370	.40
48-26	44	88	220	3.0	220	454	.48
9-39	58	110	194	3.8	206	574	.36
9-24	46	89	208	2.8	184	450	.41
9-43	46	100	144	1.0	192	378	.48
9-26	53	120	162	3.3	170	408	.41
9-22	48	105	178	2.3	222	380	.58
9-35	48	96	164	2.8	160	408	.39
9-28	44	110	120	4.0	118	320	.37
9-27	51	110	178	3.5	212	490	.43
9-33	51	110	200	2.5	174	464	.37
9-23	58	110	174	4.0	184	410	.45
8-1	52	110	132	2.8	132	296	.45
9-32	45	110	200	3.8	170	440	.38
9-25	56	105	196	2.8	204	472	.43
9-34	48	110	204	3.3	236	532	.45
9-42	55	118	212	2.8	190	472	.41
9-29	43	105	180	3.5	206	464	.44
8-21	45	88	192	2.8	208	378	.55
8-16	47	88	128	2.8	122	270	.45
8-14	48	88	146	3.3	138	272	.51
8-5	50	96	182	1.8	174	386	.45
8-12	47	100	190	2.5	188	418	.45
8-6	48	92	152	3.8	158	382	.42
8-22	44	90	130	1.0	114	222	.51
8-17	50	96	186	1.5	184	346	.53
8-3	53	100	84	1.0	56	180	.32
8-15	47	90	224	2.8	214	434	.50
8-11	52	100	158	2.3	122	300	.41
8-20	48	100	162	1.8	130	312	.42
8-10	51	96	116	1.8	116	278	.42
8-7	48	95	140	2.3	128	296	.43
8-18	46	96	186	3.3	216	454	.48
8-8	51	110	154	4.0	164	346	.50
38-8-2	55	115	104	2.8	120	274	.45
38-8-1	57	105	96	2.5	124	272	.48
39-8-1	51	98	156	1.5	190	416	.46
39-4-1	52	98	248	3.3	196	476	.41

Table 7, Appendix B (Cont.)

39-6-1	53	96	100	2.5	120	302	.41
39-11-1	52	100	160	2.8	246	508	.48
39-3-1	54	98	116	3.5	146	404	.36
38-10-1	55	98	222	1.3	198	438	.46
38-4-2	58	105	128	2.0	170	284	.60
38-7-1	59	105	180	3.3	198	484	.42
39-4-3	50	96	180	2.8	162	378	.43
38-4-1	56	98	120	3.5	144	328	.47
38-2-1	57	105	200	2.3	240	488	.49
39-11-2	53	105	132	3.8	158	288	.55
39-17-1	35	100	104	3.5	104	374	.30
39-13-1	52	101	126	3.5	168	398	.42

* Square meter.

Table 8, Appendix B. Average values of some agronomic traits of 121 bean genotypes grown under drought stress in a rainout shelter. East Lansing. MI. 1986

			Seeds						L	Days to	
Family code	IKI score	pods /m*	/pod	wt	TDM g/m*	Yield g/m*	HI	L W C	W R C	FL	PM
48-21-M	3.5	153	7.3	16.2	444	134	.29	83	61	47	125
48-21-M	3.5	137	6.3	20.1	321	127	.36	82	57	56	120
48-21-1	2.3	190	5.8	20.1	476	166	.35	83	64	64	125
PLOT-13	3.0	211	5.5	21.1	364	153	.42	81	67	37	114
PLOT-15	3.3	118	5.7	26.6	259	124	.49	81	52	39	105
48-22-1	4.0	106	6.3	23.4	321	46	.11	84	72	68	125
48-10-M	3.8	205	6.4	20.0	532	199	.37	82	63	40	122
48-15-2	3.5	142	6.6	18.2	316	103	.33	80	64	56	122
48-14-1	2.5	210	5.5	21.3	460	170	.37	78	71	38	120
48-14-2	2.3	160	6.1	21.6	411	145	.35	81	69	38	98
48-86-1	3.3	123	5.5	18.7	229	98	.42	80	70	41	93
48-86-2	3.8	181	6.0	21.1	403	167	.41	80	71	36	90
48-71-M	3.3	189	6.3	20.7	542	166	.30	82	73	58	125
48-72-1	2.5	45	5.9	19.6	60	35	.57	81	62	58	105
48-94-1	2.5	163	6.3	17.0	371	118	.31	87	55	63	122
48-78-M	3.8	166	5.8	16.6	510	82	.15	80	65	69	125
48-78-1	4.3	163	6.3	15.3	419	68	.16	81	74	67	125
38-18-2-M	2.5	260	6.3	19.4	690	216	.31	83	69	56	125
38-18-2-1	2.8	184	5.7	19.7	482	165	.31	81	65	54	125
51-6-1-1	3.3	127	4.7	24.6	323	119	.37	79	54	42	92
38-16-2-M	3.3	160	6.9	21.2	461	150	.32	83	56	54	125
51-32-1-3	4.3	187	5.8	19.4	423	130	.32	82	59	54	125
51-32-1-2	2.3	147	6.0	20.8	281	136	.46	82	58	37	120
51-32-1-1	4.3	174	5.3	21.3	370	121	.32	85	60	53	125
51-47-1-1	3.5	152	5.1	21.3	332	111	.34	78	53	39	102
31-94-M	3.3	203	6.8	20.2	536	237	.44	81	55	52	100
51-49-1-1	3.8	135	4.9	26.4	180	93	.79	78	57	37	105
51-49-1-M	4.3	119	5.5	19.9	375	49	.12	82	53	51	102
31-7-2-1	3.8	145	5.7	19.5	308	128	.43	81	58	42	95
31-7-2-2	2.8	152	3.6	20.0	360	174	.51	79	58	53	118
48-66-M	2.8	152	6.5	21.1	418	119	.26	82	61	58	125
48-66-1	2.3	118	6.8	17.3	303	83	.27	81	55	66	118
48-58-1	3.0	127	6.0	17.3	321	90	.26	80	62	60	100
9-18-1-M	3.5	137	5.8	21.2	386	126	.32	82	64	58	110
9-18-1-1	3.0	102	5.8	19.8	287	65	.15	79	67	43	102
8-25-1	2.5	232	6.6	16.3	372	169	.45	77	71	56	110
8-25-2	2.8	240	6.3	20.7	587	259	.44	80	74	41	98
9-20-1	3.0	140	5.9	18.1	307	130	.40	81	65	52	108
9-20-2	2.5	118	5.4	17.0	386	105	.23	80	61	48	98
48-94B-1	3.3	121	6.1	16.5	224	77	.35	81	54	49	120
48-94B-2	2.3	160	6.3	20.0	356	147	.40	84	64	58	107

Table 8, Appendix B (Cont.)

