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IDENTIFICATION AND ESTIMATION OF HERITABILITIES
OF DROUGHT RELATED RESISTANCE TRAITS
IN DRY BEANS (Phaseolus vulgaris L.)

presented by

Porfirio Ramirez Vallejo

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Plant Breeding & Genetics-
Crop & Soil Science.

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IDENTIFICATION AND ESTIMATION OF HERITABILITIES OF DROUGHT RELATED RESISTANCE TRAITS IN DRY BEAN (*Phaseolus vulgaris* L.)

VOLUME I

By

Porfirio Ramirez Vallejo

A DISSERTATION

Submitted to
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ABSTRACT

IDENTIFICATION AND ESTIMATION OF HERITABILITIES OF DROUGHT RELATED RESISTANCE TRAITS IN DRY BEAN (*Phaseolus vulgaris* L.)

By

Porfirio Ramirez Vallejo

Direct selection for specific characteristics that confer or are related to drought has not been utilized because such traits and their genetic control have not been adequately identified. The identification of such traits to facilitate breeding for drought resistance in dry bean was the main objective of this research. Morphological, phenological and physiological traits were evaluated for their ease of measurement, genetic characteristics and relationships with yield under drought and drought resistance. Replicated experiments were conducted in and near a rain-out shelter in the summers of 1988 and 1990. In the 1988 experiment five advanced lines were tested while in 1990 four advanced and sixteen F_{3-5} generation recombinant lines were evaluated. Two soil moisture regimes representing control (normal) and drought (stress) were established each year. The water stress was applied before flowering and the drought intensities observed were 0.78 in 1988 and 0.63 in 1990. The generalized response to drought was the reduction in the expression of traits with positive effect on yield and the increase in the expression of traits with negative effects, which was intensified at severe levels of drought intensity. It was demonstrated that it is biologically possible to obtain drought resistance genotypes with high yield potential. The main strategy of drought resistance detected was dehydration avoidance, through mechanisms of either reduction of water loss or maintenance of transpiration. It was shown that each mechanism is related to specific levels of expression of morphological, phenological and physiological traits; that each mechanism confers a specific level of drought resistance; and that both mechanisms are mutually exclusive in a single genotype. Estimates of heritability, genetic coefficients of variation and response to selection were determined. The complexity of yield under drought and drought resistance and the lack of a single trait that by itself could improve dry bean productivity under drought was demonstrated. Total biomass, harvest index, relative sink strength, days of seed filling, stomatal conductance, stem diameter, leaf orientation, specific leaf area and moisture retention capacity were identified as the most useful characteristics to consider in breeding dry bean for drought resistance and yield under drought.

TO MY WIFE, MARIA ESTHER

TO MY SONS IVAN, ERICK AND EDGAR

for their love, understanding and
encouragement

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INTRODUCTION

The common bean (*Phaseolus vulgaris* L) is the most widely grown species of *Phaseolus* from the American tropics (Laing *et al.*, 1983). Production of *Phaseolus vulgaris* accounts for approximately 95% of the total world *Phaseolus* production of 15 million metric tons. (Laing *et al.*, 1984). Common beans are grown extensively in five major continental areas: Eastern Africa, North and Central America, South America, Eastern Asia, and Western and South-Eastern Europe (Adams *et al.*, 1985). However, 91% of the total world production is located in developing countries, while only 9% is produced in developed countries (Kadam and Salunkhe, 1989). The edible seed of *P. vulgaris* is an important source of protein and calories in human diets in the tropical and subtropical developing countries, particularly in the Americas and in Eastern and Southern Africa (Laing *et al.*, 1984).

Among the abiotic stresses affecting dry bean productivity, insufficient water is the most important factor causing seasonal fluctuations in yield and is recognized as one of the main causes of low productivity around the world. Throughout the bean growing regions of the world more than 60% of the cultivated area is affected by drought, causing reduction and frequent crop failure (Anonymous, 1988). This percent is even larger for Latin America since it is estimated that moderate to severe water deficits after flowering affect the productivity of approximately 70% of the area under cultivation in this region (Laing *et al.*, 1983). Although dry beans are grown in regions subjected to water stress, the species is not particularly tolerant to long-lasting water stress (drought) (Adams *et al.*, 1985).

Since bean plants are sensitive to soil water conditions, both yield and quality can suffer greatly from even brief periods of water shortage (Wallace, 1980; Halterlein, 1983), particularly if the period of water stress occurs during the reproductive stage. Since virtually all plants are exposed to stress at some time during their life cycle (Parsons, 1979), availability and distribution of water restricts the realization of the genetically determined potential for growth, development, reproduction and productivity of the crop. Yield is reduced because water stress disturbs physiological processes and alters plant morphology. The level of yield reduction depends on the intensity, duration and timing of drought, and genotypic differences may help reduce the effects of drought on yield.

The improvement of productivity under water stress conditions may be achieved through the development of cultural practices, including supplemental irrigation, and/or drought resistance genotypes. The development of cultural practices directed toward the improvement of water retention and conservation in the soil are usually expensive and temporal. Instead, the development of genotypes that resist or are less susceptible to the effects of water stress seem to be a more practical, long-term and economical approach to overcome the negative effects of drought on the potential productivity of the crop. Under this strategy breeding for drought resistance would be directed to the attainment of drought resistance genotypes with good yield under nonstressed conditions and the lowest reduction in yield under water stress. However it should be recognized that yield under drought may help reduce the effect of the water stress but is not a guarantee of an acceptable yield under nonstressed conditions.

Despite the overwhelming importance of drought as a major constraint of crop productivity, there has been little progress in breeding for drought resistant cultivars. Selecting for drought resistance is difficult, as the response is complex and interactions with other biotic and abiotic factors occur. Moreover, plants have evolved a wide range of different response "strategies" to survive and reproduce in the face of water stress that occurs at different periods throughout the growth cycle of the crop. In addition, there are problems in obtaining a consistent response to environmental conditions which either simulate or represent actual drought conditions in the field (McWilliam, 1989; Ludlow and Muchow, 1990).

The application of empirical breeding methods, based mostly on yield under drought *per se* as the main selection criterion, has permitted some limited progress in the development of improved cultivars. However, the efficiency of selection under environmental stress based solely on yield is low. Yield under stress generally has lower genetic variance components resulting in lower heritability estimates than under nonstressed yield. (Johnson and Frey, 1967; Rosielle and Hamblin, 1981; Rambaugh *et al.*, 1984; Atlin and Frey, 1989). Furthermore, yield under drought is a poor drought resistance estimate because of the failure to estimate accurately yield potential under non-stress.

Breeding to improve drought resistance and increase yield under drought may be facilitated if morphological, phenological and physiological criteria for the identification of high yielding genotypes are applied. For this purpose a suitable trait or plant response has to be highly causally related with yield under drought, easy and rapid to assess with higher heritability than yield under drought. From a breeding perspective the value of a trait is determined not only by its relationships either with yield or with yield related physiological processes or with any other agronomic attribute, but also depends on the genetic properties and practicability of measuring the trait. Hence, traits showing strong relationships with yield or yield-related physiological processes will have a minimum value in breeding dry bean for drought resistance if they exhibit low heritability and are highly affected by environmental changes.

The use of secondary traits in breeding dry beans for drought resistance may be a potentially useful breeding method since yield under drought is a poor selection criterion, highly affected by drought stress, and extremely variable under environmental fluctuations. However, direct selection for specific characteristics that confer or are related to yield under drought have not been used because such traits and their genetic control have not been adequately identified. Information obtained about the relationships between yield and morphological and physiological traits in dry bean has suggested that several of these characteristics could be used as selection criteria. However, estimates of genetic variability and heritability of such traits are lacking because most of the research has been oriented either toward traditional empirical selection or the physiological approach which targets a single trait not always related to actual yield.

The present research determined the effects of drought on morphological, phenological and physiological characteristics; the biological and practical implications of drought resistance estimates; the relationships between yield and its components with morphological, phenological and physiological characteristics; the relationships between morphological, phenological and physiological characteristics; the dynamics of the relationships between components of variation at different levels of water stress; and the effects of drought on heritability and genetic variability.

The objectives and hypothesis evaluated in this research were as follows:

The main objective of the study, set forth in chapter 2, was the identification of morphological, phenological and physiological traits to assist breeding for drought resistance in dry bean. The main hypothesis tested in this study was that drought resistance, defined as the lowest reduction in yield due to water stress, and yield under drought in dry bean (*Phaseolus vulgaris* L.) are associated with morphological, phenological and physiological traits, that these traits exhibit sufficient genetic variability, and are practical enough to be integrated into a breeding program for drought resistance as selection criteria.

In chapter 3, the main objective of the research was directed at the estimation of heritabilities of morphological, phenological and physiological traits of dry bean genotypes grown under two contrasting water stress regimes: drought and non-stress conditions. The main hypothesis tested in this study was that morphological, phenological and physiological traits related with yield under drought and/or yield drought resistance in dry bean are more highly heritable than yield and less affected by water stress.

CHAPTER 1

PHYSIOLOGY OF DROUGHT AND DROUGHT RESISTANCE IMPROVEMENT IN DRY BEAN (*Phaseolus vulgaris* L.): A CRITICAL REVIEW.

Economic and Social Importance of Common Bean

The common bean *Phaseolus vulgaris* L. is the most widely grown of the four cultivated species of *Phaseolus* from the American tropics (Laing *et al.,* 1983). Production of *Phaseolus vulgaris* accounts for approximately 95% of the total world *Phaseolus* production (Laing *et al.,* 1984). Common beans are grown extensively in five major continental areas: Eastern Africa, North and Central America, South America, Eastern Asia, and Western and South-Eastern Europe (Adams *et al.,* 1985). Dry beans annual world production is on the order of 15 million metric tons (mmt) or 30 percent of the total world pulse production. The major dry bean producers are Brazil with 2.9 mmt, India with 2.7 mmt, China with 1.8 mmt, Mexico with 1.1 mmt, the United States with 1.1 mmt and Thailand with 0.25 mmt (Anonymous, 1990).

The edible seed of *P. vulgaris* is an important source of protein (dry beans contains 20 to 28% protein) and calories in human diets in the tropical and subtropical developing countries, particularly in the Americas and in eastern and southern Africa (Laing *et al.,* 1984). Of the mean annual world production of 14.2 mmt in 1982, 38% was produced in America, 8.4% in Africa, 48% in Asia and 5% in Europe. 91% of the total annual production was produced in developing nations with only 9% in developed countries (Kadam and Salunkhe, 1989). Dry beans can be cooked in many different ways, and may be used for canning (processing). The beans are also used as a vegetable in Africa, and the immature seeds can be used as soup beans or as a source of shelled beans (Adams *et al.,* 1985).

The common bean is not a high-yielding species. The national average yield is less than 0.5 $t.ha^{-1}$ in most developing countries and below 1.7 $t.ha^{-1}$ in developed nations (Laing *et al.,* 1983; Adams *et al.,* 1985; Summerfield and Lawn, 1987; Kadam and Salunkhe, 1989). Drought, temperature extremes, salinity, poor soil aeration and toxicity, or deficiency of certain elements are abiotic stresses affecting beans productivity (Adams *et al.,* 1985).

Insufficient water is the most important factor causing seasonal fluctuations in yield and is one of the main causes of low productivity around the world (Anonymous, 1988). Moderate to severe water deficits after flowering affect the productivity of 70% of the area under cultivation in Latin America (Laing *et al.,* 1983). Although dry beans are grown in these regions under restricted water supply the species is not particularly tolerant to long-lasting water stress (drought) (Laing *et al.,* 1983; Laing *et al.,* 1984; Adams *et al.,* 1985). Bean plants are very sensitive to soil water conditions and quality and yield suffer greatly from even brief periods of water shortage (Wallace, 1980; Halterlein, 1983). Soils at field capacity are optimum for bean crops.

Drought-Water Stress Relationship

Crop plants rarely attain their full genetic potential for yield because of the limitations imposed by the environment, especially unfavorable temperatures and lack of water (Kramer, 1980). Virtually all land plants are exposed to water stress at some times during their life cycles (Parsons, 1979).

A period without significant rainfall, meteorological drought (May and Milthorpe, 1962), leading to an insufficient supply of moisture either from precipitation and/or soil storage for optimum plant growth (Mather, 1968), produces in the plant an internal water deficit or water stress (Kramer 1980) because the evaporative demand of the atmosphere upon leaves (potential transpiration) exceeds the capacity of the roots to extract water from the soil (actual transpiration) (Edmeades *et al.,* 1989). Although plant water stress always accompanies drought, it may occur in absence of drought, either because of excessive transpiration or because absorption is inhibited (Kramer, 1983). Water deficits occur when the water potential of the cell, tissue or organ drops below zero potential (Slatyer, 1969). Water stress may occur due to atmospheric or soil conditions. It is reflected in a gradient of potentials developed between the soil or the soil-root interface and the transpirating organ. Along this gradient a differential drought stress in different organs occurs (Kramer, 1983; Blum, 1988).

The effects of water deficits on crops are highly dependent on timing and duration and both contribute to the severity of stress due to the dynamic nature of plant water balance (Hsiao, 1982). Water stress causes disturbance of physiological processes and changes in morphology, restricting the plant from realizing its genetically determined potential for growth, development, and reproduction (Jones and Qualset, 1984). The degree of plant water stress or deficit depends on the extent to which water potential and cell turgor are reduced below their optimum values (Kramer, 1980). Several patterns of plant moisture adequacy and stress can be identified (Edmeades *et al.,* 1989). Drought is a meteorological and environmental event that can be classified as permanent, seasonal or unpredictable based on the duration of the water stress (Kramer, 1980).

Given the definition by Sinha (1987) and the concepts discussed above, drought in plant breeding could be defined as "the shortage in water availability and distribution, occurring during the life of the crop, that restrict the realization of its genetically determined potential for growth, development, reproduction and productivity."

Drought Resistance

Drought resistance in ecological terms is the ability of a plant to stay alive during periods of low water supply (Levitt et al., 1960, as cited by Turner, 1979). Under this definition, drought resistant plants evolved for survival and the morphological characteristics, growth behavior, and biomass production were selected for low production in return for a high level of survival. Their selective fitness in the evolutionary sense must have resulted from the ability to produce at least one seed per growth cycle, or retention of the ability of their meristems to regenerate in spite of extreme water-stress conditions (Blum, 1988).

A plant species selected for crop production must have the ability to produce an adequate stable yield besides the ability to survive water deficits. Under this condition the ability of a crop species or variety to grow and yield in areas subjected to periodic water deficit is called drought resistance (May and Milthorpe, 1962). Drought resistance is not a simple response because it is conditioned by a number of component responses which interact and differ for different crops and in response to different types, intensity and duration of water deficits (McWilliam, 1989).

Drought resistance is conferred by a number of morphological and physiological characteristics of the plant (May and Milthorpe, 1962; Begg and Turner, 1976). Each trait is related to a specific mechanism of resistance. These mechanisms and their related characteristics have been classified by different authors (May and Milthorpe, 1962; Levitt, 1980; Kramer, 1983; Blum, 1985, 1988; Ludlow and Muchow, 1990). However, a concensus about the most useful breakdown of categories of drought resistance has not yet been reached (Levitt, 1980; Kramer, 1980; Turner and Burch, 1983; Turner, 1986). In most of the cases the classifications are either modifications or expansions of those elaborated originally by May and Milthorpe (1962) and Levitt (1980).

The mechanism of drought resistance in crop plants has been divided into three categories: drought escape, dehydration avoidance and dehydration tolerance (May and Milthorpe, 1962; Kramer, 1980, 1983; Levitt, 1980; Turner, 1986; Blum 1988; Ludlow and Muchow, 1990). Drought escape or evasion has been incorrectly equated to drought avoidance (May and Milthorpe, 1962; Levitt, 1980; Blum, 1982).

It is generally recognized that resistance to water stress can be achieved by escape or tolerance. (May and Milthorpe, 1962; Levitt, 1980; Blum, 1982, 1985, 1988; Ludlow and Muchow, 1990). Drought escape or evasion usually involves early maturity to avoid the onset of severe water deficits, whereas tolerance involves dehydration avoidance or postponement and dehydration tolerance (McWilliam, 1989).

Drought escape is the ability of a plant to complete its life cycle before serious soil and plant water deficits develop (May and Milthorpe, 1962; Turner, 1986). Rapid phenological development, developmental plasticity and photoperiod sensitivity are specific factors related to this mechanism (Turner, 1986).

Dehydration avoidance or postponement is the maintenance of a higher water or turgor potential under conditions of water stress. Dehydration postponement can be obtained through either maintenance of turgor and/or maintenance of volume. Maintenance of water uptake, reduction of water loss and osmotic adjustment are specific ways by which plants maintain both total or turgor potential. Increases in elasticity is directly related to the maintenance of volume (Turner, 1986; Blum, 1988).

Dehydration tolerance arises at the molecular level and depends on membrane structure and enzyme activity. It depends on the ability of the membranes to withstand degradation, and the ability of both the membranes and cytoplasm to withstand denaturation of proteins (Turner, 1986).