9-2-1	3.0	168	5.8	20.7	384	145	.37	80	50	54	110
9-10-1	3.3	85	7.2	19.5	305	93	.29	80	72	58	118
9-10-M	3.5	166	6.3	15.2	368	112	.30	79	64	63	125
9-7-1	3.0	63	6.3	15.3	152	42	.28	83	73	65	125
9-7-M	2.3	161	6.0	18.0	400	115	.27	82	64	65	122
9-11-1	3.3	110	5.7	21.7	234	98	.41	81	59	51	100
48-23-M	2.5	152	6.5	19.1	377	129	.34	82	64	41	110
48-46-1	3.0	163	6.0	21.6	389	163	.41	82	59	38	90
9-39-1	2.3	182	6.4	14.9	403	146	.37	81	65	64	125
9-22-1	3.3	108	6.5	18.5	310	111	.34	84	65	62	125
9-22-M	2.5	208	6.5	19.3	500	148	.30	80	67	61	125
9-27-1	3.0	161	5.5	16.2	397	112	.27	84	65	64	125
9-27-M	3.0	147	6.7	16.5	353	113	.32	81	54	60	125
9-29-1	2.8	102	6.3	22.2	352	94	.27	84	68	35	99
9-29-M	1.8	200	6.5	18.4	509	198	.39	82	57	44	102
8-21-1	3.0	77	6.0	18.8	190	74	.40	81	60	67	125
8-21-2	2.8	203	6.7	22.9	560	257	.46	80	60	63	120
8-3-M	4.0	124	6.1	19.6	317	116	.41	77	62	43	95
8-15-2	3.3	198	6.2	21.5	461	197	.42	80	74	42	102
8-15-1	2.0	29	6.0	22.0	81	27	.34	84	56	60	125
39-17-1-M	3.0	92	5.5	23.6	311	87	.30	80	50	62	125
39-11-1-M	3.3	161	6.5	23.3	629	177	.28	82	63	64	120
PLOT-36	3.5	113	5.5	23.5	239	62	.28	82	64	38	105
PLOT-36-1	4.0	148	6.0	26.4	368	129	.35	80	53	37	120
8-42-M	2.8	174	6.5	25.2	511	232	.47	80	40	45	98
41-25-1-M	3.3	123	5.8	21.6	284	97	.34	81	71	60	118
8-40-M	2.5	203	7.1	20.3	492	217	.45	81	60	54	112
41-18-1-M	2.5	282	6.4	23.1	552	304	.55	77	65	43	108
41-10-2-M	3.3	195	5.7	21.8	432	187	.43	78	69	34	93
41-12-1-M	3.3	132	7.0	20.6	339	138	.41	83	69	51	115
41-39-M	3.8	319	6.3	24.3	893	398	.45	79	63	51	105
8-46-M	3.0	271	5.9	20.7	546	249	.45	79	70	45	105
45-5-2-M	3.0	166	5.2	22.7	427	179	.40	81	67	40	90
8-30-M	3.0	263	6.1	23.7	534	266	.50	82	69	51	102
8-4-M	2.3	281	7.0	18.5	761	260	.34	80	71	61	120
41-48-1-M	2.3	281	5.7	21.8	570	288	.51	80	70	42	100
41-18-3-M	2.8	213	5.8	22.6	463	229	.49	78	63	40	100
41-52-2	2.5	208	6.5	18.9	510	195	.38	78	67	63	120
41-6-1-M	3.8	171	5.7	23.5	371	185	.51	82	54	37	105
8-35-M	2.8	253	6.0	22.2	551	240	.42	77	59	44	93
8-47-M	3.3	258	6.5	18.0	565	246	.44	78	70	61	125
41-32-1	2.8	218	6.1	20.3	403	175	.43	81	51	42	110
41-48-1-M	2.5	173	5.0	13.8	295	113	.39	73	75	54	120
41-37-1-M	3.0	221	6.2	22.3	437	203	.46	81	71	50	102
8-29-M	2.8	184	5.4	23.2	386	180	.46	81	71	42	95
41-14-1-M	3.0	181	5.5	18.6	394	170	.44	78	72	54	92
41-36-3-M	2.5	200	6.0	18.4	406	167	.41	79	59	49	125
41-58-3-M	2.3	174	6.5	18.1	468	135	.30	82	73	62	125
41-39-3-M	2.8	208	5.3	17.6	311	128	.41	81	71	53	105
48-109-M	3.5	184	6.4	24.6	430	250	.52	83	72	35	100

Table 8, Appendix B (Cont.)

51-1-1-M	2.5	227	4.7	23.6	439	198	.45	79	61	34	90
51-29-3-M	2.8	89	5.3	21.3	209	86	.44	77	55	45	100
48-19-1	2.3	139	6.6	19.3	328	134	.40	83	74	55	102
48-98-M	2.5	206	5.8	20.2	481	184	.38	81	64	39	87
9-24-M	2.5	219	6.0	21.5	566	206	.36	80	54	55	108
8-6-1	3.5	229	6.8	21.5	554	220	.38	81	77	52	116
48-105-1	2.3	185	7.0	23.0	445	203	.45	80	71	45	125
31-90-M	2.5	168	6.1	24.4	375	181	.48	81	57	55	118
51-8-2-M	3.0	144	4.9	26.3	289	116	.40	80	45	35	95
51-5-3-M	2.8	258	5.3	19.4	557	238	.43	81	53	44	90
8-17-M	3.0	231	6.4	21.6	504	234	.46	79	76	51	102
8-14-2	3.3	160	6.0	15.3	364	160	.42	82	68	44	102
48-48-M	3.0	176	5.5	20.0	367	127	.34	81	70	50	108
48-34-1	3.8	98	5.3	25.4	201	87	.43	80	43	37	105
51-1-2-M	3.3	226	5.2	23.0	399	161	.38	81	60	39	100
48-36-M	2.3	165	6.0	22.7	390	132	.33	83	69	36	125
8-10-2	3.0	276	5.8	20.5	469	229	.47	80	57	43	100
8-26-M	2.3	155	5.6	22.1	497	198	.40	80	59	44	99
LEF-2-RB	3.5	210	5.8	21.4	645	278	.42	79	74	42	98
II900-5-M	2.8	90	6.0	15.2	234	54	.24	82	67	63	125
N81064	3.3	124	5.5	20.7	197	108	.55	80	46	52	100
UW.23-61	3.3	166	5.3	21.0	268	134	.50	78	69	55	108
UW.21-54	3.0	181	6.5	16.1	329	137	.41	80	47	54	120
UW.21-58	2.8	160	7.1	18.9	361	158	.44	81	49	53	105
DGO-222	4.5	8	3.0	10.0	503	1	.01	84	54	90	125
BAYO MAD.	4.5	134	4.5	32.8	453	128	.29	81	58	63	125
1213-2	3.5	44	5.5	11.8	435	15	.03	85	56	90	125
N81017	3.5	148	5.9	22.0	292	152	.49	79	66	47	95
PINTO N.1	3.3	123	4.4	35.4	323	126	.39	82	69	33	85
39-11-1	2.5	61	5.0	15.4	149	34	.22	80	55	69	125

LWC = Leaf water content in %.

LWRC = % of moisture lost after 24 hours.

FL = Days to flowering.

PM = Physiological maturity.

* Square meter.

Table 9, Appendix B. Average values of some agronomic traits of 121 bean genotypes grown under irrigation. East Lansing, MI. 1986

Entry code	IKI score	Pods /m*	Seeds pod	Seeds wt	TDM g/m*	Yield g/m*	HI	LLWC	WRC	Days to FL	Days to MP
48-21-M	3.5	215	6.8	14.5	523	127	.25	84	79	63	125
48-21-M	2.5	448	6.8	13.0	937	331	.35	82	81	56	125
48-21-1	3.3	298	6.8	16.2	597	183	.31	85	83	60	125
PLOT-13	4.0	216	6.6	15.0	404	154	.38	83	82	50	118
PLOT-15	3.3	208	5.5	27.9	450	194	.43	82	72	40	107
48-22-1	4.0	119	6.8	13.6	366	40	.11	87	77	64	125
48-10-M	3.0	218	6.6	19.5	650	184	.31	85	74	56	125
48-15-2	4.0	224	7.0	14.5	458	145	.33	84	79	69	125
48-14-1	4.5	166	5.8	15.1	311	77	.25	84	84	55	125
48-14-2	3.3	166	5.7	22.5	320	163	.50	83	89	43	108
48-86-1	3.8	171	6.3	17.1	287	120	.42	86	74	47	118
48-86-2	3.0	235	5.8	16.2	417	176	.43	84	80	49	112
48-71-M	3.5	242	6.0	15.5	634	144	.23	83	80	62	115
48-72-1	4.0	103	6.0	15.7	228	52	.23	86	75	50	115
48-94-1	2.8	235	6.3	16.2	487	159	.33	84	82	62	125
48-78-M	4.3	292	6.8	12.4	677	114	.17	86	80	61	125
48-78-1	4.0	79	5.5	8.8	324	16	.05	83	77	65	125
38-18-2-M	4.0	292	7.1	18.1	746	217	.29	84	75	60	125
38-18-2-1	3.0	219	6.8	15.0	519	133	.23	87	75	56	125
51-6-1-1	3.5	234	6.8	20.5	479	192	.39	85	84	40	95
38-16-2-M	3.8	371	6.5	18.3	848	336	.39	83	77	62	115
51-32-1-3	4.0	237	6.7	13.4	457	117	.25	83	81	43	125
51-32-1-2	3.3	165	6.0	16.4	460	119	.22	84	82	39	125
51-32-1-1	4.0	168	5.5	15.1	568	82	.15	85	79	64	115
51-47-1-1	3.5	147	6.1	16.7	258	86	.34	84	80	43	95
31-94-M	2.0	239	7.2	17.6	590	227	.38	84	79	54	120
51-49-1-1	2.8	187	5.6	23.6	500	162	.33	82	82	47	95
51-49-1-M	3.5	252	6.0	16.4	251	139	.92	83	78	52	125
31-7-2-1	3.0	258	6.6	16.4	425	187	.41	85	77	64	112
31-7-2-2	2.5	310	7.1	17.0	654	280	.43	83	78	47	105
48-66-M	3.5	271	6.3	16.0	597	181	.30	83	75	58	125
48-66-1	2.5	218	6.7	15.0	538	173	.31	84	84	64	125
48-58-1	3.0	252	6.6	14.9	608	186	.32	83	84	59	125
9-18-1-M	3.8	116	6.7	16.1	338	61	.20	87	71	50	125
9-18-1-1	3.3	232	7.1	16.4	588	215	.37	87	72	47	125
8-25-1	2.3	303	7.0	13.8	541	225	.40	82	79	53	125
8-25-2	3.3	340	6.6	16.0	515	247	.47	85	81	50	115
9-20-1	2.8	348	6.6	16.3	859	254	.31	85	73	47	120
9-20-2	2.3	105	6.0	11.8	369	85	.23	83	74	52	118
48-94B-1	3.5	126	6.4	16.7	227	88	.40	82	75	43	118
48-94B-2	3.3	258	6.9	14.9	465	179	.38	86	74	53	118
9-2-1	3.0	290	6.0	15.9	736	196	.26	83	81	61	125
9-10-1	2.3	150	7.4	16.9	368	139	.36	85	80	55	118

Table 9, Appendix B (Cont.)