There are several individual morphological, physiological and biochemical traits related to each mechanism, however, resistance to drought depends on a complex interaction of attributes that confer both survival and a range of productivity potential at various stages of the life cycle (Sullivan and Ross, 1979; Simpson, 1981; Ibarra, 1985; Elizondo, 1987; Acosta-Gallegos, 1988). The mechanisms of adaptation are not mutually exclusive because one kind of plant can possess more that one category of adaptation (May and Milthorpe, 1962; Kramer, 1980). It seems that no single trait confers stress resistance but there are responses due to a combination of traits (Turner, 1986; Morgan, 1984; Acevedo, 1987; Singh, 1989). Thus, in legumes, major differences in adaptation to photo-thermal-regime, to edaphic conditions and to the amount and seasonal distribution of water have been possible through the combination of physiological adaptations, anatomical variations, morphological patterns, symbiotic associations in addition to the structure and genetics of the population (Adams and Pipoly, 1980).

Effects of Drought on Growth and Development

While the ultimate effect of drought is limitation of growth and yield, specific physiological effects of water stress vary depending on the history of the crop, and timing and intensity of stress (White and Izquierdo, 1989). Inadequate availability of water in quantity and distribution leading to water deficits has a profound effect on various plant processes. These processes have different time scales in their responses to water stress or drought. Change in leaf water potential, turgor pressure and stomatal resistance are influenced within seconds or minutes while cell growth, accumulation of proline and betaine, degradation of proteins and polysacharides are affected in hours. Leaf expansion, shoot growth and root growth might take days while reproductive biology and grain yield are influenced in days or months. Under field conditions a crop experiences the effects of water deficits gradually, leaf water potential drops at a rate of -0.04 to -0.01 MPa per day (Sinha, 1986, 1987; White and Izquierdo 1989).

Sensitivity at Different Stages of Development

Growth and development in most crops proceed completely unimpaired and crop yield is maximal only when high water status is maintained throughout the life of the crop (Slatyer, 1969). Most determinate crops are specially sensitive to water deficits from the time of floral initiation during flowering, and, to a lesser extent, during fruit and seed development. The situation is less clear in indeterminate crops where the stages overlap (Begg and Turner, 1976).

In legumes, anthesis and seed set are the most critical stage in reproductive development, which is characterized by a large number of aborted flowers. In *Phaseolus* sp. as many as two thirds of the flowers produced may abscise. This stage of development is unfavorably affected by water stress, low and high temperatures, relative humidity and photoperiod (Summerfield 1980a).

In dry bean the most sensitive phase of development to water stress is from flowering to early pod set (Dubetz and Mahalle, 1969; Laing *et al.,* 1983; Laing *et al.*, 1984; Halterlein, 1983; Sheriff and Muchow, 1984) and prolonged stress before flowering restricts canopy development, which in turn limits yield (Laing *et al.,* 1984). The effect of water stress on growth and yield is more severe at the reproductive stage than at the vegetative stage (Robins and Domingo, 1956; Dubetz and Mahalle, 1969; Stansell and Smittle, 1980; Laing *et al.*, 1984; Favaro and Palatti, 1988; Acosta-Gallegos and Kohashi-Shibata, 1989). The direct effects of water stress and stage of growth interact to influence the time and amount of floral initiation and pod development (Dubetz and Mahalle, 1969). The relative sensitivity of different stages of development to stress vary with the degree of stress (Begg and Turner, 1976).

Effects of Drought on Morphology

The most common effect of water deficit is the reduction in plant size and yield (Kramer, 1983). The reduction in leaf area is the most obvious morphological change. Leaf area index, the most usual 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 (Sheriff and Muchow, 1984). Leaves are smaller because leaf expansion due to cell enlargement is very sensitive to water deficits (Slatyer, 1969; Begg, 1980; Kramer, 1983). While leaf senescence is not as sensitive as leaf area development (Turner, 1982, 1986; Muchow, 1985b), the differences in sensitivity have been observed in grain legumes grown under deficit water regimes (Muchow, 1985b) and corn under water stress (Muchow and Carberry, 1989).

Even short periods of diurnal water deficits inhibit stem elongation or leaf enlargement (Slatyer, 1969). Since leaf growth is more sensitive to water stress than stomatal conductance and CO_2 assimilation, crop growth can be reduced by water deficits too small to cause a reduction in stomatal aperture and photosynthesis (Begg, 1980; Kramer, 1983). Enlargement of leaves in maize, sunflower and soybean is lowered by any reduction in leaf water potential to values approaching -.2 MPa (Turner, 1982).

A reduction in leaf area will reduce crop growth, particularly during establishment when there is incomplete light interception (Begg, 1980) and crop evaporation, since below a leaf area index of about 3 crop transpiration is reduced linearly with leaf area, provided that the soil surface is dry (Ritchie, 1974). Decrease in leaf expansion and increase in leaf senescence are irreversible. The combination of both responses result in incomplete radiation interception and yield reduction (Sheriff and Muchow, 1984).

There is a very close dependence of growth on water status since growth is very sensitive to stress. In sunflower, maize and soybean, growth is completely halted by a drop of leaf water potential to about -0.4, -0.7, and -1.2 MPa, respectively (Turner, 1982). In dry beans, soils at field capacity are optimum for plant growth; soil water potentials of -0.03 MPa reduces plant growth and plant growth ceases about -0.5 MPa (Wallace, 1980).

Yield under non-stressed conditions is positively correlated to maximum leaf area index, number of nodes and leaf area duration in dry beans (Laing *et al.,* 1983; Laing *et al.,* 1984), thus any reduction in leaf area by water stress affect yield. This was confirmed by Acosta-Gallegos and Kohashi-Shibata (1989) who reported a high positive correlation between leaf area index and yield under stress in indeterminate dry bean cultivars. The reduction in leaf area enhanced by an increase in leaf senescence is another common effect of water deficit during grain filling.

The relative significance of both reductions in leaf initiation and expansion and increases in leaf senescence and shedding depends on the timing and severity of plant water deficits (Sheriff and Muchow, 1984). Field studies in grain legumes have shown that crops grown on stored moisture produced fewer, smaller leaves which did not senescence until near maturity than crops well watered for the first half of vegetative growth. The latter showed a reduction in leaf production and expansion and marked leaf senescence as soon as water was withheld (Muchow, 1985b). The relative significance of changes in leaf expansion and leaf senescence with water deficits varies with species and cultivars (Lawn, 1982c).

After seedling establishment, the bean plant grown under non-stress condition generally follows a near exponential growth phase until the onset of rapid pod growth, then growth is slowed. At this point some cultivars reach zero crop growth and then decline while others obtain the maximum weight near maturity (White and Izquierdo, 1989).

In pigeon bean, duck bean and other legumes the plant produces only 1/3 of its final dry matter about the time of flowering, and almost two-thirds or more of its dry matter is acquired when early pod development starts (Summerfield, 1980b; Sinha, 1987). Under water stress significant reduction in leaf area could lead to decreased dry matter production (D'Souza and Coulson, 1988). The changes in total leaf area or LAI are due to changes in both the number of leaves and leaf size. Although, total leaf area could be more sensitive to water stress than leaf size, as in cowpea (Turk and Hall, 1980), Bonnano and Mack (1983) have found that the greatest contributor to the reduction of total leaf area under water stress in snap beans was individual leaf area (leaf size).

Changes in either leaf size (leaf expansion) and/or leaf number have been reported for snap beans (Bonnano and Mack, 1983) and dry beans (Bascur *et al.,* 1985; Ibarra, 1985; Markhart, 1985; Lopes *et al.,* 1987; Mkandawire, 1987; Acosta-Gallegos, 1988; D'Souza and Coulson, 1988; Acosta-Gallegos and Koshashi-Shibata, 1989). Similar results have been found for sorghum and cotton (Rosenthal *et al.,* 1987), cowpea (Turk and Hall, 1980), soybean, green gram, black gram, lablab bean and pigeon pea (Muchow, 1985a), tepary bean (Markhart, 1985) and corn (Muchow and Carberry, 1989). In these studies concomitant reductions in total dry matter were caused by reductions in both leaf and stem weight.

Water stress hastens the rate of senescence (Begg and Turner, 1976). Increased leaf senescence due to water stress has been observed in snap beans

(Bonnano and Mack, 1983), dry beans (Samper, 1984; Ibarra, 1985; Sponchiado, 1985 as quoted by White and Izquierdo, 1989; Acosta-Gallegos and Kohashi-Shibata, 1989;), cowpea (Turk and Hall, 1980; Ibarra, 1985; Sinha, 1987), tepary bean (Samper, 1984; Ibarra, 1985), mungbean (Sinha, 1987), and other crops such as sorghum (Rosenthal *et al.*, 1987) and corn (Muchow and Carberry, 1989). Increased senescence in dry beans affects yield by reducing leaf area index (Acosta-Gallegos and Kohashi-Shibata, 1989) and leaf area duration (LAD). Leaf area duration of individual leaves is not seriously altered by water deficits that develop gradually, but rapid development of water deficits may accelerate senescence of lower leaves. However, water deficits that develop after anthesis appear to elicit a more dramatic senescence, as that found in snap beans (Bonnano and Mack, 1983), dry beans (Sponchiado, 1985 as quoted by White and Izquierdo, 1989), cowpea (Turk and Hall, 1980), cotton and sorghum (Rosenthal *et al.*, 1989), and corn (Muchow and Carberry, 1989). The demand of a strong reproductive sink for photosynthates and reduced nitrogen may exceed that available through current metabolism, specially since water deficits may limit nutrient uptake and photosynthesis. This is particularly important in legumes because the nodule activity involved in nitrogen fixation and supply of amino acids generally becomes drastically impaired after flowering, and the adjoining leaves and distant tissues are left as the major contributors of reduced nitrogen. Thus, a gradual loss of RuBisCo occurs during senescence, reducing the RuBisCo activity, net photosynthesis rate and chlorophyll content. Leaf senescence is the result of drain of leaf nitrogen and perhaps other nutrients (Grover *et al.,* 1985). Mungbean and cowpea plants with developing pods have shown faster senescence under water stress than when the pods were excised. So, the plant uses its resources for seed development when its survival its threatened due to drought (Sinha, 1987).

A major disadvantage of a decrease in leaf expansion and an increase in leaf senescence is that they are irreversible. Their combined effects result in the incomplete interception of radiation and in yield reduction. This is particularly important in determinate crops because there is no opportunity for compensation through an increase in leaf number or leaf size after floral initiation and yield is reduced even if the water deficit is removed. However, indeterminate crops may compensate for leaf area loss by additional vegetative growth, but this occurs less when water deficits are removed after flowering, because the seed and other structures in the plant compete for assimilates (Sheriff and Muchow, 1984). D'Souza and Coulson (1988) argue that a decline in leaf area would allow increased light penetration into the crop, which is available for stem and pod photosynthesis because both are green at this time. The response may play a compensation role.

Since leaf senescence may affect productivity in sorghum, Duncan *et al.* (1981) proposed the use of non-senescent genotypes to increase LAD, although the relation of this character with yield was not consistent. Most crops undergo nearly complete leaf senescence before maturity, but some non-senescent genotypes occur in dry beans. However, these genotypes have poor pod or seed set, thus the lack of senescence in this species probably reflects a weak sink demand. In temperate regions, such a pattern of delayed senescence may involve problems of photoperiod-temperature adaptation (White and Izquierdo, 1989).

Studies in corn have suggested that in view of the small amount of reserves made available to the grain and the small amount of transpiration that is prevented by accelerated senescence of the leaf tissue, it appears that this trait is undesirable for agriculture. Genetic improvement of crop performance under dry conditions could be based at least in part, on genotypes that retain leaf tissue during drought by reducing premature leaf shedding, but undergo the usual senescence at maturity (Boyer, 1983).

Effect of Drought on Physiological Processes

The responsiveness of stomata to water deficits has been known for many years. Since guard cells occupy a key position in the pathway for gaseous exchange between the plant and atmosphere, their importance as regulators of water loss and carbon dioxide uptake has long been recognized (Begg and Turner, 1976).

A reduction in soil water potential results in a reduction in leaf water potential and a concomitant increase in diffusive stomatal resistance for any given set of conditions with respect to light, temperature, nutrition, and other environmental factors (Kanemasu and Tanner, 1969). Diffusive resistance measures the "difficulty" with which molecules diffuse along a path and is the reciprocal of diffusive conductance (cm s^{-1}). It is often preferable to use diffusive conductance rather than diffusive resistance because diffusive conductance is directly proportional to transpiration rate (Sheriff and Muchow, 1984).

Begg and Turner (1976) have indicated that stomata do not close until a threshold value of leaf water potential or leaf turgor pressure is reached and that stomata close over a narrow range of leaf water potential or relative water content. Hsiao (1973) suggested that there is a threshold level of water potential or relative water content above which leaf resistance, and therefore stomatal opening, remain constant. Thresholds of -0.5 to -0.7 MPa (Walton *et al.* 1977) and -0.8 to -1.1 MPa (Begg and Turner, 1976) have been reported for common beans.

Differential responses in stomatal resistance between adaxial (upper) and abaxial (lower) surfaces of the leaflet of common beans have been found. Kanemasu and Tanner (1969) showed that abaxial stomata is not significantly affected as leaf water potential changed from 0 to -1.1 MPa, but as leaf water potential changed from -1.1 to -1.2 MPa resistance increased rapidly. The resistance of the adaxial stomatal did not increase from 0 to -0.8 MPa, but is increased sharply from -0.8 to -1.2. At leaf water potentials between -1.0 to -1.2 MPa, the average stomatal resistance for both surfaces of the leaf acts as an on-off switch to prevent further decline in leaf water potential. Hsiao (1973) has indicated threshold values of -0.7 to -0.9 MPa for the adaxial stomata and -1.0 and -1.2 MPa for the abaxial stomata. Solarova *et al.* (1977) found that the response to progressive increases in water stress was parallel for both surfaces and that the conductance of the abaxial epidermis was 50% higher than the conductance of the adaxial epidermis. Abaxial stomata were 25% smaller than adaxial stomata. Comparisons between common bean and tepary bean under drought condition have shown that stomatal resistance in both tepary bean and common beans increased 5 days after the beginning of the drying cycle with resistance of the upper surfaces increasing faster and to a greater extent than the lower surface. The stomata of the common bean did not close appreciably until water potentials between -1.3 to -1.8 MPa were reached. In contrast, in tepary bean the stomata closed completely between -0.8 to -1.0 MPa. Stomatal closure allows maintenance of higher leaf water potential in tepary bean (Markhart, 1985).

The number of stomata differ between both leaf surfaces. The abaxial surface has been reported as having 7 times more stomata than the adaxial surface, with 28,100 and 4,000 stomata, respectively (Meyer *et al.,* 1973; Solarova *et al.,* 1977). Drought stress in soybean cultivars decreased the number of stomata in both the adaxial and abaxial surfaces (Ciha and Braun, 1975). The decrease could be explained by a restricted leaf expansion. The stress/cultivar interaction was significant for stomatal leaflet surface and total number of stomata per leaflet in this study. The genotypic differences in stomatal frequency could be related to varietal differences in gas exchange, recognizing that stomatal sensitivity should be considered.

There is evidence in different legumes that adaxial stomata close more rapidly under stress, thus water loss from stressed plants probably occurs via the abaxial leaf surface (Muchow as quoted by Lawn, 1982a).

Sometimes no threshold response is observed, with stomatal conductance decreasing linearly or almost linearly with the leaf water potential or leaf turgor pressure (Turner, 1986). There is not a unique relationship between stomatal conductance and leaf water potential or leaf turgor pressure, since a variety of factors affect the water potential at which stomata close including age, growing conditions, leaf position and orientation, and the stress history of the plant (Begg and Turner, 1976).

A threshold value of leaf water potential for stomatal closure was not found in snap beans by Bonnano and Mack (1983). As water potential became more negative, a greater range of diffusive resistance values occurred. The authors suggested that water potential at which stomata close is environmentally dependent and can be increased by moisture stress hardening (osmotic adjustment); it is possible that stomatal adaptation to moisture stress occurred in the dry treatment. As leaf diffusive resistance values are more responsive to plant water stress conditions the trait can be very useful in the day-to-day monitoring of relative plant stresses.

Lawn (1982a) found that a significant proportion (34-62%) of the variation in conductance accounts for the change in leaf water potential in three species of *Vigna* and soybean, and differences in the response of conductance to leaf water potential and in stomatal sensitivity were detected among cultivars under drought. Acosta-Gallegos (1988) under controlled conditions and Elizondo (1987) and Mkandawire (1984) under field conditions did not detect differences in stomatal conductance among cultivars of common bean. However, differences in stomatal conductance among genotypes in *Phaseolus* have been reported (Laing *et al.*, 1983; Laing *et al.*, 1984; Bascur *et al.*, 1985; Ehleringer, 1990).

Plants growing under field conditions are subjected to a high radiation load for most of the day. Leaf temperature, interval temperature gradients, and the leaf-air temperature are increased. The latter has a large effect on transpiration and in the development of water deficits, while high temperatures are often deleterious to metabolic processes, and sometimes are lethal. Thus, the amount of radiation absorbed by a leaf can be an important determinant of its metabolic activity and even its survival. The energy received by the leaf is removed as sensible heat by convective cooling and by latent heat transfer through transpiration. The ability of a plant to maintain low leaf temperature by transpirational cooling depends very much on water availability and on the long term "strategy" adopted by the plant. If the plant normally maintains high stomatal resistance to conserve soil water, then transpirational cooling must be limited. When water loss is not limited by the energy available for dissipation of latent heat, leaf movement can be an effective alternative mechanism of limiting leaf temperature maxima (Sheriff and Muchow, 1984). Pubescence and leaf movement can be very powerful mechanisms to reduce leaf temperature (Ehleringer and Forseth, 1980; Sheriff and Muchow, 1984).

Differences between cultivars in leaf temperature and the association of stomatal conductance with leaf temperature have been reported in common beans. Laing *et al.* (1983 and 1984), working with two contrasting genotypes, found that the resistant genotype exhibited a higher water potential than the susceptible cultivar. Stomatal resistance was extremely high in the susceptible cultivar in the warmer period of the day. The differential of temperature between the irrigated and stressed treatments rose by 6.5 °C for the susceptible cultivar and by 2.5 °C for the tolerant cultivar. A high correlation was found between the canopy temperature differential and stomatal resistance. The differential of temperature was highly correlated with the reduction of yield. Likewise, Bascur *et al.* (1985) reported a strong correlation between lower stomatal resistance and yield performance under drought. Negative correlation between canopy temperature and yield has been reported in soybean (Harris *et al.*, 1984) and wheat (Blum *et al.*, 1989). Genotypic differences for canopy temperatures have been found in soybean (Harris *et al.*, 1984), *Brassica* sp. (Singh *et al.*, 1985) and wheat (Blum, 1989). Mkandawire (1984) reported differences in leaf temperature in Malawian dry bean landraces and no evident relationship between stomatal conductance and leaf temperature.

An inverse relationship between trend in leaf temperature and conductance, for the evaporative cooling associated with water loss in transpiration, was observed by Lawn (1982a) under drought in four legumes. Leaf temperatures were highest when conductances were lowest in stressed treatments and in cowpea. Conversely, leaf temperatures were lowest and conductances were highest in irrigated plots and in soybean. Within cultivars a large amount of the variation in temperature of individual leaves was accounted for by variations in air temperatures and conductances, regardless of sampling time or date. Leaf temperature was strongly associated with air temperature and the inverse of conductance. The differences found between three species of *Vigna* and soybean suggest that leaf temperature in soybean rises more rapidly as conductance falls (Stevenson and Shaw, 1971).

Paraheliotropism may play an important role reducing temperature in legumes like cowpea (Lawn, 1982a). Radiation load on leaves with a reflective surface is lower than the load on relatively non-reflective leaves. A higher reflectance is produced by pubescence or by wax layer depositions (Sheriff and

Muchow, 1984). Some plants have the ability either to move their leaves diaheliotropically, to face the sun, under well watered conditions in order to maximize photosynthesis, or to avoid direct solar radiation by moving them vertically or rolling them when they experience water stress (Ehleringer and Forseth, 1980). The avoidance of direct solar radiation may be important not only for reducing temperature and transpiration and therefore water stress, but also for reducing photo-inhibition when the stomata are closed.

Paraheliotropism may help lower leaf temperature under stress and presumably further restricts water loss. Differences among species in the degree of expression of paraheliotropism were observed by Lawn (1982a). Three species of *Vigna* and soybean showed paraheliotropism in the following order: cowpea > black and green gram > soybean. An interdependency in the degree of expression and the stomatal response to declining leaf-water potential was detected. The lack of paraheliotropism in soybean relative to *Vigna* cultivars may be related in part to the lower leaf water potentials developed and the apparent loss in turgor of stressed soybean leaves (Lawn, 1982a).

Paraheliotropism is associated with improved plant water status (Dubetz, 1969; Oosterhuis *et al.*, 1985; Berg and Hsiao, 1986; Berg and Heuchelin, 1990) and lower leaf temperatures. The association with stomatal conductance is less clear. Paraheliotropic leaf movement and stomatal closure may act in parallel without any association between them, nor do they show a relationship (Oosterhuis *et al.*, 1985). Although, both mechanisms can reduce transpiration under conditions of low water potential (Dubetz, 1969; Berg and Heuchelin, 1990). Since leaf movement is easily measured and has been shown to be related with leaf water potential and stomatal resistance in soybean (Oosterhuis *et al.,* 1985), dry bean (Dubetz, 1969; Berg and Hsiao, 1986) and cowpea (Lawn, 1982a), the response has been suggested as an useful indicator of the crop water status (Oosterhuis *et al.,* 1985).

In addition to contributing to the reduction of transpiration and leaf temperature, paraheliotropism plays a role in increasing light penetration and transpiration efficiency. Since, light avoidance by leaves at the top of the canopy increases light penetration to the lower leaves, where vapor pressure may be less (Shackel and Hall, 1979; Travis and Reed, 1983), water use efficiency and possibly photosynthesis may be increased (Fukai and Loomis, 1976). Likewise, paraheliotropic leaf movements by individual plants, or a combination of paraheliotropic movements by a plant canopy, may enhance carbon balance by maximizing sunlight intercepted on a diurnal basis (Forseth and Ehleringer, 1983), by compensating rates of photosynthesis during the day and improving water use efficiency (Mooney and Ehleringer, 1978; Berg and Hsiao, 1986).

Although paraheliotropic movements have been associated with water stress, leaf movements have been observed in absence of changes in soil and plant water status, because paraheliotropic movements are influenced also by air temperature in the presence of light (Fu and Ehleringer, 1989). Paraheliotropic movements have been associated with drought resistance in soybean (Lawn, 1982a), tepary bean (Parsons and Davis, 1978) and cowpea (Shackel and Hall, 1979; Lawn, 1982a). Studies to characterize genotypic differences within species are scarce. Significant variation among soybean cultivars in the degree of orientation of the center and the side leaflets of trifoliate leaves at different times of the day during the vegetative and reproductive stages have been reported (Wofford and Allen, 1982). It is possible that leaf movements may confer different benefits at different stages of development (Berg and Hsiao, 1986). Leaf movements may contribute to the stability of yield in environments with intermittent water stress. Since leaf movements are essentially survival traits, it is expected that they have little influence on the yield components directly (Ludlow and Muchow, 1990).

Some species have highly pubescent leaves, but in many cases the degree of pubescence increases with water stress, and to some extent with temperature occurring during leaf development. Thus, low water potentials and high temperatures cause leaves to be reflective, and therefore to have a lower absorption than do leaves developed under milder conditions. The increase in reflectance reduces the energy input to the leaf reducing both temperature and transpiration, so the mechanism may be important in increasing growth and yield (Sheriff and Muchow, 1984). In soybean, pubescence reduces evapotranspiration and increases water use efficiency, although, it does not alter the net radiation balance, turbulent mixing, canopy CO_2 exchange or plant water status. Leaf pubescence, in this case, appears to alter the spectral characteristics of the leaf and, thus, to facilitate the penetration of solar radiation into the canopy, under non-stress conditions (Baldocchi *et al.*, 1983). Under water stress a linear reduction in apparent photosynthesis occurs when leaf water potential is reduced, but the rate of reduction is in the order of glabrous > normal > dense pubescent isolines of soybean, indicating a relation between the level of pubescence and the photosynthetic ability of the genotype (Ghorashy *et al.,* 1971).

In common beans pubescence has been studied for phytopathological purposes, but not for its possible relation with water status of the plant. Studies have detected genetic variation in pubescence among cultivars and lines. In these studies pubescence (long, straight hairs) has been found to be determined by a single major gene or by duplicate recessive epistatic genes, depending on the cross involved. Trichome density (number of trichomes per mm^2), however, was found to be a quantitative trait. Therefore, pubescence is a discrete trait, but trichome density ranges from low to high (Zaiter *et al.,* 1990).

Accumulation of wax under water stress has been demonstrated in common and tepary beans. Anderson *et al.* (1984) found that the amount of phytol, which is bound as an ester in mature leaves is increased 10-20 times by drought, after seven days of water stress. Watering the plants before permanent wilt reverses the trend. Tepary bean produces greater amounts of these substance than common bean under drought.

Since leaf and canopy temperature have been found to be related to physiological and morphological responses of the plant to water stress and yield, it seems possible to utilize them as a possible selection criteria. In dry beans an infrared thermometer was used to calculate an index of drought based on means of canopy temperatures, Bascur *et al.* (1985) found a good correlation between the drought index with leaf water potential, stomatal resistance and yield reduction. Infrared thermometry is a rapid method for the characterization of homogeneous genotypes in field plots which may be used for the identification of drought resistant cultivars (Laing *et al.*, 1983). In common bean (Laing *et al.*, 1983, 1984; Bascur *et al.*, 1985), wheat (Blum *et al.*, 1989), soybean (Harris *et al.*, 1984), oil seed *Brassicas* (Singh *et al.*, 1985) and other crops genotypic differences have been found through this method.

Stomatal behavior is not an independent response and maintains a strong relationship with the root system. Thus, it has been suggested that the root can act as sensor of plant water deficits. Photosynthetic rate and/or stomatal conductance is more closely correlated to soil water content or soil water potential than with leaf water potential or leaf turgor (Turner, 1986; Henson *et al.*, 1989).

A similar pattern has been observed in common beans, where there appears to exist a tight linkage between gas exchange activity under water stress and rooting density. This suggests that genotypic differences in root growth could allow prolonged maintenance of relatively large stomatal conductances (Sullivan and Brun, 1975; White and Castillo, 1989; DeVries *et al.*, 1989; Sponchiado *et al.*, 1989; White *et al.*, 1990), maintenance of high water status and rates of photosynthesis (DeVries *et al.*, 1989; White *et al.*, 1990), and maintenance of nitrogenase activity (DeVries *et al.*, 1989).

Once the stomata are closed, the plant losses water through the cuticle. However, some stomata may be incompletely closed and additional water can be lost. The mechanism has been called epidermal conductance. Low epidermal conductance enhances avoidance of dehydration of leaves and, therefore, promotes leaf survival (Sinclair and Ludlow, 1986). Thus this mechanism should contribute to stability of yield, without any cost to yield. The mechanism may be equally important in either intermittent or temporal stress. Substantial differences in epidermal conductances have been found among different species of legumes (Sinclair and Ludlow, 1986) and among soybean genotypes (Paje *et al.*, 1988).

Excised leaf water-retention has been used as a screening method for drought resistance. As the method uses long periods of dehydration, it is in a large extent a reflection of cuticular transpiration as controlled by cuticular resistance (Blum, 1988). Differences in leaf moisture retention capacity between resistant and susceptible genotypes of cowpea have been found (Walker and Miller Jr., 1986). Leaf moisture retention capacity (MRC) was different among dry bean genotypes, although it was not significantly related to economic yield (Mkandawire, 1987). Acosta-Gallegos (1988) reported significant differences among genotypes of common beans under drought for MRC and low positive significant correlations of MRC with yield, pods, seeds and total matter weight.

Among the assimilatory processes, photosynthesis is important for determining growth and yield. Since CO_2 fixed by photosynthesis represents most of the dry matter accumulated by the plant any factor that affects the photosynthetic activity of the leaves is likely also to affect the total dry matter and, within broad limits, the grain production by the crop (Boyer and McPherson, 1975). The total photosynthate production is the result of the multiplicative interaction between the photosynthetic rate and the leaf area or the photosynthetic surface (Sinha *et al.*, 1982). After flowering growth is characterized by the photosynthetic activity of the leaves and the translocation of the photosynthetic products to the seed rather than by leaf development. During this stage of development changes in the photosynthetic activity of the leaves are important means by which the photosynthetic capacity of the crop is influenced by drought (Boyer and McPherson, 1975).

Stomatal closure may be the primary mechanism by which water stress reduces net photosynthesis under natural conditions, directly by impeding CO_2 supply and indirectly by increasing leaf temperature (Slatyer, 1969). The resistance to CO_2 uptake in most of the leaves are primarily stomatal and secondly the non-stomatal limitations associated with the liquid phase, inducing the physical diffusion of CO_2, the biochemical limitations, and the effects of dark respiration and photorespiration (Pearcy, 1983). In common beans a parallel decrease in net photosynthesis and transpiration has been reported, indicating that stomatal closure is the principal cause in water stress mediated reduction of net photosynthesis (O'Toole *et al.*, 1977; Velasquez-Mendoza, 1986). The influence of non-stomatal factors based on increases in the CO_2 compensation point and a reduction in RuBisCo activity decreases photosynthesis (O'Toole *et al.*, 1976).

Remobilization of nitrogen and stored carbohydrates (starch) may be enhanced under drought stress, and this would permit greater root growth or capacity for osmotic adjustment (White and Izquierdo, 1989). Under condition of adequate water supply, photosynthesis after flowering is the major contributor to grain yield and only a small proportion of the grain comes from assimilates stored in the stem and the root. When stress occurs in the seed filling period an increased proportion of the assimilates is transferred to the seed, so pre-anthesis photosynthesis becomes more important provided that a source limitation exists (Hsiao *et al.*, 1976; Turner, 1979). Since photosynthesis is inhibited more than translocation during stress, dry matter produced before flowering may be transferred from the stem and roots to the grain during grain filling, the process is called "compensatory translocation" (Sheriff and Muchow, 1984). In dry beans the process is possible because the ray tissue in stems and roots is a primary site of the deposition of starch which may be remobilized later and utilized elsewhere in the plant (Adams and Pipoly, 1980).

Studies of carbohydrate remobilization under drought conditions suggest that yield under drought is related to remobilization of photosynthate stored before flowering, and the process is hastened by water stress (Samper, 1984). Remobilization could be triggered by the stress and then be available to support seed filling instead of the impaired photosynthetic leaf area, as suggested by the negative relationship between stem dry weight and yield described by White and Izquierdo (1989). D'Souza and Coulson (1988) studying dry matter production and partitioning in two cultivars of common beans under different watering regimes found that photosynthate from the leaves was primarily accumulated in the root and the stem. Dry matter was subsequently re-translocated to the reproductive organs, first from the root and then from the stem. A change in root-shoot partitioning, with relatively more carbohydrates being allocated to the root system (temporarily) than to the canopy is one of the possibilities for survival during dry periods (Hoogenboom *et al.*, 1988). The remobilization of assimilates may explain the observed correlation between yield under stress and dry weight of biomass found in common beans under drought after flowering (Samper, 1984; Elizondo, 1987; Acosta-Gallegos, 1989).

The partitioning of stem and root dry matter to the seed is beneficial to yield under water deficits, provided the stem does not become so weak that lodging and disease infection occur. Thus, under water stress conditions both stem dry weight and stem diameter could have the same positive relationship with yield that was shown under non-stress conditions by Acosta-Gallegos (1988). He suggested that stem diameter could be used as an indirect indicator of the weight of the stem, since it was a preponderant morphological trait in resistant genotypes evaluated by him under drought. A thick stem could have a dual function. Before anthesis, the stem may provide enough water supply and support for higher levels of photosynthesis and canopy development and provide a storage site of photosynthates. After anthesis the stem would be a source of photosynthates by increasing remobilization and partitioning to the seed.

The ability of plants to transfer assimilate accumulated prior to seed filling to the seed during the seed filling stage is an important aspect of developmental plasticity (Turner, 1979). Varietal differences in the amount of stem reserves transferred to the seed under water deficits were observed in common beans (Samper, 1984; White and Izquierdo, 1989). An additional advantage of a large stem with thick hypocotyl diameter is that it may indicate a larger root system and better storage by allowing a greater portion of photosynthate to be translocated to the roots (Stofella et al., 1979a,b).

Nitrate reduction and nitrogen fixation are drastically reduced when leaf water potential falls below 0.2 to 0.5 MPa. If stress continues, plant proteins begin to breakdown, sometimes accompanied by release of ammonia. For many species, proline is a major product of the disruption of the nitrogen metabolism process in water-stressed plants (Hanson and Hitz, 1983). Nitrate reductase loses its activity when plants undergo stress. The decrease in nitrate reductase activity is accompanied by an increase in free aminoacids and a decline in protein synthesis (Sinha *et al.*, 1982). Velasquez-Mendoza (1986) found a reduction in nitrate reductase activity and increased levels of free amino-compounds, specially proline, under drought stress in common beans.

Nitrogen fixation is reduced under drought stress (Laing *et al.*, 1984). Water stress decreases specific nodule activity and dry weight of nodules. The inhibition of nodule activity under long term water stress is caused by the decrease in photosynthesis and by changes in photosynthate pool sites when current photosynthate is lacking due to reduced leaf expansion and foliar processes (Finn and Brun, 1980).

Effect of Drought on Root Growth

Although total growth is reduced during water stress, root growth is generally favored relative to shoot growth. It is frequently assumed that root dry matter is typically 10% of total crop dry matter after flowering under non-stress conditions producing root/shoot ratios of 0.1 in temperate regions. However, in drier regions the root proportion maybe as high as 20% in crops such as barley or 45% in wheat without fertilization (Gregory, 1989). The root/shoot ratio under drought conditions will increase up to 0.3 (Passioura, 1983).