9-10-M	3.0	194	6.5	15.7	400	159	.35	85	71	55	125
9-7-1	3.5	171	6.8	15.7	624	125	.24	83	76	54	125
9-7-M	3.3	384	7.0	17.0	847	285	.34	84	83	54	118
9-11-1	2.5	248	6.6	16.9	520	236	.44	83	79	51	115
48-23-M	3.8	240	6.5	14.9	506	148	.29	85	81	53	125
48-46-1	3.3	168	6.3	18.2	351	172	.48	83	74	43	95
9-39-1	4.3	176	7.0	11.5	425	110	.26	83	79	51	125
9-22-1	3.3	197	7.0	13.0	524	133	.25	86	77	61	125
9-22-M	3.3	337	6.2	17.3	834	281	.33	84	78	66	125
9-27-1	4.0	140	6.5	12.6	307	68	.22	87	78	59	125
9-27-M	3.8	302	6.9	16.6	702	288	.42	85	82	54	125
9-29-1	3.0	265	6.8	13.5	607	172	.29	83	84	56	118
9-29-M	3.5	277	6.7	17.5	624	239	.39	86	76	60	125
8-21-1	2.5	244	6.4	13.9	464	175	.35	88	76	51	118
8-21-2	2.3	313	7.0	23.5	762	384	.54	84	77	49	115
8-3-M	3.5	150	6.3	16.4	354	124	.37	84	80	48	115
8-15-2	2.3	218	6.6	18.8	459	203	.44	86	80	51	115
8-15-1	2.5	323	6.8	17.8	913	246	.28	86	75	51	115
39-17-1-M	3.3	144	6.0	24.3	335	166	.45	84	64	51	115
39-11-1-M	3.8	416	7.5	22.8	1114	501	.45	86	68	56	118
PLOT-36	4.3	166	6.0	14.3	474	110	.22	85	76	48	125
PLOT-36-1	3.3	258	6.5	17.4	567	184	.32	84	81	49	120
8-42-M	3.0	436	6.8	24.3	975	498	.51	84	77	43	102
41-25-1-M	2.8	155	6.0	16.4	268	96	.34	83	76	54	112
8-40-M	3.8	271	6.8	15.9	686	210	.31	84	83	48	115
41-18-1-M	3.3	292	7.1	22.8	608	311	.51	83	74	48	118
41-10-2-M	2.8	245	6.3	20.1	422	216	.51	84	81	43	95
41-12-1-M	3.8	198	6.5	15.2	392	138	.35	84	75	43	112
41-39-M	4.0	508	7.0	19.1	1315	503	.38	85	80	53	115
8-46-M	3.3	395	5.6	17.8	711	331	.47	85	83	50	115
45-5-2-M	3.5	281	7.1	20.4	579	288	.50	84	78	43	100
8-30-M	2.3	281	6.3	20.6	586	275	.47	87	79	51	115
8-4-M	2.0	423	6.8	16.3	879	413	.47	84	78	56	112
41-48-1-M	2.8	342	5.9	20.6	642	356	.54	83	80	41	95
41-18-3-M	2.8	316	6.2	20.2	557	267	.48	84	77	49	115
41-52-2	3.5	386	7.1	14.2	829	279	.31	83	85	43	125
41-6-1-M	3.0	287	6.0	20.2	505	223	.44	84	82	40	94
8-35-M	3.5	318	7.3	20.5	695	309	.44	85	83	56	118
8-47-M	3.3	486	7.0	18.5	767	465	.67	83	85	47	105
41-32-1	3.0	192	6.5	15.5	419	87	.21	86	78	43	115
41-48-1-M	3.3	226	5.8	12.6	348	153	.44	83	81	42	90
41-37-1-M	2.5	287	6.5	17.8	573	203	.36	85	86	58	125
8-29-M	2.5	321	5.9	20.0	577	238	.41	84	86	48	100
41-14-1-M	2.5	286	6.2	21.7	559	165	.34	85	79	47	118
41-36-3-M	4.0	342	7.0	18.1	712	280	.38	83	81	49	118
41-58-3-M	3.0	374	7.0	14.0	650	276	.68	83	86	60	115
41-39-3-M	2.8	323	5.8	15.4	499	201	.41	83	85	51	110
48-109-M	3.5	227	6.7	20.8	549	218	.40	81	73	47	106
51-1-1-M	3.5	84	5.5	15.3	201	65	.28	84	81	37	90
51-29-3-M	3.3	137	6.3	21.4	382	139	.37	84	70	43	90

Table 9, Appendix B (Cont.)

48-19-1	2.8	195	6.0	17.3	369	113	.31	87	81	49	112
48-98-M	3.3	173	6.6	15.2	348	118	.33	84	78	57	115
9-24-M	3.3	258	6.8	20.5	575	258	.45	82	75	44	98
8-6-1	3.8	448	6.7	18.5	916	398	.44	86	80	52	112
48-105-1	3.3	374	7.3	19.9	764	373	.48	83	84	47	115
31-90-M	2.8	329	6.0	23.1	757	359	.47	86	77	44	110
51-8-2-M	4.0	85	5.6	22.6	225	47	.20	83	82	43	115
51-5-3-M	3.5	147	5.4	18.4	258	127	.37	83	75	43	90
8-17-M	3.3	497	7.0	19.0	995	454	.46	85	79	54	125
8-14-2	2.8	332	7.0	18.7	712	340	.46	84	84	46	118
48-48-M	4.0	300	6.8	18.5	632	228	.36	85	77	50	125
48-34-1	2.3	224	6.5	22.4	399	206	.52	78	74	47	108
51-1-2-M	3.0	177	5.7	16.8	338	148	.41	85	81	44	104
48-36-M	2.8	258	7.3	14.4	458	165	.36	86	81	41	118
8-10-2	3.3	356	6.8	17.5	780	329	.44	86	83	52	125
8-26-M	2.0	387	6.9	21.3	804	412	.51	82	80	43	103
LEF-2-RB	2.8	221	6.8	23.2	478	214	.45	84	84	43	115
II900-5-M	3.5	111	6.3	14.6	302	75	.23	85	79	61	125
N81064	2.5	277	6.3	18.3	521	235	.45	86	78	43	103
UW.23-61	3.5	227	6.1	20.8	396	181	.48	81	82	42	97
UW.21-54	2.8	527	7.5	16.9	1037	505	.49	83	85	56	112
UW.21-58	3.0	302	7.8	17.2	792	283	.37	83	80	58	125
DGO-222	4.5	119	6.0	15.0	800	30	.06	89	85	90	125
BAYO MAD.	4.0	155	5.0	29.5	441	149	.34	83	81	52	120
1213-2	4.0	126	6.0	13.5	724	55	.07	84	87	90	125
N81017	2.5	452	6.5	16.9	873	433	.49	82	84	47	95
PINTO N.1	3.5	137	4.4	35.8	331	172	.53	86	85	37	90
39-11-1-M	3.0	269	5.8	15.6	563	169	.30	82	85	63	125

LWC = Leaf water content in %.

LWRC = % of water lost after 24 hours.

FL = Days to flowering.

PM = Days to physiological maturity.

* Square meter

APPENDIX C

Table 1, Appendix C. Combined analyses of variance for growth and yield related variables of 26 bean genotypes grown under drought stress and non-stress conditions at Durango (Mexico) and Michigan (USA). 1987

	Significance of F-values							CV
Variable	$L^{@}$	C	LC	G	LG	CG	LCG	%
df	1	1	1	25	25	25	25	
TDM 40 DAE	***	NS	**	**	***	NS	NS	21.9
TDM 61 DAE	***	***	***	***	*	NS	NS	20.9
Senes leaves	***	***	NS	**	***	***	***	32.9
LAI 40 DAE	***	***	***	***	***	NS	NS	24.1
LAI 61 DAE	***	***	***	***	***	NS	NS	24.1
CGR 40 DAE	***	NS	NS	**	***	NS	NS	22.0
CGR 61 DAE	***	***	***	***	*	NS	NS	20.9
Leaf expans	***	***	***	***	***	**	**	39.8
Days flowering	NS	NS	NS	***	***	***	***	3.3
Days maturity	***	***	NS	***	***	***	***	2.7
Rep. phase	***	***	NS	***	***	***	***	6.0
Seed yield	***	***	***	***	***	**	NS	23.4
Pods/m^2	***	***	***	***	***	NS	NS	23.5
Seeds/pod	***	***	***	***	***	NS	**	15.6
100 seeds wt.	***	NS	*	***	***	*	*	9.8
Seed protein	***	NS	***	***	NS	**	NS	5.6
N seeds (g/m^2)	***	***	***	***	***	**	NS	22.6
TDM maturity	***	***	***	***	***	***	**	20.4
Harvest Index	***	***	***	***	***	***	***	9.0

*,**, *** F is significant at $P<0.05$, 0.01, and 0.001, respectively.
@ L= location, G= genotype

Table 2, Appendix C. Analyses of variance for growth and yield related variables of 26 bean genotypes grown under drought stress and rainfall conditions. Kellog Biological Station, Battle Creek, MI. 1987

Variable		Mean squares			
		Regime	Genotype	R x G	
	df	1	25	25	CV %
TDM at 40 DAE		3096	3628*	2909	18.3
TDM at 61 DAE		77247	9959**	5954*	17.8
Senesced leaves		4675**	424**	398**	30.1
LAI at 40 DAE		8.77*	1.37**	0.75	21.7
LAI at 61 DAE		6.12	2.48**	0.60	22.8
CGR at 40 DAE		1.93	2.27*	1.81	18.3
CGR at 61 DAE		20.7	2.68**	1.60*	17.9
Leaf expansion		132**	3.04**	1.36**	35.3
Days to flowering		0.16	1799**	202**	3.0
Days to maturity		592**	418**	42**	2.8
Length reprod. phase		573**	185**	57**	6.3
Seed yield (g/m^2)		945131**	5832**	3216*	22.4
No. pods/m^2		294756**	8338**	1869	23.4
No. seeds/pod		100**	1.45**	0.54*	14.2
100 seeds weight		16.9	73.2**	8.73*	10.5
N seed yield (g/m^2)		623**	7.2**	4.1**	22.0
TDM at maturity		1640528**	22362**	13524**	18.7
Harvest Index		1.0**	0.018**	0.007**	11.6

*,** F-value significant at P<0.05 and 0.01, respectively.

Table 3, Appendix C. Analyses of variance for growth and yield related variables of 26 bean genotypes grown under drought stress and rainfall conditions. Durango, Mexico. 1987

	Mean Squares			
Variable	Regime	Genotype	C x G	
df	1	25	25	CV %
TDM at 40 DAE	37	3169**	40	30.1
TDM at 57 DAE	393462**	2883	2540	24.5
Senesced leaves	2632*	109**	96**	32.8
LAI at 40 DAE	0.011	1.12**	0.011	27.2
LAI at 57 DAE	71**	0.54**	0.26	23.9
CGR at 40 DAE	0.023	1.98**	0.025	30.1
CGR at 57 DAE	121**	0.88	0.78	24.5
Leaf expansion	65**	0.28	0.17	43.6
Days to flowering	2.6	17.8**	2.96	3.7
Days to maturity	845**	38.8**	8.77**	2.5
Length rep. phase	754**	11.3**	8.80	5.6
Seed yield (g/m^2)	86625**	1008**	454	19.9
No. pods/m^2	110005**	1010**	491	16.8
No. seeds/pod	5.39*	1.24**	0.76*	16.7
100 seeds weight	2.64	97.2**	4.60	8.4
N in seeds (g/m^2)	163**	1.81**	0.89	20.8
TDM at maturity	218997**	1636**	735	16.3
Harvest Index	0.46	.011**	.002*	6.3
IKI score	2.92**	1.02**	0.43**	15.1

*,** F-value significant at $P<0.05$ and 0.01, respectively.

Table 4, Appendix C. Percent soil moisture at three soil depths during the growing season. Kellogg Biological Station, Battle Creek, MI. 1987

Days after planting	Soil depth in cm.					
	0 - 15		16 - 30		31 - 45	
	I*	S*	I	S	I	S
40	15.5	6.1	13.6	8.7	13.0	15.2
46	12.1	4.8	11.3	8.0	12.2	10.7
55	12.0	6.8	12.4	7.8	13.3	8.0
61	13.1	4.9	8.7	7.0	8.6	7.1

* I = Irrigated, S = Stressed.