A slow decrease in water content of soil containing the roots causes: a) a reduction in the solute potential of the roots, thereby causing osmotic adjustment within the root; b) a reduction in cell extensibility; c) a reduction in water uptake; and d) an increase in the mechanical constraint of the soil. Osmotic adjustment allows the root to continue growing but the other factors listed tend to reduce root growth rates (Taylor, 1983). The main effects of water deficits on root growth are the reduction in rates of meristematic activity and root elongation and suberization on roots (Slatyer, 1969). Tap root elongation is affected neither by plant water potential nor soil water potential as long as they remain above -1.0 to -1.5 MPa. Root weight is much more affected by soil water stress than root length. Lower water potentials are usually required to reduce root elongation. Root shedding may be accelerated by reductions in soil water content. Although root shedding occurs normally during different periods of the plant growth cycle, shedding usually is accelerated during periods of rapid reproductive development. Since roots grow faster where soil water contents are high and soil strengths are lowest and root shedding is lowest where water contents are highest, plant roots are concentrated in the soil's wettest zones (Taylor, 1983). Before maturity a proportion of the roots dies, but the effect is more pronounced in the top soil, which suggests that earlier formed laterals closer to the soil surface die sequentially in a manner comparable to the lower leaves above ground. The main axes of the root system remain alive to provide vascular continuity in the same manner as stems (Fisher and Dunham, 1984). Whenever the top soil is wet (by rain or irrigation) new roots develop, inhibiting the growth of existing roots, irrespectively of the moisture content in deeper soil layers. A high root density is then found in the upper soil layers. When the top soil is continuously dry, new roots do not develop in the upper soil layers. Assimilate partitioned to the roots is then used for growth and root branching into the soil (Blum, 1988). Lower soil water content reduces root elongation rates (which reduces rooting depths), increases root shedding, decreases soil hydraulic conductivity, reduces root diameter, reduces the water potential of the surrounding soil and increases root suberization (Taylor, 1983).

Root development and capacity of plants to absorb water are closely related. Generally, as width, depth, and branching of root systems increase, plant water stress decreases (Hurd, 1976). Deep rooted plants show greater drought avoidance than shallow rooted ones, if ground water is available; but they may show lower avoidance, if deeper soil moisture is not present (Levitt, 1972). Relevant attributes of root systems for drought prone environments are rooting depth, root length in specific layers (root length density, cm roots/cm^3 soil) and the resistance to water flow within the root (Taylor, 1980). Axial flow is not likely to limit the uptake of water in legumes because their facility for secondary growth normally ensures abundant vessels. Only a vascular disease or a large resistance at nodes or at the junctions between roots is likely to cause a problem (Passioura, 1982).

Maintenance of root water uptake requires the development of roots into soil containing water and their continued extraction of water in absence of rain. The growth of roots into deeper soil layers is a function of both genotype and environment. The continued exploration of soil when water content decreases and mechanical impedance increases depends on osmotic adjustment which prevents a decrease in turgor pressure of the root cells. The osmotic adjustment capability depends on both the species and the genotype within the species (Turner, 1986).

The type of growth of root systems is determined genetically and modified later by environmental factors. Interactions between shoot and root are important in determining the size of root systems (Kramer, 1983). Soil strength, aeration, temperature, salinity and toxic concentration of aluminium or other substances are environmental factors, other than water available in the soil, affecting root growth (Taylor, 1983; Gregory, 1989).

Roots have an obvious effect in the response to drought in securing a supply of water and this is most commonly characterized by the depth of rooting and the root length in a particular layer (Passioura, 1982; Taylor, 1983; Sheriff and Muchow, 1984; Gregory, 1989). The characteristics of a desirable root system will vary with edaphic and climatic conditions. When the root system is limited to a drying soil with no additional moisture reserves at deeper soil layers, soil-to-leaf water flux, and the associated water potential will be affected by root length density, root axial resistance, and root adaxial resistance (Hurd, 1976; Passioura, 1982; Sheriff and Muchow, 1984; Blum, 1988; Gregory, 1989). Small root resistance and a large root-length density would contribute to the maintenance of a higher leaf-water potential (Blum, 1988).

Dry Bean Root System

Stofella et al. (1979 a,b) described morphologically and physiologically the root system of black beans. They indicated that the total root biomass consists of adventitious roots, arising from the upper region of the hypocotyl; taproot or radicle; lateral roots, arising from the taproot; and basal roots, arising from the basal region of the hypocotyl. Under non-stress field conditions, adventitious, taproots together with lateral roots, and basal roots represent 4%, 58% and 38% of the total root biomass, respectively, at the seed initiation stage. At this stage total root weight, basal root weight and taproot weight were maximum. Maximum growth occurs during seed initiation stage after which root senescence begins. Stem and taproot diameters respond similarly.

Dry beans have a shallow root systems and so they are particularly responsive to frequent irrigation to maintain the levels of available soil water (Halterlein, 1983). Halterlein *et al.* (unpublished) (as quoted by Halterlein, 1983) found that maximum root depth for adequately watered plants was between 81 and 102 cm in three bean cultivars. Maximum root extension occurred by full flowering. At all growth stages at least 50% of roots were found to be in a zone bounded by a depth of 30 cm and lateral extension of 20 cm. Less than 10% of roots ever extended laterally beyond 20 cm. Likewise, less than 10% of roots extended to a depth exceeding 46 cm.

Maximum root depth of different cultivars grown at different locations under irrigation or well watered conditions have been reported. Sponchiado *et al.* (1989) have shown that the root growth of adapted and sensitive lines to drought was similar under irrigation, reaching 0.8 m in one location and only 0.4 m in another location due to soil limitations. Hoogenboom *et al.* (1988) working with two genotypes found roots at 1.2 m of depth irrespective of the irrigation treatment, in Florida. Stansell and Smittle (1980) observed that water extraction from depths greater than 45 cm in a sandy soil was minimal irrespective of irrigation regime, although water was extracted from the 30-45 cm soil profile depth. Snap bean production was maximum with water management to a depth of 30 cm, indicating that the maximum density of functional roots was between 0 and 30 cm. Thus, the maximum density reported in dry bean is between 0 and 30 cm irrespectively of genotype (Markhart, 1985; Hoogenboom *et al.*, 1988; Sponchiado *et al.*, 1989), level of water stress (Ibarra, 1985; CIAT, 1988; Hoogenboom *et al.*, 1988; Sponchiado *et al.*, 1989) or environmental constraint (Sponchiado *et al.*, 1989).

D'Souza and Coulson (1988) found that after flowering, limited photosynthate from the leaves resulted in the cessation of root growth. Dry matter was accumulated in the root before flowering but was accumulated in the shoot after flowering. Although root dry matter accumulation declined after flowering, the decline was less under reduced watering. The adaptation in the root and shoot growth takes place to ameliorate the effect of the stress. Thus, under reduced watering and prior to flowering, this adaptation takes the form of an increase in the root dry matter *per se* but after flowering reduced watering results in a lowering of the rate of root dry matter reduction. Ibarra (1985) found that in three out of seven genotypes, the maximum root dry weight peaked at mid-pod filling, while in four other genotypes the maximum point was detected at physiological maturity. In three stages of development (pre-flowering, mid-pod filling and physiological maturity) more than 90% of the root weight was between 0 and 30 cm of depth. A reduction in root dry weight in eleven dry bean genotypes from flowering to physiological maturity under both normal and water stress condition was reported by Elizondo (1987).

The depth of rooting is often cited as an important criterion of crop performance but is rarely measured or selected for specifically. Under ideal conditions, the depth of rooting is genetically controlled but, in practice, many soil factors affect the extension of root axes. In deep soils where water is stored throughout the whole soil profile, the rooting depth has a major influence determining the potential supply of water (Gregory, 1989).

Genotypic differences for depth of rooting have been found in dry beans. Sponchiado *et al.*, (1989) have shown that genotypes differing in their ability to resist water stress have different capabilities to reach deeper soil profiles. Thus, drought adapted genotypes have the ability to produce deeper roots than the susceptible lines, so, drought resistant genotypes extracted more soil water. The ability to continue growing is only detected under drought conditions. In the adapted genotypes a larger proportion of roots was produced between 0.8 to 1.2 m. Sensitive genotypes did not show the ability to produce roots at soil profiles deeper than the maximum depth reached under non-stress conditions. To verify these results on a wider range of genotypes, root growth under stress was analyzed for 10 small to medium seeded genotypes of indeterminate growth habits. At the location without soil constraints (Palmira) root length density was correlated with yield, but at the site with soil constraints (Quilachao) no relation was detected. Root growth at the two sites did show a significant correlation. The results confirm the importance of root growth under certain soil conditions, and suggest that cultivar differences in root growth may show similar patterns in contrasting soil environments (CIAT, 1987).

Studying two cultivars of dry beans in Florida, Hoogenboom *et al.* (1988) did not find genotypic differences in root growth responses to drought at the seed filling stage. However, both cultivars showed a change in root-shoot partitioning, with relatively more carbohydrates being allocated to the root system than to the canopy. The highest root density for depths below 0.45 m were found in the lower water availability regimes, and the shoot biomass production was significantly less in the rainfed treatment than in the well watered level. The root/shoot partitioning rates was significantly changed under drought conditions. Lack of differences in rooting depth between genotypes may be explained by the date of sampling, which were taken at the seed filling stage. It is possible that the number of roots developed before the seed filling stage could be more important, since root weight was increased.

Differences in root growth may be detected before the seed filling stage. The comparison of root growth at different dates after planting in drought resistant and susceptible genotypes under water stress showed no differences between genotypes at 33 days after planting (DAP) and a more rapid root establishment between 0 to 20 cm in the drought resistance genotype than in the susceptible genotype at 45 DAP. The susceptible genotype also produced a larger number of roots at soil depth of 0.5 - 1.2 m at 45 and 60 DAP. The drought resistant genotype had a more rapid establishment of root superficially and a larger number of roots in all the sampling (CIAT, 1988).

Differences in root growth due to water stress, on a dry weight basis, were reported in dry bean under both controlled (Ibarra, 1985 and Velasquez-Mendoza, 1986) and field conditions (Ibarra, 1985; Markhart, 1985; Elizondo, 1987; Hoogenboom *et al.*, 1988; D'Souza and Coulson, 1988). Reduction in the root dry weight was observed under drought conditions after flowering in all the studies. Similar response was observed in tepary bean (Markhart, 1985) and faba bean (El-Shazly and Warboys, 1989), with an exception in case of soybean where an increase in root dry weight was reported (Finn and Brun, 1980). Markhart (1985) found that the dry bean cultivars Pinto and Half White Runner (HWR) behaved similarly in depth of rooting under drought conditions, reaching a maximum depth of 70 cm. The pinto cultivar exhibited approximately 50% of the roots between 0 and 16 cm of depth while HWR had only 35% of the roots at the same soil profile. Both cultivars showed more than 50% of the root system between 0 and 30 cm (until 75% in the pinto bean). HWR had more roots (25% approximately) than pinto bean (10% approximately) in a deeper soil profile, from 48 to 70 cm. The average penetration rate was 0.92 cm/ day from 10 to 60 DAP. Markhart (1985) compared both cultivars with tepary bean and found a deeper root system in tepary bean even at the first sampling (8 DAP) and a faster continued elongation, averaging 2.0 cm/day during the first 20 days of growth and 1.2 cm/day from day 30 to 50. The deeply penetrating root system of the tepary bean resulted in a greater percentage of the root dry weight within deeper layers of soil.

Deeper rooting and larger number of roots at deeper profiles of the soils under drought are generalized responses in legumes like peanut, soybean and pigeon pea (DeVries *et al.,* 1989); green gram, black gram, cowpea, and lablab bean (Muchow, 1985a); faba bean (El-Shazly and Warboys, 1989) and tepary bean (Markhart, 1985). Although, Turk and Hall (1980) found that root growth in cowpea increased linearly throughout the season to a depth of 135 cm under well-watered conditions, growth was restricted greatly under dry conditions. The response is a mechanism of the plant to maintain the nutrition balance and water supply necessary to achieve the best possible yield under stress conditions.

Through this mechanism water supply is guaranteed to the plant by increasing the extraction of water (Muchow, 1985c; CIAT, 1987; El-Shazly and Warboys, 1989; Sponchiado *et al.*, 1989). Higher levels of available water maintain the performance of the shoot in transpiration, higher leaf water status, stomatal conductance and nitrogenase activity (Sponchiado et al., 1989; DeVries *et al.*, 1989; White *et al.*, 1990), maintaining maximum productivity under water stress (CIAT, 1987; Sponchiado *et al.*, 1989; White *et al.*, 1990).

Shoot-Root Relationship

In some respects, the plant is able to modify its rooting behavior in response to water deficits, so it is very common to find an increase in the root-shoot ratio with the increase in water stress (Hsiao, 1973; Turner, 1983; Blum, 1988). The ratio increases largely because shoot growth is inhibited relatively more than root growth under stress. Wetsgate and Boyer (1985) demonstrated in maize that growth was inhibited as the water potential in the region of cell expansion decreased in each organ. The water potential required to stop growth was -0.50, -0.75 and -1.00 MPa, in this order, in the stem, silks and leaves. However, the roots grow at these water potentials and ceased only when water potential was lower that -1.4 MPa. The difference in turgor and gradient maintenance could contribute to the increase in root/shoot ratios generally observed in water limiting conditions.

The increase in root/shoot rates of crops under water deficits may reflect an increase in the proportion of assimilates allocated to roots, as demonstrated by D'Souza and Coulson (1988) for dry beans and by Finn and Brun (1980) for soybean. Turner (1983) has indicated that an increase in root-shoot ratio can be often ascribed to an absolute increase in root weight and root depth. Ibarra (1985) found genotypic differences in the way the ratio could change. Some genotypes exhibited an absolute increase in root weight, others maintained the root weight but reduced shoot weight, while others had a greater reduction in shoot dry weight relative to root weight.

The changes in root/shoot ratio are caused by changes and adjustments in source-sink relationships. As long as roots remain the major sink, with a lower sensitivity to water stress, they grow and explore soil for more water, thus increasing water availability. When flower or seed development commences the major sink changes and the root is transformed into a source reducing or stopping its growth (Sinha, 1986). This is shown perfectly by the results of D'Souza and Coulson (1988) in dry bean in which the root growth is increased under drought conditions before flowering as a function of the level of stress. At flowering, root growth is stopped. After flowering the root weight is reduced but this reduction is slower in the greatest level of stress, thereby changing the root/shoots ratio. The ratio root/shoot is changed by the levels of stress through the different stages of development because of the dynamic source-sink relationship.

Increases in the root/shoot ratio brought about by water stress in dry bean under controlled conditions have been reported by Ibarra (1984) and Lopez *et al.,* (1987) and under field conditions by Elizondo (1987), Hoogenboom *et al.,* (1988), Markhart (1985) and Ibarra (1985). In tepary bean (Markhart, 1985) and faba bean (El-Shazly and Warboys, 1988) similar behavior was detected. When two dry bean cultivars, pinto and HWR, were compared to tepary bean, the results showed that pinto bean had the highest root/shoot ratio under well watered and water stress conditions. The pinto cultivar reduced the shoot dry weight but the root dry weight was not changed by water stress and the reduction in shoot weight was proportionally less than HWR or tepary bean. Tepary bean exhibited the maximum root weight under well-watered conditions but the reduction of weight under drought was the greatest. The shoot weight of tepary bean was drastically reduced, almost twice that of pinto bean, by water stress. The combination of these factors contributed to highest root/shoot ratios in the pinto bean.

The root/shoot ratio is usualy larger at the vegetative stage and is reduced throughout the whole life cycle of the crop until maturity, irrespective of genotype, level of water stress and location (Stofella *et al*., 1979b; Ibarra, 1985; Elizondo, 1987; D'Souza and Coulson, 1988).

Besides the effect of the environment on root growth, there is evidence that at certain physiological stages of growth, especially during flowering and fruit formation, root growth is retarded or stopped completely (Begg and Turner, 1976). Thus, Summerfield (1980b) found that the duration of reproductive growth in chick pea is strongly correlated with, and may depend on, the proportion of roots which senescence during the latter half of the life of the crop, emphasizing the importance of a functional root system for a longer time.

Grafting experiments in soybean (Sullivan and Brun, 1975) and dry bean (CIAT, 1987; White and Castillo, 1989) have shown that root characteristics are of primary importance in determining drought response in both crops and that shoot characteristics are less important. However, the response of specific genotypes varies greatly with environment. Root genotypes may differ in their ability, morphological or physiological, to supply water to the top and may cause partial stomatal closure, reduced photosynthesis, and potential yield loss.

In addition, roots send cytokinins to the shoot. It is highly possible that the root tips, which are thought to contain the site of cytokinin synthesis, may be able to sense the water potential of the soil and adjust the production of cytokinins accordingly. The variation in the production of cytokinins may influence plant behavior in relation to water supply (Passioura, 1982). It has similarly been suggested than in dry soil ABA can move from the roots to the epidermis and restrict stomatal aperture even when leaf water potentials and turgor pressure remain constant. A comparatively small increase in ABA production by the roots can provide a precise measurement of the moisture status of the soil surrounding the roots (Zhang *et al.*, 1987).

Effect of Drought on Development and Differentiation

The direct effect of water stress and stage of growth interact to influence the time and the amount of floral initiation and pod development (Dubetz and Mahalle, 1969). Depending on the intensity and timing of water deficits the time between planting and maturity may be shortened or lengthened (Sheriff and Muchow, 1984). This mechanism provides the crop with two possible adaptive responses. Under moderate water deficit the crop produces grain which matures before the soil water is depleted. Such early maturity response may be advantageous in dry years and yet permit the plant the ability to exploit a longer season and larger yield in wetter years. When severe water deficit occurs early, 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). In wheat mild drought has caused earlier flowering while severe water stress has delayed flowering (Fisher and Turner, 1978). Similar responses have been observed in cowpea (Turk and Hall, 1980; Lawn, 1982a). The responses vary with the species and genotype, and the stage of development. Lawn (1982a) studying the response of soybean, black gram, green gram and cowpea found a substantial differential effect of water stress on cultivar phenology. Water stress induced more rapid maturity; particularly in *Vigna* species, the reduction in crop duration varied from 12 to 28% depending on cultivar and level of stress. In soybean, the effect of water stress was small with only 6 to 7 day difference between extreme treatments. In all cultivars, most of the variation in phenology was associated with variation in the duration of flowering. In *Vigna* species there was a shortening in the length of the post-flowering period. In another study conducted by the same author on seed legumes grown under different soil water stress, the water deficit had little effect on the date of flowering, although there was a tendency to hasten flowering in all seed legumes, in pigeon-pea flowering was delayed. The duration of flowering was significantly reduced by water shortage in all grain legumes except soybean. The duration of pod-filling (time from end of flowering to maturity) was markedly reduced leading to shorter growth duration in response to water deficits for all seed legumes.

In common bean an acceleration of maturity of 10 days was found in 72 genotypes due to drought in the driest condition evaluated. In the same season with severe water stress occurring 35 days after planting, days to maturity and drought were negatively correlated, but a stronger relationship between yield with the difference in days to maturity between irrigated and stress conditions was detected. When the stress was applied allowing rainfall after 35 days after planting, later maturity cultivars gave higher yields, and genotypes showing a delay in maturity under drought had higher yields. Four Type I genotypes showed the least ability to adjust their growth cycle under stress, explaining partially their generally poor drought adaptation in the season with severe drought (CIAT, 1987). The length and the rate of the seed filling period were regarded as important determinants of varietal differences in seed yield by Samper (1984). The top yielding cultivars under stress and irrigated conditions were those which had a higher than average seed growth rate accompanied by a seed filling period that was not significantly different in length due to water treatments. All cultivars had a reduction in the length of seed filling period and the genotype variability was hastened at higher stress. Acosta-Gallegos (1988) detected a significant reduction in days to physiological maturity and length of seed filing period under drought as compared to irrigated treatments in a study carried out in Michigan and Durango, Mexico. The level of reduction was very similar in both locations 4.3 and 8.0% in Michigan, and 5.2 and 8.5% in Durango, for days to physiological maturity and flowering, respectively. The absolute reduction in the duration of the cycle was 10 days in Durango and 8 days in Michigan.

The sensitivity of growth reduction varies among species of legumes. Muchow (1985a) described a direct relationship between the increase of yield reduction with increasing growth duration. The order in sensitivity for several species was as follow: black gram > lablab bean > pigeon pea > soybean > cowpea > green gram.

Major developmental adaptations found in plants to resist water stress are rapid phenological development and developmental plasticity (Turner, 1982, 1986). Rapid phenological development is achieved by earliness, while developmental plasticity is obtained by extending vegetative growth through tillering, branching and indeterminacy. When the probability of drought increases with the life of the crop, the shorter the crop duration the greater the yield will be in most years (Turner, 1983). However, under conditions of adequate moisture, crops with early flowering and maturity frequently have lower yields than later season crops (Turner, 1982).

Later maturing bean genotypes typically out-yield similar, but earlier maturing materials by substantial amounts in the absence of marked seasonal variations in stresses, notably drought or low temperatures in common bean. White (1987) has shown that differences in maturity were associated with a yield difference of nearly 2000 kg/ha in a set of 42 genotypes varying in maturity from 52 to 83 days grown at CIAT (Palmira, Colombia), with a linear correlation between yield and days to maturity of $r=0.8$. Likewise, Laing *et al.* (1984) using photo-period treatment to delay flowering of Porrillo Sintetico cultivar, showed that a 10 day delay in maturity was associated with a 1000 kg/ha increase in yield. Turner (1979) has pointed out that in crop plants there is no doubt that the greatest advances in breeding for water limited environments have been achieved by shortening the life cycle, thereby allowing the crop to escape drought. One limitation of earliness and determinate plants, is the lack of plasticity to recover once the stress is removed. Phenological coupling of plants to their environment is a critical aspect of adaptation (Fisher and Turner, 1978). Earliness has been associated with improved adaptation of determinate crops to semiarid environments, especially for crops subjected to drought after flowering (Hall *et al.*, 1979). However in different environments and genetic backgrounds, specific times of flowering and maturity are selected to be optimal, whereas extremely precocious strains may not be well adapted (Hall, 1981). Thus, earlier flowering and shorter duration of pod filling to match crop phenology does not mean higher yields (Muchow, 1985a). In addition to modifications of phenology in response to water deficits, the matching of crop phenology to environment to escape serious water shortage should be advantageous in situations of prolonged water deficit (Muchow, 1985a).

Developmental plasticity, in ecological terms, facilitates the matching of crop growth and development to the constraints of the environment, especially to optimize the occurrence of the reproductive phase during drought periods (Lawn, 1982a). The approach, in agronomic terms, may raise difficulties of uneven maturity of the crop in capital intensive mechanized agriculture, particularly for harvesting, where flowering is delayed in some plants but not in others or where successive flushes of flowering occur. In labor intensive agricultural systems such plasticity reduces the risk of complete crop failure for subsistence farmers (Lawn, 1982a). Short term growth is reduced presumably as a consequence of lower rates of CO_2 exchange and photosynthesis. Escape can be achieved by developmental plasticity, usually in the form of more rapid development, but occasionally as delayed development. Crop duration may be either shortened or extended, depending of species and seasonal occurrence of the stress period.

The ability of plant to transfer assimilates accumulated prior to seed filling to the grain during the seed filling stage through remobilization is one important characteristic of developmental plasticity. When water supply is adequate only a small proportion of the seed dry weight comes from the stored assimilates in the stems and roots, but when stress occurs in the seed-filling stage an increased proportion of the stored assimilates is transferred to the seed (Turner, 1979).

Indeterminacy can be an useful growth mechanism for drought conditions as shown by the results of Grantz and Hall (1982) studying earliness of an indeterminate crop like cowpea , as affected by drought. They found that time to maturity was progressively decreased by increasing severity of drought imposed throughout the season. Very severe drought at flowering increased the time from germination to maturity but only when weather conditions and late irrigation allowed plants to exhibit a second period of leaf growth, flowering and pod development. The effect of drought may be adaptive since these plastic responses appear to be suited to the indeterminate growth habit and to the alternation of humid and arid periods that characterize semiarid environments. Studies with common bean 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 reproductive stage is one of the most sensitive stages of development to water stress. In this stage three steps are important to be considered: floral initiation and inflorescence development when the potential seed number is determined; anthesis and fertilization when the degree to which this potential is realized or fixed; seed filling when seed weight progressively increases (Slatyer, 1969).

The abscission of reproductive organs during flowering and fruiting period is often greater that 50% under non-stress condition in legumes. Abscission varies greatly with growing conditions. Abscission may result from water stress or from competition among developing pods for nitrogen, carbohydrates and other nutrients (White and Izquierdo, 1989). The tendency is more marked in determinate bush types than in indeterminate bean genotypes.

Abscission under drought was studied in Kenya in five determinate and three indeterminate cultivars in two seasons and two levels of irrigation; well watered and watering for only three weeks after planting, in one experiment. In a second experiment a low and high level of irrigation was established 42 days after planting using the line source sprinkler method. Under water stress the number of flowers per plant was significantly reduced and the total number of flowers produced was correlated with number of pods per plant ($r=0.69$). The percentage of abscission was significantly increased under drought and abscission was correlated with the number of pods per plant. Indeterminate cultivars had a lower abscission of flowers and pods than determinate genotypes. Under drought a large reduction in the number of flowers per plant was correlated with either a large increase in abscission or a large decrease in the number of flowers per plant. Additionally, differences among cultivars in the level of sensitivity were detected (Floor-Drees, 1984). Stress at anthesis can markedly reduce fertilization and seed set. In common bean it has been found that the pollen is adversely affected by drought. The critical period occurs between 10 and 13 days after emergence, during the transition from the vegetative to reproductive stage. Pollen abortion is increased, and the percentage of pollen germination and total pollen production are reduced (Shen and Webster, 1986).

Weaver (1988) has pointed out that the maintenance of optimal available soil moisture during periods of high temperature stress would favor survival of higher number of pollen grains and thereby enhance the potential for successful pollination and fertilization and increased seed set and yield.

Effect of Drought on Yield

Yield Potential, Components and Partitioning

Crop yield can be characterized as a function of an organism's adaptation to its environment, its ability to effectively harvest light through the photosynthetic apparatus, and effectively partition and translocate photosynthates to the economic organs. Phenological adaptations are best measured by days to maturity and the concomitant days to flower and pod filling period. Biomass and biomass growth rate are indicative of the light harvesting ability of the crop canopy. Harvest index measures assimilate distribution, and seed growth measures the rate of assimilate translocation and sink strength. Additionally, economic growth rate relates the length of crop cycle to yield (Scully and Wallace, 1990).

Crop yield can be expressed as a function of its components. In beans (Adams, 1967) such components may be defined as follow :

$$\text{Yield} = PN \times SP \times SW$$

Where PN, SP, and SW represent number of pods, seeds per pod and seed weight, respectively. According to this equation if the yield components were completely independent, improvement of any component would result in an increase in yield, but because they are negatively related, particularly under conditions of environmental stress, the individual effect is compensated (Adams, 1967; Sinha, 1986; White and Izquierdo, 1989). A "yield compensation" mechanism occurs, where positive variation in one component tends to compensate for negative variation in another, allowing the maintenance of a more stable yield (Adams, 1967).

Among the yield components in beans, the most important is pod number, which exhibits a strong association with yield. Pod number varies greatly while seeds per pod and particularly seed size show comparatively small changes across environments and treatments . This suggests that the common bean is more conservative in an evolutionary sense. Thus, bean plants apparently adjust potential sink size (pod number) to the available source and then proceed to fill that sink as rapidly as possible. The process in turn influences the rapid rate of senescence of the leaf canopy (Laing *et al.*, 1983). In beans a positive yield component like the weight of seed has been found to be negatively correlated to yield (Nienhuis and Singh, 1986; White and Izquierdo, 1989).

In common bean the importance of morphological traits such as biomass (Laing *et al.*, 1983; Scully and Wallace, 1990; Scully *et al.*, 1991), leaf area duration (Laing *et al.*,1983,1984), leaf area index (Laing *et al.*, 1983, 1984), growth habit (Laing *et al.*, 1983,1984), basal internode diameter and basal internode length (Davis and Evans, 1977), hypocotyl diameter (Davis and Evans, 1977; Acquaah *et al.*, 1991) and phenological traits such as days to flowering, days to maturity and days to pod fill (Laing *et al.*, 1983, 1984; Scully and Wallace, 1990; Scully *et al.*,1991) have been recognized as contributing significantly to determining final yield.

Thus an increase in the length of growth cycle increases the number of nodes formed and the leaf area duration; consequently there are more reproductive nodes and a larger leaf area to support the extra fruits formed. At the same time fewer flowers are shed and these factors combine to substantially increase yield (Laing *et al.*, 1984).

Harvest Index

Yield can be expressed as a function of harvest index (HI) as follows:

$$\text{Yield} = \text{Biological Yield} \times \text{HI}$$

The substantial advance in the productivity of the cereals over the past half-century have been made primarily through increases in HI rather than through increases in total biomass (Donald and Hamblin, 1976). It is possible that the productivity improvements made in soybean and groundnut were largely the consequence of improvements in their HI (Lawn, 1989). However, in common bean White (1987) has indicated that any increase of the yield potential in common bean through the improvement of the HI is not feasible, because they already possess a high HI and there is a lack of variability for this trait within cultivars grown in the tropics. In addition, a lack of correlation between HI and yield has been found.

Lawn (1989) has pointed out that HI is a much more stable parameter than yield over a range of densities and that in absence of stress HI is primarily a function of genotype and the (latitude/sowing) date in which the plant is grown. Thus for any given set of comparisons, HI may or may not be simply correlated with seed yield, depending on the density of the canopy involved in the comparison. Harvest index (HI) in the tropical legumes is affected by environmental stress, such as water deficits and temperature extremes. Generally the effect of stress is to reduce HI, although occasionally it can be enhanced by stress depending on its timing relative to crop ontogeny and the consequently differential effects on vegetative and reproductive growth (Lawn, 1982a; Chapman and Muchow, 1985). HI is more likely to be enhanced when stress occurs prior to reproduction and is subsequently relieved.

The sensitivity of HI to environmental stress poses specific problems for the plant breeder because the environmental effects are confounded with the measurements of differential genotypic performance. Selection efficiency is reduced by environmental effects in situations where the nature, timing and or intensity of stress is largely uncontrollable and unpredictable. The improvement in HI in legumes reduces opportunities for dual or multi-purpose crops, reduces potential for yield homeostasis through indeterminateness and increases requirement for management input and crop protection (Lawn, 1989). In terms of water stress, Passioura (1977) has indicated that we might expect the harvest index to depend on the proportion of the total water supply which is used after anthesis.

Harvest index depends on the relative duration of the vegetative and reproductive phases, and during the reproductive phase, on the relative partitioning, and remobilization of stored assimilates, to the reproductive organs. HI will be enhanced when the duration of reproductive growth represents a greater proportion of total growth, where most of the assimilation after flowering is partitioned into pods, and where there is substantial remobilization of assimilates from vegetative tissues into pods (Lawn, 1989).

Yield under Drought

The effect of drought on the morphology, physiology and phenology of the plant is generally the reduction in the expression of specific traits. The effect of drought on economical yield follows a similar pattern. The level of yield reduction will depend on the intensity, duration and timing of drought, although genotypic differences may ameliorate the effect of water stress. Yield reduction is generally a function of a lower number of pods and to a lesser extent, to changes in the number of seeds per pod and seed size. Of the yield components seed size undergoes the least significant changes. The importance of pod set as a prime factor of drought resistance in dry bean has been emphasized by Stocker (1974).

Yield Potential and Drought Resistance Relationships

In crop production drought resistance should not be referred to in terms of physiological mechanisms but rather as a stability parameter which allows seed yield to be maintained in spite of imposed water stress. So, drought resistance may be defined by the percentage of reduction in yield between non-stress and stressed conditions (Blum, 1973). Thus, higher yield in dry environments can be considered as a "residual" effect of high yield potential (Blum, 1988). In the absence of genotype x stress interactions of the crossover type, yield under drought is positively correlated with yield potential (Fisher and Maurer, 1978).

Estimation of Drought Resistance.

To separate the effects of yield potential from drought susceptibility, Fisher and Maurer (1978) proposed a susceptibility index (**S**). In this model yield under drought is represented by:

$$Y_d = Y_p (1 - \mathbf{S} \mathbf{D})$$

Where Y_d is stressed yield, Y_p is potential yield under non-stress conditions, and **D** is drought intensity calculated by $\mathbf{D} = (1 - X_d / X_p)$, where X_d and X_p are the mean yield of all varieties under stressed and nonstressed conditions, respectively. The susceptibility index is defined by the following equation

$$\mathbf{S} = (1 - Y_d / Y_p) / \mathbf{D}$$

In these expressions it is assumed that Y_d is made up of two components, Y_p and **S**. In Fisher and Maurer's original study, **S** and Y_p were positively correlated, however, independence of these traits has been observed (Fereres *et al.*, 1986). Although **S** appears to account for yield-potential variations among cultivars, it must include an effect due to the potential yield level. Thus, in wheat, **S** was found unrelated to plant water relations but was related to various non-stress attributes affecting yield (Fisher and Wood, 1979).

Varieties with average susceptibility to drought have an **S** value of 1.0. Values of **S** less than 1.0 indicates less susceptibility and greater resistance to drought with a value of **S**=0 indicating maximum possible drought resistance (no effect of drought on yield). Genotypic differences in **S** would be most readily detected in experiments where the intensity of drought is intermediate (e.g. **D** values of 0.5). The variation in **S** in a set of genotypes indicates that they are better adapted to certain types of drought and environmental conditions (Hall and Patel, 1985).