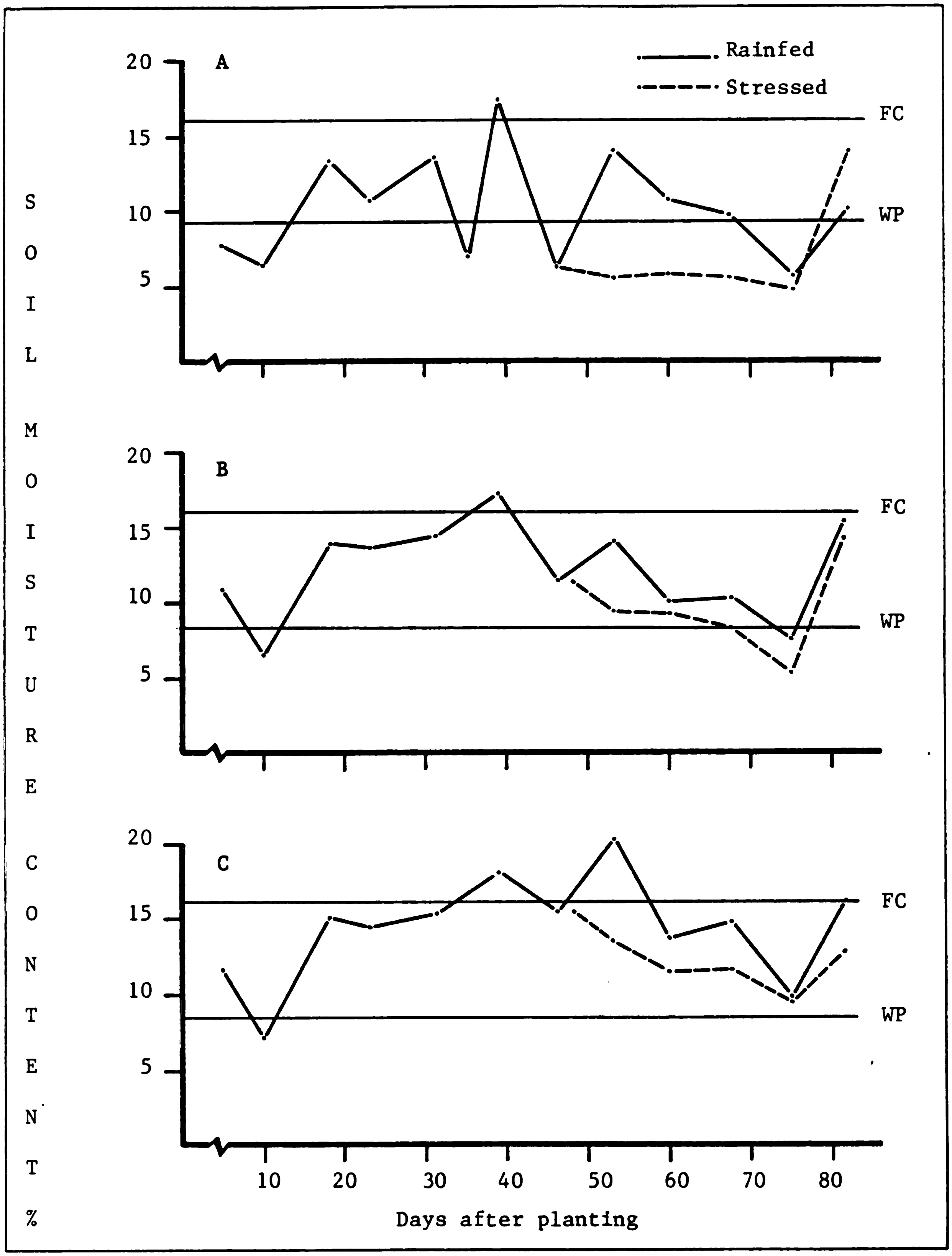


Figure 1. Soil moisture content during the growing season at three different depths, A = 0-15 cm, B = 16-30 cm, C = 31-45 cm (FC= field capacity, -0.03 bars and WP= wilting point, -15 bars). Durango, Mexico. 1987.

Table 5, Appendix C. Climatic conditions recorded at Kellogg Biological Station, during the growing season. Battle Creek, MI. 1987

	Temperature °C		
Period	maximum	minimum	Rainfall in mm.
May			
16 - 20	24.7	10.8	22.0 *
21 - 25	22.3	10.1	00.0
26 - 31	30.8	18.2	2.0 *
June			
1 - 5	25.9	13.8	3.0 *
6 - 10	26.8	12.3	0.0 +5
11 - 15	32.1	16.5	3.0 *
16 - 20	34.4	16.2	40.0 *
21 - 25	28.5	17.4	13.0 *
26 - 30	24.5	15.0	3.0 *
July			
1 - 5	26.9	14.6	2.0 *
6 - 10	30.7	19.3	28.0 *8
11 - 15	26.0	15.6	21.0
16 - 20	30.6	16.1	8.0
21 - 25	32.0	20.2	19.0
26 - 31	30.5	15.4	11.0
August			
1 - 5	31.3	18.9	12.0
6 - 10	27.4	16.3	23.0
11 - 15	30.2	17.2	7.0
16 - 20	27.5	14.9	55.0 *40
21 - 25	23.2	11.3	14.0
26 - 31	19.8	11.7	58.0
September			
1 - 5	24.6	8.6	4.0
6 - 10	26.7	14.2	20.0
11 - 15	24.6	11.4	38.0
16 - 20	20.6	14.0	22.0
21 - 25	19.0	8.2	12.0
26 - 30	23.3	10.2	19.0
October			
1 - 5	15.3	2.7	6.0
6 - 10	10.8	2.8	4.0
11 - 15	15.4	0.5	00.0
16 - 20	15.4	4.9	28.0

* Rainfall (+) plus irrigation under rain shelter.

Table 6, Appendix C. Climatic conditions recorded at "Los Llanos" Experimental Station, during the growing season. Durango, Mexico.1987

Period	Temperature °C		Rainfall in mm.
	maximum	minimum	
June			
1 - 10	25.7	10.9	33.5 *
11 - 20	29.8	13.7	0.1 *
20 - 30	30.4	14.2	28.5 *
July			
1 - 10	30.7	14.7	11.8 *
10 - 20	25.8	14.8	50.2 *
20 - 31	21.5	12.4	5.3 *
August			
1 - 10	24.5	13.3	52.5 *16.5
11 - 20	26.6	14.3	26.1
21 - 30	25.8	14.1	46.9
September			
1 - 10	24.0	12.9	24.0
11 - 20	28.3	11.5	4.0
21 - 30	22.5	13.2	74.5
October			
1 - 10	20.5	7.9	0.0
11 - 20	22.7	6.3	0.0
21 - 31	25.6	9.4	10.5

* Rainfall for stressed plots.