The commonly used stability analysis can also be useful in defining drought resistance in terms of yield, provided that the major component of variation in the environmental index as used in the analysis can be attributed to the water regime (Blum, 1982). The level of plant stress in a given environment is measured by the mean yield of the population grown in that environment, compared with other environments. The biological effects of the different undefined environments are integrated into one statistical parameter of stability in yield performance over changing environments (Finlay and Wilkinson, 1963). Drought resistance is one component of this stability and in cases where environments are variable mainly in the water regime, stable genotypes could indeed be physiologically classified as drought resistant (Blum, 1989).

Samper (1984), working with dry bean, found that the mean yields of a group of genotypes selected by their geometric mean were higher than the mean yields of groups selected on the basis of yield differential. She concluded that the use of the geometric mean $(Y_d * Y_p)^{1/2}$ as selection criterion rather than yield differential $(Y_p\text{-}Y_d)$ or the drought susceptibility index (**S**) proved to be very advantageous in the selection of genotypes.

In common bean, genotypic differences in susceptibility index and geometric mean were found by Samper (1984), Mkandawire (1987) and Acosta-

Gallegos (1988), although its practical usefulness in a breeding program has not been validated.

Breeding for Drought Resistance

Despite the overwhelming importance of drought as a constraint of dry-land crop production, there has been little progress in breeding for drought resistant cultivars. Selecting for drought resistance is difficult as the response is complex and the interaction with other factors such as high temperature and nutrient uptake confounds the problem. Moreover, plants have evolved a wide range of different response "strategies" to survive and reproduce under water stress occurring at various periods throughout the growth cycle of the crop. In addition, it is difficult to obtain a consistent response following the exposure of large plant populations to conditions which either simulate or represent realistic drought conditions in the field (Mc William, 1989; Ludlow and Muchow, 1990).

Breeding improved genotypes by selecting solely for seed yield is difficult. Absolute plant yield under stress is a poor estimate of drought resistance (Blum, 1982). Since yield under stress can be considered a function of yield potential, maturity and a susceptibility index (Edmeades *et al.*, 1989), it may be affected by any given non-stress environmental factor, masking the genotype x stress interaction. The genetic component of variation relative to the environmental component of variation in yield is usually low under stress (Frey, 1964). Under drought prone environments the inter-annual and location-to-location variation in rainfall is larger, and both variability of yield and response to inputs and management are high. Under these conditions, the heritability of yield is lower than under better environments because plant characteristics that are optimal for yield in a given season will be suboptimal in another season. Heritabilities for yield often are low under stress because genetic variance drops more rapidly with increasing stress than environmental variances, though the decline may not be great until yield levels are severely reduced (Blum, 1988).

Selection for yield under moisture stress is generally considered less efficient than selection for yield under well watered conditions (Rosielle and Hamblin, 1981). Since drought is normally an uncertain condition varying with its incidence, severity and timing, it is necessary to select for performance in both well watered and moisture stressed environments (Edmeades *et al.*, 1989). The efficiency of selection based on yield under drought alone is correspondingly low and genotype x environment interactions are always more important under these conditions than under more uniform environments. Therefore, an increase in the effort devoted to plant breeding can only partly overcome the consequences of low heritability (Austin,1989).

Breeding for drought resistance has been limited by the identification of specific parameters that represent the significant traits that collectively confer survival and productivity at each stage of the life cycle; the development of a single practical method for screening and selection; and the development of routine, large scale methodology for creating defined and repeatable water stress in the environment to screen large populations (Simpson, 1981).

Resistance to drought depends on a complex integration of attributes that confer both survival and a range of productivity potential at various stages of the life cycle. It is doubtful that only one criterion will be adequate for selection against water stress (Sullivan and Ross, 1979; Simpson, 1981). In seed legumes, Lawn (1982, a, b, c) has pointed out that there is no absolute character functional as a drought resistance mechanism, rather there are at least several alternative pathways to productivity in rain-fed treatments, with the relative agronomic success of each depending of the seasonal pattern of water availability. The most appropriate strategy for a particular environment will be that which simultaneously maximizes production and minimizes risk in that environment. In dry beans the complexity of drought resistance has been recognized by Ibarra (1985), Elizondo (1987) and Acosta-Gallegos (1988). Strategies for improving drought resistance through breeding should include both avoidance and tolerance mechanisms (Boyer and McPherson, 1975; Parsons, 1979; Sullivan and Ross, 1979; Simpson, 1981). Turner (1979) has indicated that only those mechanisms involved in drought escape, maintenance of water uptake and maintenance of turgor pressure do not reduce photosynthesis, crop growth and yield. In breeding for drought resistance the best traits would be those which cause no sacrifice in growth and yield (Boyer and McPherson, 1975).

Selection for earliness may not be advantageous because there is little evidence that early cultivars are more drought tolerant that late cultivars of a similar genetic background. Since escape should not be equated with drought tolerance, the breeder must take considerable care in selecting for drought tolerance among cultivars which vary in flowering date and in maturity, using perhaps, a selection index to maintain maturity constant if that is desired (Edmeades *et al.*, 1989). In order to overcome the low efficiency in traditional programs some plant breeders resort to the expensive solution of growing huge populations and performing repeated testing over years and locations to secure results. In these programs the probability for success becomes a function of investment rather than a function of science (Blum, 1989).

In breeding for drought resistance four basic methods have been followed: 1) To breed for optimum yield under optimal conditions; 2) To breed for maximum yield under optimal conditions; 3) To select and to incorporate physiological and morphological mechanisms of drought resistance; 4) To incorporate a specific, single drought resistance character that benefits yield under water-limited conditions (Blum, 1985; Turner, 1986).

Breeding for drought resistance can have opposing objectives. For the subsistence farmer, breeding for plant survival in the worst years may be the major objective to ensure some seed production. For other dryland farmers, the major objective may be high yields in the best years, since they contribute the most to long-term yields. It is unlikely that factors that contribute to plant survival in the most extreme dry environments also contribute to high yield in wetter environments. Therefore, the focus would be applied on maximizing long-term yields in dryland environments by developing drought resistant cultivars able to yield more seed under drought without sacrificing yield potential in wetter years. The emphasis should be applied on developing cultivars with the highest absolute yield under drought rather that the highest relative yield (Y_d/Y_p), because long term yields are influenced more by the wetter years (Richards, 1982).

Yield has been, and always will be, an important criterion in breeding for drought resistance, since performance at the whole-plant level integrates genotypic and environmental factors. In environments with considerable year-to-year variation in precipitation, highly drought-resistant genotypes may not be desirable, given that such genotypes are often unresponsive to favorable moisture conditions. Genotypes with a high yield potential buffered by a few drought resistance traits will yield well under favorable conditions and not substantially less than highly drought-resistant genotypes under drought conditions. The challenge under this situation is to improve the success of selecting genotypes with high and stable yields under drought stress (Clarke, 1987).

In breeding for high yield under drought two very different approaches have been used. The traditional or empirical approach, which relies on seed yield as selection criterion, since this integrates all the components that determine yield of the economic product, and the analytical approach which relies on selecting the different physiological mechanisms of adaptation in a drought environment, with the possibility that these adaptations will contribute to growth and yield under drought (Richards, 1982).

The traditional approach to selection has resulted in gains in performance under stress in wheat and corn (Edmeades *et al.*, 1989), dry bean (Acosta-Gallegos, 1988) and other crops. Although drought resistant varieties have been developed using the empirical breeding method employing yield as selection index, these methods are costly and require a long period of testing and evaluation.

High yield potential under stressed conditions, even with a relatively high drought susceptibility index (S) (Fisher and Maurer, 1978) has given superior performance under dry conditions. Edmeades *et al.*, 1989, have indicated that in wheat and corn the gains for selection apparently are due to changes in biomass partitioning rather than changes in plant water status or in tolerance of tissues to moisture deficits. However, this trend of improvement has biological limits, and subsequent improvements will require the improvement in water status under drought for further gains in biomass and grain yield. Further improvements through this method will require larger investments. Therefore, breeding for drought resistance must depart from the use of yield as the exclusive selection index (Blum, 1989).

Selection for yield under optimal conditions results in marked improvements under less optimal conditions. However, it could be possible that some traits which are yield positive under dry conditions, are neutral or even negative in their effect under optimal conditions which may result in their lost in breeding programs carried out under good conditions. One such trait is deep roots (Richards, 1982).

To combine yield potential with drought resistance may be difficult physiologically because of the trade-off between yield potential and resistance to stress (Fisher and Wood, 1979). However, this could be made possible when the susceptibility index is independent of yield potential (Fereres *et al.*, 1986).

Two analytical approaches can be distinguished, the deductive approach in which underlying causes of yield differences are sought and the approach based on the ideotype concept in which predictions are made of possible causes of yield differences based on a morpho-physiological design (Fisher, 1981). Acevedo and Ceccarelli (1989) have indicated that a practical approach to physiological breeding to improve drought resistance or yield under stress is forced to start from yield and move towards underlying processes.

The utilization of morphological and physiological adaptations require suitable screening methods. The major problem with many methods developed for the screening of these traits is that they are too slow and laborious for use in screening large plant populations. Some of the current screening techniques available to the breeder to use in the identification of drought tolerant plants are: 1) Multilocational testing; 2) Drought plots, with shelter screen; 3) Line source sprinkler system; 4) Use of slopes and drains in the field; 5) Greenhouse screening in pots or tubes; 6) testing through hydroponics and aeroponics methods, by creating varying levels of water stress. Each technique has limitations yet the first two are the most conventional and reliable. Other techniques are available for studying root pattern, canopy temperatures, leaf waxiness, and osmotic adjustment (Turner, 1981).

The ideotype approach has been analyzed using the general Passioura's (1977) framework, which has been considered suitable for the analysis of yield under drought (Richard, 1982, 1987, 1989; Blum, 1989; Ludlow and Muchow, 1990). Under this model yield of a grain crop can be analyzed as the product of three components: the amount of water used by the crop (transpiration), the efficiency with which the water is used in producing dry matter (the amount of dry matter produced per unit of water transpirated), and the harvest index (the proportion of dry matter that ends up in the grain) which depends on the amount of water used after anthesis (Passioura, 1977). Attributes of root may influence these components (Passioura, 1982). The Passioura's model in its basic form is:

$$\text{AGDM} = \text{T} \times \text{WUE}$$

Where AGDM, T, and WUE represent above ground dry matter, amount of water transpirated and water use efficiency, respectively. When the grain is the important economic product a partitioning component is introduced in the model and the expression becomes:

$$\text{Grain yield} = \text{T} \times \text{WUE} \times \text{HI}.$$

To assist in trait identification, each of these components can be further expanded (Richards, 1987, 1989). The model is useful when considering ways to increase yield by breeding because the components are largely independent of each other, thus improvement in any component should improve yield, and because the model focuses directly on the processes that affect productivity in dry environments, indiscriminate recommendation of selection criteria is avoided (Richards, 1987). The framework has been validated experimentally by Richards (1983) in wheat, who stressed the importance of the pre-anthesis water use, showing that kernel number is influenced most by pre-anthesis events, whereas kernel weight is influenced by events after anthesis. Richards (1982, 1987, 1989) and Ludlow and Muchow (1990) have analyzed the implications of the model for plant breeding and the possible components and traits that could be useful to consider.

The amount of water used by the crop can be increased by increasing the depth of rooting to increase the soil water extraction and also by the early vigor to increase early leaf cover of interrow leaf display to decrease surface water evaporation.

The most useful traits for water use efficiency would be those affecting the assimilation ratio by affecting photosynthesis and transpiration. These traits are likely to be under simpler genetic control. Thus any trait that influences the resistance to diffusion of carbon dioxide and water vapor, respiration rate, or energy loads on the leaf may influence the assimilation ratio. Some of these traits are: specific leaf weight and traits related with leaf morphology, such as pubescence and waxiness. These traits are controlled by single genes whose contrasting expression are easily identified. Other traits like leaf rolling, leaf size, leaf erectness and leaf movements, and stomatal sensitivity are less important, because, with the exception of erectness, they are more susceptible to environmental fluctuations and are more complex genetically.

Harvest index is perhaps the most important component of the model. Maximizing AGDM at maturity under water limited conditions is achieved by first maximizing its components i.e. water transpirated and water use efficiency, followed by maximizing grain yield. Since the latter is a function of the harvest index, ways to increase HI of water limited crops by genetic manipulations need to be considered. Three findings are relevant in this regard: 1. In cereal crops improving yield has been possible by the improvement of the HI rather than the improvement of dry matter (Austin *et al.*, 1978); 2. HI under good conditions is about 0.5, and under drought conditions is typically around 0.35 and often less. Thus a considerable amount of potential yield is not realized; 3. In dryland crops it is the balance between dry matter produced and hence water used before and after anthesis that it is important in determining HI (Passioura, 1977).

Ludlow and Muchow (1990) have concluded that the best prospects at the moment for improving yield of crops appears to be increasing the amount of water transpirated and maintaining harvest index, remarking that in plant breeding the interest is on how the plants survive drought and how traits influence yield by enhancing the determinants of survival through either escape or tolerance (dehydration avoidance or dehydration tolerance).

Blum (1988) has pointed out that no single drought resistance factor can indicate an advantage in plant productivity under stress, therefore, one solution is to apply multiple selection criteria for drought resistance to advanced-stage high-yielding populations (Blum, 1983). This approach is based on the assumptions that genetic variation for drought resistance exists within the population and that high yield potential is not negatively associated with the selection criteria involved. Alternatively, the importance of singular drought-adaptive traits should be established and quantified for a given agricultural ecosystem (Blum,1982).

Simpson (1981) has indicated conditions to be meet about the introduction of desirable traits into breeding programs such as : 1) The physiological response within the plant to a specific water stress at a specific stage must be accurately described; 2) A single physical parameter in the plant, easily monitored, that correlates highly with the observed physiological response must be identified; 3) Proof that sufficient genetic variability exists within a population for the specific parameter to warrant a plant selection program; 4) Establishment of a specific water stress that simulates the ultimate field conditions for crop growth under large scale laboratory or field conditions to elicit the parameter; and 5) Demonstration that selection for the physical response and its recombination with other characters does not have negative effects on such prime characters as yield, disease resistance, or quality of vegetative and seed products.

Austin (1989) has pointed out that while some traits may have optimum levels of expression that are very season and location specific (tillering and flowering time), others are likely to be beneficial under most conditions. Although selection for yield tends to concentrate and fix the relevant genes, individual genes will generally have only minor effects which are difficult and costly to assess experimentally (waxiness and leaf posture). Other traits may be adverse and/or exhibit compensatory pleiotropic effects (rate of photosynthesis vs leaf size, and stomatal size vs frequency) or useful genetic variation may not exist (e.g. for depth of rooting).

Determining the effort that should be applied to breeding morphological traits, Rasmusson (1987) has suggested that where enhanced yield potential is a major breeding goal the breeder might consider making 75% of the breeding effort traditional and 25 % trait oriented. Richards (1989) suggested that 30% of the breeding effort in a crop be physiologically oriented.

The utility of a particular trait as a selection criterion for drought resistance in a breeding program depends upon its heritability. Singh (1989) reviewed experimental results and found that the traits studied for heritability included leaf water potential, osmotic potential, relative water content, leaf diffusive conductance, osmotic adjustment, transpirational cooling and leaf moisture retention capacity. These studies indicated that the various component characters (water potential, osmotic potential, relative water content and diffusive conductance) have significant digenic interactions, but these are absent for osmotic adjustment and transpiration cooling. This suggests that osmotic adjustment and transpiration cooling are controlled by single genes and their component characters by two or more genes. In fact, the additive and dominance effects are interallelic in nature. Alternatively, the osmotic adjustment and transpirational cooling may be governed by a block of inter-linked genes, which may be behaving as if they were controlled by a single gene. Osmotic adjustment and moisture retention capacity have been reported under single gene control in wheat. Ludlow and Muchow (1990) reviewed experimental evidence and found that heritability estimates are known for traits such as matching phenology for water supply, photoperiod sensitivity, developmental plasticity, rooting depth and density, low root hydraulic conductance, leaf area maintenance, osmotic adjustment, reduced stomatal conductance, leaf reflectance and transpiration efficiency.

In dry beans the evidence about specific traits related to drought resistance that could aid in the selection process is incomplete, however phenological, physiological and morphological plant attributes have been either found or suggested to be related to yield under water limiting conditions. Studies carried out by Stocker (1974), Parsons and Howe (1983), Laing *et al.* (1983, 1984), Samper (1984), Ibarra (1985), Markhart (1985), Elizondo (1987), Mkandawire (1987), Acosta-Gallegos (1988), Acosta-Gallegos and Kohashi-Shibata (1989), Sponchiado *et al.* (1989) and White and Castillo (1989) have either found or suggested putative drought resistance related plant attributes, which are important in yield. Those are described in Table 1.1. The most frequently cited characteristics are: root traits, pod set, biomass at anthesis, leaf temperature and stomatal resistance, stomatal conductance and stomatal sensitivity. However, these traits have not been validated and their relationships with yield have not been proved experimentally.

No definitive information about the genetics and heritability of specific traits, screening techniques and breeding methods to guide a breeding program in dry beans is available, because most of the research conducted until now has been oriented toward either traditional empirical selection or the physiological approach which targets a single trait not always related to actual yield.

Table 1.1. Dry bean plant attributes suggested as drought resistance related traits.

TYPE OF TRAIT	ATTRIBUTE	ROLE
Phenological	Delayed Flowering	T, HI
	Seed Filling Period	T, HI
Morphological	Root	T, HI
	Vigor and Development	T
	Biomass at Anthesis	WUE, HI
	Stem Weight	HI
	Hypocotyl Diameter	T, HI
	Leaf Area Index	T, HI
	Pod Set	HI
Physiological	>Stomatal Resistance	T, WUE
	Stomatal Sensitivity	T, WUE
	Leaf Transpiration	T, WUE, HI
	Leaf Temperature	T, WUE, HI
	Osmotic Adjustment	T, WUE, HI
	Leaf Senescence	T, WUE
	Harvest Index	HI
	Seed Growth Rate	HI

T = Transpiration.
WUE = Water use efficiency.
HI = Harvest Index.

CHAPTER 2

IDENTIFICATION OF DROUGHT RESISTANCE RELATED TRAITS IN DRY BEANS (*Phaseolus vulgaris* L.).

INTRODUCTION

Insufficient water is one of the most important non-biotic factors causing seasonal fluctuations in yield and one of the main causes of low productivity in common bean around the world (Anonymous, 1988). Since bean plants are very sensitive to soil water conditions, both quality and yield can suffer greatly from even brief periods of water shortage (Wallace, 1980; Halterlein, 1983). In common beans, stress at flowering is particularly deleterious (Wallace, 1980). The development of genotypes that resist or are less susceptible to the effect of water stress is a practical and economical alternative to overcome the negative effects of drought on the potential productivity of the crop.

Drought resistance has been defined in different ways but for crop production an appropriate definition should not be characterized by physiological mechanisms but rather as a stability parameter which allows seed yield to be maintained despite imposed water stress. Thus, drought resistance may be defined as the percentage of reduction in yield between nonstressed and stressed conditions (Blum, 1973). Since yield under water limited conditions may be considered as a residual effect of high yield potential (Blum, 1988), the susceptibility of a genotype to water stress can be measured as a function of the reduction in yield. Therefore, from an agronomic perspective a drought resistance genotype would be one with high yield under nonstressed conditions and the lowest reduction in yield under water stress, as compared to a drought susceptible genotype which would exhibit high performance under nonstressed conditions but a large yield reduction under drought. Yield under drought may help to reduce the effect of the water stress but by itself is not a guarantee of an acceptable yield under nonstressed conditions.

Two estimates of drought resistance based on the yield reduction have been proposed: the susceptibility index and the geometric mean. The susceptibility index (S) was developed by Fisher and Maurer (1978) to separate the effects of yield potential from drought susceptibility itself. The geometric mean of yield performance under drought and nonstressed yield was used as an estimate of drought resistance by Samper (1984). In common beans genotypic differences in susceptibility index and geometric mean were found in studies conducted by Samper (1984), Mkandawire (1987) and Acosta-Gallegos (1988) and the importance and usefulness of these parameters as potential selection criteria have been recognized (Samper, 1984). However, the biological implications of these estimates of drought resistance, their relationships with yield and other plant characteristics, and their practical usefulness in a common bean breeding program for drought resistance have not been well studied and defined.

Despite the overwhelming importance of drought as a major constraint of crop productivity, there has been little progress in breeding for drought resistant cultivars. Selecting for drought resistance is difficult, as the response is complex and interactions with other abiotic and biotic factors occur. Moreover, plants have evolved a wide range of different response "strategies" to survive and reproduce in the face of water stress that occurs at various periods throughout the growth cycle of the crop. In addition, there are problems in obtaining a consistent response to environmental conditions which either simulate or represent realistic drought conditions in the field (Mc William, 1989; Ludlow and Muchow, 1990).

Breeding improved genotypes by selecting solely for seed yield under stress is difficult because absolute yield under stress is a poor estimate of drought resistance (Blum, 1982) and the low heritability of yield under drought leads to low selection efficiency (Austin, 1989). The application of empirical breeding methods, based on yield under drought *per se* as the main selection criteria, has permitted some limited progress in the development of improved cultivars with drought resistance. However breeding for drought resistance has been limited by at least three conditions: 1) Identification of specific parameters that represent the significant traits that collectively confer survival and productivity for each stage of the life cycle; 2) Establishment of a single practical method for screening and selection; and the 3) Development of routine, large scale methodology for creating defined and repeatable water stress in the environment to permit the screening of large populations (Simpson, 1981).

Empirical selection of genotypes with improved productivity under water stress has been the most important approach in breeding for drought resistance in dry beans. Direct selection for specific characteristics that confer or are related to drought resistance or yield under drought has not been used because such traits and their genetic control have not been adequately identified. Although drought resistant varieties have been developed through the empirical breeding method using yield as selection index, these methods are costly and require a large period of testing and evaluation. Additional improvements using yield as the selection criteria will require additional investments. Therefore, breeding for drought resistance must depart from the use of yield as the exclusive selection index in the future (Blum, 1989). The improvement of the empirical approach could be possible by applying physiological and morphological criteria for the identification of high yielding families (Paroda, 1986). Thus, breeding for drought resistance could be improved through the identification of traits regulating the mechanism of drought resistance and/or yield under drought.

If such traits are to be suitable in a breeding program they have to meet the following criteria over a range of environments, seasons and locations: 1) Higher heritability than yield and 2) A significant correlation with yield. In addition, they should be: 3) Causally correlated to yield and 4) Easy and rapid to measure (Austin, 1989). Non-destructive methods with possible replicated sampling rather than destructive ones would be preferred. In common beans several traits have been suggested as possible selection criteria and those characteristics that are related to yield under drought in this crop have been studied (Samper, 1984; Ibarra, 1985; Mkandawire, 1987; Acosta-Gallegos, 1988). Lacking however is definitive information about the genetics and heritability of specific traits, and about the screening techniques and breeding methods because most of the research conducted until now has been oriented towards either traditional empirical selection or the physiological approach which targets a single trait not always related to actual yield.

The present research was directed to study the biological and practical implications of drought resistance estimates and their relationships with yield potential and yield under drought; the genetic variability of morphological, phenological and physiological traits in common beans under normal and drought environments; and the relationships of those traits with either yield under drought, or productivity related traits, and drought resistance estimates.

The main objective of the research described in this chapter was specifically directed at the identification of morphological, phenological and physiological traits to assist breeding for drought resistance in dry bean. Traits related to drought resistance and yield under drought; that are non-destructive and easy to measure; and that exhibit sufficient genotypic variability are suitable for this purpose.

The basic hypothesis tested in this study was that drought resistance, defined as the lowest reduction in yield due to water stress, and yield under drought in dry bean (*Phaseolus vulgaris* L.) are associated with morphological, phenological and physiological traits; that these traits exhibit sufficient genetic variability and are practical enough to be integrated into a breeding program as selection criteria for drought resistance.

MATERIALS AND METHODS

Experimental Location

The experiments were carried out at the Crop Science Teaching and Research facility at Michigan State University located in East Lansing, MI., in a Capac fine-loamy soil (mixed, mesic, Glassoboric Hapludolfs) (USDA, Soil Conservation Service) during the summers of 1988 and 1990. The experiments were grown near and under a rainout shelter to study the performance of dry bean genotypes under nonstressed and drought environments, to evaluate their drought resistance.

Environmental Conditions

The climate in the area alternates between continental and semi-marine, depending on the meteorological conditions. The marine type is due to the influence of the Great Lakes and is governed by the force and direction of the wind. Without wind the weather becomes continental, with fluctuations in temperature, hot weather in summer and severe cold in winter. The winter cold lasts longer in the spring and the summer heat lasts longer in the fall. The average first occurrence of frost in the fall is September 30. Precipitation is fairly well distributed through the year; although, there is about 1 inch less per month in winter than in summer. The heavier rainfall amounts in summer occur during thunderstorms. The wettest months are May and June. Sunshine is abundant during the summer months.

Climatological data for the crop growing season for the years 1987 to 1990 are presented in Table 1A of the Appendix A. The precipitation from June to August for the years of evaluation, 1988 and 1990, was 199 and 216 mm, respectively. The precipitation from June to September was 345 and 312 mm for 1988 and 1990, respectively.

Soil moisture content was regularly monitored during the seed filling period after the application of the stress. In 1988 soil moisture content was recorded on dry weight basis. Soil samples were taken at four depths: 0 - 15, 16 - 30, 31 - 45 and 46 - 60 cm. Nine soil sampling measurements were collected, weighed and immediately placed into a oven at 120 °C for 48 h. The sampling period was between 32 to 99 days after planting. Soil moisture contents in percentage of fresh weight are shown in Table 2A.

In 1990, the soil moisture content was estimated by the Neutron-probe method using a Hydroprobe model 503DR. The Neutron Depth Moisture Gauge measures the sub-surface moisture in the soil by the use of a probe containing a source of high energy neutrons and a slow (thermal) neutron detector. The probe is lowered into a pre-drilled and cased hole (3.7 or 5.0 cm diameter). Hydrogen as present in the water in the soil slows down the detection of neutrons allowing measurement of water content (USDA, Soil Conservation Service). In the two experiments six sites were randomly chosen in each of two replications. At every site a 1m long transparent plastic tube was inserted. Seven readings at the depths of 30, 60 and 90 cm were taken in the period between 44 and 92 days after planting. Soil moisture records in percentage of volume are shown in Table 3A.

Germplasm Evaluated

Five genotypes were chosen for testing in 1988. They were selected for their known response to drought, their plant characteristics and their yield under drought in 1987. Seed yield, number of pods per plant, pod wall weight, leaf moisture retention capacity, growth habit, seed type and origin of the genotypes evaluated in 1987 are described in Table 4A of the Appendix A.

In 1988 the cultivars Sierra and Seafarer, the breeding line LEF2RB from Mexico, and the progeny accessions AC1028 and AC1022 selected for their performance under drought (Acosta-Gallegos, 1988) were tested under drought and nonstressed conditions.

In 1990 the genotypes Sierra, Seafarer, AC1022 and AC1028 and sixteen $F_{3\ 5}$ derived lines from two populations, chosen based on their yield performance under drought in 1989, were tested under drought and nonstressed environments (Table 2.1). The sources of lines were generated by crossing the cultivar Sierra with the genotypes AC1028 and LEF2RB, respectively designated as AS and LS populations. From each population four lines from each group classified as both high and low yielders were selected to be incorporated in this experiment. Special care was taken to choose different genetic families to incorporate as many different families as possible into the experiment. The availability of seed was an additional factor in the selection of families with poor seed yield.

Cultural Practices

The soil for planting was conditioned with a rototiller. The experiments were planted on June 17, 1990 and on June 21 and 25, 1988 for the drought and nonstressed treatments, respectively. The seed was hand planted, and supplementary irrigation was applied to assure even germination. In all the experiments an extra number of seeds were planted and the stand was adjusted to ten and twenty plants per square meter at seedling stage in 1988 and 1990,

Table 2.1 Origin and geneology of progenies, progenitors and check genotypes evaluated under drought and non-stress conditions. East Lansing, MI, 1990.

GENOTYPE	POPULATION SOURCE	PEDIGREE	DROUGHT PERFORMANCE[a]
AS-11	(AC-1028 x Sierra)	(3053-2) F3	Good
AS-6	" "	(3025-1) F3	Good
AS-3	" "	(3216-1) F3	Good
AS-1	" "	(3001-1) F3	Good
AS-104	" "	(3035-1) F3	Poor
AS-101	" "	(3027-2) F3	Poor
AS-102	" "	(3029-2) F3	Poor
AS-103	" "	(3031-1) F3	Poor
LS-7	(LEF2RB x Sierra)	(3135-1) F3	Good
LS-11	" "	(3152-2) F3	Good
LS-4	" "	(3116-1) F3	Good
LS-6	" "	(3120-1) F3	Good
LS-103	" "	(3125-2) F3	Poor
LS-102	" "	(3119-1) F3	Poor
LS-101	" "	(3114-2) F3	Poor
LS-104	" "	(3134-2) F3	Poor
Sierra	Parent		Good
LEF2RB[1]	Parent		Good
AC-1028[2]	Parent	41-39-M	Poor
AC-1022[3]	Check	8-42-M	Poor

1. (VER10/CHIs143)/Pue144
2. (UW21-58 x A411)
3. N81017 x LEF2RB

[a] Based on yield under drought.

respectively. In all the experiments, the experimental unit was a plot 1.0 m long with 50 cm distance between rows. Fertilizer was applied 10 cm to the side of the seeded row, using the equivalent of 250 kg per hectare of the formula 19-19-19. Weed control was manual. Pests, mostly leafhopper (*Empoasca spp.*) and Mexican bean beetle (*Epilachna varivestis* Mulsant), were controlled by applying Sevin, following commercial recommendations, once or twice as required during the vegetative stage.

Experimental Design

In each year of evaluation two experiments containing the same set of genotypes were grown under two treatments: drought and nonstressed control. The creation of the treatments was facilitated by growing the experiments in and near a rainout shelter with supplementary irrigation in the control experiment. Irrigation was applied every week during the driest period of the growing season when rainfall was inadequate. The drought condition was applied at 33 and 32 days after planting in 1988 and 1990, respectively. Water stress was initiated 12 and 17 days before average flowering in 1988 and 1990, respectively. The drought treatment was continued through the reproductive stage of development up to physiological maturity in both years of evaluation. In the drought environment water accumulation due to rainfall or dew was avoided by covering the experiment with the shelter during periods of rainfall and at night. Otherwise the experiment was uncovered during the day as long as the weather permitted.

In 1988 the five tested genotypes were planted in a completely randomized design inside the shelter while a completely randomized block design was used in the experiment planted outside the shelter, using six replications in both experiments. In 1990, the twenty genotypes were planted in a completely randomized block design with two replications in each of the two treatments of evaluation.

A combined analysis over treatments for each year was utilized (McIntosh, 1983). A random model was assumed for environments and genotypes according to Steel and Torrie(1980), Wricke and Weber(986) and Fehr(1987).

Variables under Study

Variables measured included yield and biomass components, partitioning indices, phenology, and water use and water relations characteristics in both years. A set of five supplementary traits was measured in 1990. The designation, units of measurement and stage of development when the sampling of the recorded variables was conducted are described in Table 2.2.

Data Recording

At physiological maturity, when 75% to 90% of the pods lost their green pigmentation and began to dry, a sample of four or five plants grown under full competition was taken from each plot. Every plant was dissected into various plant parts and the stem was cut at the base. All plant parts, except seeds, were oven-dried at 70^{o} C for at least 72h and the data for stem weight, pod wall weight, pods with seed, pods without seed, seeds per pod and seed size were obtained. Stem diameter was recorded in 1990 but not in 1988. The diameter of the stem was determined at the first lowest node of the stem by using a template of circles calibrated on a progressive scale to an approximation of 0.5 mm diameter. The data were recorded in all the replications in both years.

Partitioning variables such as harvest index, biomass growth rate, economic growth rate, seed growth rate and relative sink strength were estimated using the procedure and equations described in Table 2.3. The data were recorded in all the replications.

Water use variables were measured using the instrumentation and methodology described in Table 2.3. In 1988, four replications of both leaf surfaces were sampled at 41, 50, 55, 62 and 69 days after planting. In 1990, two

Table 2.2. Designation, units and stage of sampling of variables measured in experiments grown under drought and non-stressed conditions in 1988 and 1990. East Lansing, MI.

VARIABLE	DESIGNATION	UNITS	STAGE OF SAMPLING
Yield and Yield Components			
Yield	SY	g/plant	At maturity
Pods with Seed	PWS	#	" "
Pods w/o Seed	PWOS	#	" "
Total Number of Pods	PTN	#	" "
Seeds/pod	S/P	#	" "
Seed Number	SN	#	" "
Seed Size	SS	100 seed weight	" "
Biomass			
Stem Weight	STW	g/plant	At maturity
Pod Weight	PW	" "	" "
Total Biomass	TB	" "	" "
Partitioning			
Harvest Index	HI	----	At maturity
Biomass Growth Rate	BGR	g/day/plant	" "
Economic Growth Rate	EGR	g/day/plant	" "
Seed Growth Rate	SGR	g/day/plant	" "
Relative Sink Strength	RSS	----	" "

Table 2.2. (cont'd)...

VARIABLE	DESIGNATION	UNITS	STAGE OF SAMPLING
Phenology			
Days to Flower	DF	Days	At flowering
Days to Maturity	MAT	Days	At physiological maturity
Days of Seed Filling	DSF	Days	" "
Water Use			
Stomatal Conductance	SC	cm/s	Pod filling period (1)
Transpiration Rate	TR	mg$H_2$0/cm^2/s	" "
Leaf Temperature	LT	°C	" "
Water Relations			
Water Content	WC	%	Pod filling period (1)
Relative Water Content	RWC	%	" "
Water Potential	WP	MPa	" "
Leaf Moisture Retention Capacity	MRC	%	" "
Other Traits			
Leaf Orientation	LO	Visual estimation (2)	Vegetative and Pod filling period
Specific Leaf Weigth	SLW	mg/cm^2	Pod filling period
Leaf Size	LS	cm^2	" "
Leaf Area Index	LAI	-----	" "
Stem Diameter	SD	mm	At maturity
Leaf Retention	LR	g/plant	" "

(1) Between flowering and late pod filling
(2) Scale: 1.0 (Horizontal; 5.0 Vertical)

replications of the lower surface of the leaf was sampled at 39, 51 and 68 days after planting in the drought treatment, and at 47, 55 and 76 days after planting under nonstressed conditions. Three plants were sampled in all experiments.