Table 7, Appendix C. Loading coefficients of 25 traits on five principal components for 26 bean genotypes grown under irrigation. Kellogg Biological Station, Battle Creek, MI.1987

	Principal Components				
Trait	1	2	3	4	5
CGRAV	0.945	-0.259	-0.122	0.027	0.010
CGR2	0.927	0.306	-0.063	0.155	0.012
PodWt	0.757	0.104	0.064	-0.170	0.169
LWR2	-0.707	-0.153	0.203	0.115	0.099
Flow	-0.657	0.042	-0.064	0.270	-0.042
PhyMa	-0.656	-0.351	0.193	0.131	0.073
NAR2	0.645	0.007	-0.304	-0.029	-0.008
CGR1	0.047	0.952	0.090	0.223	0.004
StWt1	0.246	0.897	-0.198	0.175	-0.033
LeWt1	-0.055	0.792	0.532	0.219	0.028
RePha	-0.428	-0.555	0.339	-0.029	0.143
LWR1	-0.179	0.040	0.926	0.046	0.017
NAR1	0.288	-0.010	-0.695	-0.044	0.480
HI	0.212	0.032	0.576	0.281	0.493
Nitro	0.063	0.197	0.234	0.925	0.034
Yield	0.079	0.326	0.151	0.904	0.023
TDM	-0.078	0.303	-0.200	0.821	-0.253
Seeds	0.013	0.070	0.051	0.204	-0.888
Sewt	-0.114	0.128	-0.016	0.197	0.638
LeWt2	-0.095	0.206	0.151	0.236	0.080
StWt2	-0.020	0.195	-0.235	0.348	-0.342
WtSeLe	-0.494	-0.057	0.210	-0.275	0.031
Pods	0.329	0.091	0.125	0.172	0.178
LER	-0.393	-0.060	0.430	0.335	0.012
SePro	-0.123	-0.488	0.172	-0.055	0.027
Variance %	21.976	16.821	10.366	12.108	7.262
Cumulative variance	21.976	38.797	49.193	61.271	68.533

Table 8, Appendix C. Loading coefficients of 25 traits on five principal components for 26 bean genotypes grown under drought stress. Kellogg Biological Station, Battle Creek, MI.1987

Trait	Principal Components				
	1	2	3	4	5
LWR2	0.946	0.027	-0.077	-0.054	-0.150
PhyMa	0.942	-0.045	-0.016	-0.028	0.044
Flow	0.900	-0.132	-0.025	-0.138	-0.037
PodWt	-0.899	0.081	0.264	0.183	0.005
RePha	0.892	-0.008	-0.012	0.018	0.073
NAR2	-0.870	-0.000	-0.074	0.095	0.196
LeWt2	0.813	0.188	-0.007	0.455	-0.164
LER	0.739	-0.088	0.210	0.088	0.107
SeWt	0.655	-0.272	-0.204	0.042	0.116
StWt2	0.630	0.224	-0.121	0.560	0.256
TDM	0.627	-0.094	0.172	0.237	0.330
Pods	-0.589	0.243	0.551	0.249	0.122
HI	-0.506	0.006	0.711	-0.025	-0.287
CGR1	-0.030	0.980	-0.078	0.060	0.026
LeWt1	0.005	0.934	0.040	0.111	-0.292
StWt1	-0.254	0.897	-0.175	0.070	0.182
Yield	0.027	-0.099	0.935	0.212	0.011
Nitro	-0.074	-0.177	0.905	0.153	0.064
Seeds	0.310	-0.221	0.570	-0.215	-0.275
CGR2	-0.019	-0.019	0.146	0.921	-0.028
CGRAV	0.004	-0.426	0.200	0.856	-0.047
SePro	-0.248	-0.107	-0.030	0.539	-0.184
LWR1	0.130	0.216	0.254	0.163	-0.797
WtSeLe	0.105	0.450	0.260	0.044	0.677
NAR1	-0.020	-0.298	-0.470	-0.134	0.440
Variance %	30.518	17.290	12.039	13.407	7.103
Cumulative variance	30.518	47.808	60.847	72.254	81.357

Table 9, Appendix C. Loading of 25 traits on five principal components for 22 bean genotypes grown under irrigation. Kellogg Biological Station, Battle Creek, MI.1987

	Principal Components				
Trait	1	2	3	4	5
CGR1	0.957	0.100	0.190	0.033	0.134
StWt1	0.915	-0.056	0.188	-0.053	-0.130
RePha	-0.805	-0.212	-0.201	0.059	0.319
LeWt1	0.789	0.116	0.163	0.120	0.547
PhyMa	-0.732	0.477	-0.001	-0.159	0.197
SePro	-0.517	-0.106	-0.020	0.006	0.198
LWR2	-0.005	0.924	0.003	-0.003	0.167
LeWt2	0.210	0.879	0.169	0.008	0.171
NAR2	0.018	-0.870	0.057	0.037	-0.283
Flow	0.180	0.828	0.258	-0.261	-0.181
PodWt	0.032	-0.784	-0.186	0.326	0.073
StWt2	0.176	0.757	0.366	-0.423	-0.141
WtSeLe	-0.127	0.660	-0.347	0.040	0.131
Nitro	0.203	0.044	0.917	0.095	0.197
Yield	0.318	0.138	0.865	0.076	0.113
TDM	0.363	0.250	0.795	-0.233	-0.144
Seeds	-0.015	0.147	0.257	-0.833	0.147
Pods	0.145	-0.275	0.284	0.798	0.017
HI	-0.079	-0.145	0.270	0.602	0.431
LWR1	-0.001	0.101	-0.010	0.143	0.930
NAR1	0.013	-0.423	-0.055	0.263	-0.764
LER	-0.085	-0.067	0.391	-0.451	0.542
SeWt	0.099	0.055	0.140	0.068	0.036
CGR2	0.330	-0.216	0.269	0.051	0.010
CGRAV	-0.480	-0.296	0.104	0.022	-0.103
Variance %	20.870	20.710	12.348	9.147	10.290
Cumulative variance	20.870	41.580	53.928	63.075	73.365

Table 10, Appendix C. Loading of 25 traits on five principal components for 22 bean genotypes grown under drought stress. Kellogg Biological Station, Battle Creek, MI.1987

	Principal Components				
Trait	1	2	3	4	5
LWR2	-0.924	-0.124	-0.046	0.240	0.022
PodWt	0.891	-0.059	0.228	-0.001	-0.262
PhyMa	-0.874	0.103	0.120	0.010	0.271
NAR2	0.848	0.063	0.147	-0.249	0.186
Flow	-0.808	0.127	-0.061	0.029	0.064
RePha	-0.746	0.069	0.205	-0.003	0.343
LeWt2	-0.741	-0.274	0.508	0.218	-0.059
SeWt	-0.737	0.270	0.079	-0.158	-0.189
Pods	0.703	-0.206	0.159	0.029	-0.529
StWt2	-0.630	-0.230	0.563	-0.330	0.117
HI	0.519	0.028	0.020	0.237	-0.562
TDM	-0.507	0.097	0.152	-0.209	-0.372
CGR1	0.020	-0.980	0.040	-0.038	0.066
StWt1	0.135	-0.945	0.055	-0.220	0.075
LeWt1	0.037	-0.924	0.107	0.306	0.025
CGR2	-0.042	-0.315	0.917	0.009	-0.190
CGRAV	-0.055	0.412	0.852	0.036	-0.230
SePro	0.327	0.149	0.619	0.304	0.176
LWR1	0.036	-0.143	0.202	0.848	-0.053
WtSeLe	0.215	-0.365	0.054	-0.753	0.010
NAR1	0.193	0.271	0.021	-0.533	0.514
Yield	0.130	0.142	0.206	0.041	-0.929
Nitro	0.280	0.244	0.161	0.008	-0.848
Seeds	-0.204	0.214	-0.113	0.147	-0.316
LER	-0.455	0.089	0.342	-0.198	0.015
Variance %	27.449	17.509	14.140	8.418	11.873
Cumulative variance	27.449	44.958	59.098	67.516	79.389

Table 11, Appendix C. Loading coefficients of 28 traits on five principal components for 26 bean genotypes grown under rainfall conditions. Durango, Mexico. 1987

	Principal Components				
Trait	1	2	3	4	5
StWt1	0.983	0.039	0.103	-0.005	-0.061
CGR1	0.971	0.049	0.148	-0.012	-0.050
LeWt1	0.956	0.055	0.176	-0.017	-0.042
LWR1	-0.889	-0.077	-0.076	-0.040	0.049
WtSeLe	0.609	-0.013	-0.147	0.246	0.084
CGR2	0.120	0.960	0.021	0.051	-0.226
StWt2	0.238	0.913	-0.054	0.067	0.030
LeWt2	0.104	0.875	0.117	0.052	0.221
CGRAV	-0.457	0.859	-0.069	0.037	-0.168
PodWt	-0.048	0.582	0.005	0.007	-0.745
Yield	-0.157	0.017	-0.976	-0.075	-0.071
Nitro	-0.189	0.034	-0.963	-0.078	-0.035
TDM	-0.040	-0.102	-0.915	0.189	0.109
HI	-0.209	0.173	-0.686	-0.460	-0.248
SeWt	-0.240	-0.176	-0.528	0.056	-0.215
PhyMa	0.043	0.109	0.226	0.912	0.234
RePha	-0.059	0.183	-0.205	0.761	-0.129
LWR2	-0.181	-0.272	0.080	0.063	0.838
LER	-0.106	0.046	0.019	0.040	0.701
LWRC	0.181	0.117	0.025	0.115	0.531
SePro	-0.136	-0.032	0.037	-0.094	0.116
NAR1	0.191	-0.278	0.110	-0.079	0.125
NAR2	0.053	0.169	-0.016	-0.147	-0.470
IKI	-0.087	-0.036	0.001	0.150	0.017
LWC	-0.117	0.217	0.370	0.223	0.477
Seeds	-0.241	0.447	-0.196	-0.465	0.032
Pods	0.331	-0.144	-0.423	0.094	0.086
Flow	0.112	-0.030	0.492	0.479	0.429
Variance %	19.135	17.057	14.366	7.777	10.330
Cumulative variance	19.135	36.192	50.558	58.235	68.565

Table 12, Appendix C. Loading coefficients of 28 traits on five principal components for 26 bean genotypes grown under drought stress conditions. Durango, Mexico. 1987

	Principal Components				
Trait	1	2	3	4	5
CGR1	0.978	0.040	0.134	0.019	0.030
StWt1	0.976	0.023	0.151	0.034	0.082
LeWt1	0.971	0.050	0.122	0.009	-0.003
LWR1	-0.840	0.066	-0.050	0.006	-0.241
CGRAV	-0.676	0.046	0.672	-0.035	0.051
TDM	0.008	-0.945	-0.134	-0.100	0.018
Yield	-0.007	-.0934	-0.175	0.247	-0.019
Nitro	0.056	-0.902	-0.185	0.259	0.030
SePro	0.238	0.666	-0.005	-0.035	0.211
HI	-0.021	-0.531	-0.082	0.717	-0.094
Pods	0.087	-0.502	0.133	0.080	0.522
LeWt2	0.103	0.051	0.963	-0.031	0.085
CGR2	0.201	0.100	0.913	-0.012	0.085
StWt2	0.140	0.253	0.897	0.093	-0.021
PhyMa	0.001	0.030	-0.010	-0.980	-0.006
Flow	0.097	0.062	0.138	-0.870	0.080
RePha	-0.091	-0.008	-0.150	-0.849	-0.088
IKI	-0.201	0.317	-0.091	-0.579	0.114
LWRC	-0.102	-0.025	0.036	0.114	-0.890
LWC	-0.148	-0.005	-0.214	0.073	-0.775
LER	0.008	-0.352	-0.044	-0.357	-0.610
LWR2	-0.205	-0.068	0.001	0.035	-0.020
PodWt	0.228	-0.029	0.479	-0.075	0.124
WtSeLe	-0.040	0.147	0.251	0.032	-0.398
NAR2	0.037	0.152	0.005	-0.017	0.051
SeWt	-0.203	-0.480	-0.106	0.006	-0.182
Seeds	0.161	-0.109	-0.139	0.289	-0.198
Variance %	18.075	13.964	14.991	12.279	8.292
Cumulative variance	18.075	32.039	47.037	59.316	67.608