Water content (WC), relative water content (RWC), leaf water potential (WP) and leaf moisture retention capacity (MRC) were obtained simultaneously following the procedure described in Table 2.3. Samples taken at 41, 50, 55, 62 and 69 days after planting in four replications were used in the analysis of 1988 results for WC, RWC, and WP, but the sample at 50 days was not used in the analysis of MRC. In 1990, the sampling dates for two replications were 39, 51 and 68 days after planting in the drought treatment, and at 47, 55 and 76 days after planting under nonstressed conditions.

The methods followed in 1990 to estimate specific leaf weight, leaf size and leaf area index are described in Table 2.3. The samples were taken from the two replications of both experiments, at 71 and 75 days after planting in the drought and control treatments, respectively.

Data Analysis

The data were analyzed using the MSTAT statistical package version C. Analysis of variance of individual variables for each drought treatment, combined analysis over drought treatments and linear correlations among the variables under study were the main statistical methods used for the analysis of the data.

F tests for the models used in this study were done following McIntosh (1984) and Steel and Torrie (1980). The LSD test at 0.05 level of probability was the multiple range test used to determine differences among genotypes.

RESULTS

The Effects of Drought

The effect of drought treatments, the differences between drought treatments, the proportion of reduction about the nonstressed treatment and the

Table 2.3. Instrumentation and methods for estimation of variables.

VARIABLE	METHOD
Harvest Index	HI is the ratio between economic yield and biological yield.
Biomass Growth Rate	BGR was calculated by dividing the seed yield by the number of days to physiological maturity.
Economic Growth Rate	EGR is the relation between the seed yield and the number of days to physiological maturity.
Seed Growth Rate	SGR is the seed yield divided by the number of days of the seed filling period.
Relative Sink Strength	RSS is the relation between seed growth rate and biomass growth rate. A seed growth rate higher than biomass growth rate suggests good translocation ability, strong sink strength, and/or that assimilates were remobilized during the reproductive phase. Genotypes with relative sink strength values equal or higher than 1.0 are regarded useful for the improvement of yield in common beans under non stressed conditions (Scully and Wallace, 1990).
Water Use Variables	These traits were measured using a steady state porometer (LiCor Inc., Lincoln, NE). The readings were performed on the uppermost young fully expanded leaf of each of three known plants in each plot at every day of sampling. The sampling were always conducted on clear days with high levels of sunlight and temperature, between the times of 11:00 AM and 2:00 PM.
Water Relation Variables	The four water relation variables were registered simultaneously in the same file sample. Young fully expanded leaves were taken from three known plants in each plot growing under full competition, at each sampling day. The samples were taken between 11:00 AM and 2:00 PM when the effect of stress was more evident. The samples were taken always in clear days with both high sunlight and temperature.

Table 2.3. (cont'd)...

VARIABLE	METHOD
Leaf Moisture Retention Capacity (MRC)	The leaves were detached from the plant, put in a sealed plastic bag and stored temporally in a portable cooler with ice. The field samples were taken to the Field Bean research facility to be processed as soon as possible, usually no longer than 1 or 2 h after the samples were taken in the field. The three leaflets of each sampled leaf were detached and used individually. A single leaflet was used as a sample in the estimation of each of the following variables: leaf moisture retention capacity (MRC), relative water content (RWC) and water content (WC), and water potential (WP). Therefore, all the measurements were performed on different leaflets of the same leaf. The method was used to avoid the use of leaves at different stages of development and relative position at the plant. MRC was determined by weighing each leaflet after field sampling to obtain the fresh weight (FW), the leaves where then placed in a closed room to dry for 24 h. After this period the leaves were weighed to get the air-dried weight (ADW). Then the leaflets were oven-dried for at least 72 h to get the oven-dried weight (ODW). Leaf moisture retention capacity was calculated using the following ratio: $\mathrm{MRC} = [\,(\mathrm{ADW}-\mathrm{ODW}) / (\mathrm{FW}-\mathrm{ODW})\,] \times 100$
Relative Water Content (RWC) and Water Content (WC)	RWC and WC were determined simultaneously on the same sampled leaflet as follows: each leaflet was weighed to obtain the fresh weight (FW), the leaflet was placed in a Petri dish and floated on distilled water. The leaflet was kept in water for at least 16 h but not longer than 24 h, under minimal illumination, to get the saturation of the tissue. The saturated weight (SW) was obtained and the leaflet was oven-dried to get the dry weight (DW). The weights were used for the calculation of both variables with the following equations: $\mathrm{RWC} = [\,(\mathrm{FW}-\mathrm{DW}) / (\mathrm{SW}-\mathrm{DW})\,] \times 100$ $\mathrm{WC} = [\,(\mathrm{FW}-\mathrm{DW}) / (\mathrm{DW})\,] \times 100$

Table 2.3. (cont'd)...

VARIABLE	METHOD
Water potential (WP)	WP was measured using a Leaf Press model J-14 (Decagon Devices, Inc.) that provides a rapid field estimates of the energy status of water in plant parts. The unit is a rugged, fast, accurate, simple to operate, and relatively inexpensive as compared to the Scholander 's pressure chamber. The press consist of a modified hydraulic jack, supplied with a pressure chamber at the top, wherein samples may be viewed through an acrylic window. The device is recommended for survey comparisons of the state of water stress in a community of plants. It was possible to determine water potential at a rate of one sample per minute in the experiments. Individual leaflets were used for the estimation of water potential.
Other Variables	The relative orientation of the leaves about the ground caused by paraheliotropic movements of the leaves was measured and called leaf orientation (LO). The orientation was estimated visually using a relative scale from 1.0 to 5.0. The value of 1.0 indicated a horizontal position of the leaf or minimum paraheliotropic movement. Values of 5.0 were for almost vertical leaf orientation of the leaves caused by a relative high paraheliotropic movements, similar to those observed in the cultivar Sierra. The leaf orientation estimation was estimated at the afternoon in days with sunshine and high temperature. The variable was recorded only in 1990 at two stages of development: vegetative and reproductive. Specific leaf weight (SLW), leaf size (LS) and leaf area index (LAI) were simultaneously estimated at mid-pod filing stage, at 75 DAP in the control experiment and 71 DAP in the drought environment. The variables were estimated in a sample of two plants, as follow: a sample of five leaflets from the uppest, the middle and the lowest levels of the stem were taken from each plant. The leaf area of ten leaflets was estimated using a leaf area meter (LI-3000, LICOR Instruments, Lincoln, NE). The dry weight was obtained by oven-drying the leaflets for at least 72 h at 70°C . Simultaneously, the remained leaflets of each sampling were removed and oven-dried. The total leaf area was estimated based on the weight and leaf area of the sample of each level. Specific leaf weight was calculated by dividing the dry weight of the leaflets by the leaf area. Leaf size was calculated as the average of the area of the leaflets. Leaf area index was calculated dividing the estimated total leaf area by the area occupied by the plants.

statistical significance of the difference between treatments for the morphological, physiological and phenological characteristics evaluated in this study are summarized in Tables 2.4 and 2.5, for the experiments carried out in 1988 and 1990, respectively.

The drought intensities (Fisher and Maurer, 1978) were 78% and 63% in 1988 and 1990, respectively, and the soil water content was lower in 1988 than in 1990 (Tables 2A and 3A). Rainfall avoidance at the water stress treatment lowered the content of water in the soil. In 1988, the soil water content after flowering in the drought treatment was 63, 50 and 37% less than in the nonstressed environment, at 0 - 15, 16 - 30 and 31 - 45 cm depths, respectively. In 1990, for the same growth period, the reduction in water content in the drought treatment compared to the nonstressed treatment was 50 and 20%, at depths of 0 - 30 and 31 - 60 cm. The soil water content in both years was slightly higher in the drought treatment than in the non-stress treatment in deeper soil layers, at 46-60 cm in 1988 and 90 cm in 1990.

The water stress applied in the drought treatment by the reduction in soil water content applied at the reproductive stage of development (Tables 2 and 3 of the Appendix A), lowered the expression of most of the variables evaluated in this study in both years. However, the number of pods without seed, days to flowering, leaf temperature and leaf moisture retention capacity increased their expression under drought conditions. The differences between treatments were more evident in the 1988 experiments.

Despite the differences in the levels of water stress attained in both years, most of the variables responded similarly to the condition of drought. Thus, the correlation between the responses in both years was significant and positive (r=0.88) regardless of the level of stress applied or number of genotypes evaluated.

Table 2.4. Effect of drought on yield, yield components, biomass, partitioning, phenology, water use, and water relations of five dry beans genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

CHARACTERISTICS	TREATMENT		DIFFERENCE	REDUCTION (%)
	Drought	Non-Stress		
YIELD AND YIELD COMPONENTS				
Yield (SY)	9.29	41.66	32.37***	78
Pods With Seed (PWS)	16.90	39.37	22.47***	57
Pods w/o Seed (PWOS)	4.93	3.93	-1.00 NS	-20
Total Number of Pods (PTN)	21.90	43.17	21.27**	49
Seeds/Pod (S/P)	2.54	3.91	1.37***	35
Seed Number (SN)	41	157	116***	74
Seed Size (SS)	21.88	28.73	6.85***	24
BIOMASS				
Stem Weight (STW)	7.52	15.53	8.01**	52
Pod Weight (PW)	4.02	11.99	7.97**	66
Total Biomass (TB)	20.83	69.22	48.39***	70
PARTITIONING				
Harvest Index (HI)	0.42	0.60	0.18***	30
Biomass Growth Rate (BGR)	0.24	0.66	0.42***	63
Economic Growth Rate (EGR)	0.11	0.41	0.30***	73
Seed Growth Rate (SGR)	0.24	0.74	0.50***	68
Relative Sink Strength (RSS)	0.90	1.09	0.19***	17

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

Table 2.4. (cont'd)...

CHARACTERISTICS	TREATMENT		DIFFERENCE	REDUCTION (%)
	Drought	Non-Stress		
PHENOLOGY				
Days to Flower (DF)	45.13	43.83	-1.30*	-3
Days to Maturity (MAT)	87	104	17**	16
Days of Seed Filling (DSF)	42	60	18***	30
WATER USE				
Stomatal Conductance				
Abaxial (SCAB)[1]	0.69	1.28	0.59***	46
Adaxial (SCAD)[1]	0.23	0.54	0.31***	58
Total (SC)[1]	0.92	1.82	0.90***	49
Abaxial % (ABC%)	76.82	70.80	-6.02***	-9
Adaxial % (ADC%)	23.18	29.20	6.02**	21
Transpiration (TR)[2]	8.72	12.50	3.78**	30
Leaf Temperature (LT)[3]	30.63	29.13	-1.50**	-5
WATER RELATIONS				
Water Content (WC)[4]	79.45	79.97	0.52 NS	1
Relative Water Content (RWC)[4]	74.71	77.86	3.15**	4
Water Potential (WP)[5]	-0.77	-0.58	-0.19**	33
Moisture Retention Capacity (MRC)[4]	27.28	15.02	-12.26***	-82

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

1. cm/s
2. mg $H_2O/cm^2/s$
3. °C
4. Percentage
5. MPa

Table 2.5. Effect of drought on yield, yield components, biomass, partitioning, phenology, water use and relations of twenty dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1990.

CHARACTERISTICS	TREATMENT		DIFFERENCE	REDUCTION (%)
	Drought	Non-Stress		
YIELD AND YIELD COMPONENTS				
Yield (SY)	7.36	19.63	12.02***	63
Pods With Seed (PWS)	6.70	17.58	10.88***	62
Pods w/o Seed (PWOS)	2.85	1.90	-0.95 NS	-33
Total Number of Pods (PTN)	9.55	19.48	9.93**	51
Seeds/Pod (S/P)	4.30	4.30	0.00 NS	0
Seed Number (SN)	29.10	76.33	47.23**	62
Seed Size (SS)	25.57	26.10	0.53 NS	2
BIOMASS				
Stem Weight (STW)	4.34	7.91	3.57**	45
Pod Weight (PW)	2.04	5.12	3.08**	60
Total Biomass (TB)	13.74	32.67	18.93***	58
PARTITIONING				
Harvest Index (HI)	0.53	0.58	0.06 NS	10
Biomass Growth Rate (BGR)	0.16	0.34	0.18	53
Economic Growth Rate (EGR)	0.09	0.20	0.12***	57
Seed Growth Rate (SGR)	0.21	0.40	0.19***	48
Relative Sink Strength (RSS)	1.24	1.14	-0.10 NS	-9

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 2.5. (cont'd)...

CHARACTERISTICS	TREATMENT Drought	 Non-Stress	DIFFERENCE	REDUCTION (%)
PHENOLOGY				
Days to Flower (DF)	48.51	46.91	-1.60*	-3
Days to Maturity (MAT)	86.43	96.95	10.52**	11
Days of Seed Filling (DSF)	37.92	50.05	12.13**	24
WATER USE				
Stomatal Conductance (SC)^1	1.51	2.00	0.49 NS	23
Transpiration Rate (TR)^2	10.98	16.33	5.35*	33
Leaf Temperature (LT)^3	26.13	25.19	-0.94**	-4
WATER RELATIONS				
Water Content (WC)^4	83.70	84.18	0.47 NS	1
Relative Water Content (RWC)^4	78.71	81.55	2.84*	1
Water Potential (WP)^5	-0.66	-0.64	-0.02 NS	3
Moisture Retention Capacity (MRC)^4	8.86	6.70	-2.16 NS	-24
OTHER TRAITS				
Leaf Orientation (LO)	3.74	3.38	-0.36 NS	-10
Specific Leaf Weight (SLW)	2.51	2.96	-0.45 NS	15
Leaf Size (LS)^6	30.11	37.73	7.62*	25
Leaf Area Index (LAI)	3.70	5.29	1.59 NS	30
Stem Diameter (SD)	4.17	5.14	0.97**	19

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

1. cm/s
2. mg $H_2O/cm^2/s$
3. °C
4. %
5. Percentage
6. cm^2

Among the groups of variables classified, yield components, partitioning indices and water use variables were the most affected by stress. Within groups, the variables with the greatest negative response were seed yield, number of pods with seed, total number of seeds, pod weight, total biomass, biomass growth rate, days of seed fill, stomatal conductance, transpiration rate, leaf size and leaf area index.

The least affected variables were number of seeds per pod, seed size, stem weight, harvest index, relative sink strength, days to flowering, days to physiological maturity, leaf temperature, water content, relative water content, leaf orientation, specific leaf weight and stem diameter.

In addition to the differences between drought treatments, differential genotypic responses due to the different drought treatments were found. The significance of the differences, expressed as percent of reduction, for variables with significant G x E interaction, in each of the two years, are presented in Tables 2.6, 2.7, 2.8 and 2.9. Two patterns of differential genotypic responses were identified. The most generalized response was a differential reduction within the expression for all the genotypes, for yield components. In another set of variables, the differential responses were demonstrated either by a reduction or an increase in each genotype for relative water content, leaf moisture retention capacity and percentage of stomatal conductance in upper leaf surface in 1988 (Table 2.8), and seed growth rate, leaf temperature, water potential and leaf size in 1990 (Table 2.9). Seed yield, total number of pods, stem weight and total biomass behaved similarly in both years in their genotypic expression caused by the drought treatment.

A consistent differential behavior between genotypes with both lower and higher yield reduction was evident in 1988. The genotypes Sierra, LEF2RB and Seafarer showed different responses to those observed in genotypes AC1022

Table 2.6. Significance of differences, as percentage of reduction, between non-stressed and drought treatments for yield and biomass components in five genotypes. East Lansing, MI, 1988.

GENOTYPE	R (1)	YIELD %	PODS W/ SEED %	TOTAL POD NUMBER %	SEED NUMBER %	SEEDS PER POD %	STEM WEIGHT %	TOTAL BIOMASS %
Sierra	1	60**	24**	17	50**	34**	38**	52**
LEF2RB	2	77**	54**	42**	68**	32**	46**	69**
AC-1028	3	86**	70**	62**	82**	41**	59**	78**
AC-1022	4	84**	67**	59**	79**	36**	57**	76**
Seafarer	5	78**	73**	53**	72**	32**	46**	68**

Level of Significance: 0.10(*); 0.05(**); 0.01(***) for the differerence between non-stress and drought environments.
1. Ranking based on yield under drought.

Table 2.7. Significances of differences, as percentage of reduction, between non-stressed and drought treatments for partitioning indices and phenological traits in five genotypes. East Lansing, MI, 1988.

GENOTYPE	R (1)	ECONOMIC GROWTH RATE %	SEED GROWTH RATE %	BIOMASS GROWTH RATE %	MATURITY %	DAYS OF SEED FILLING %
Sierra	1	57**	50*	48**	5	16
LEF2RB	2	72**	67*	63**	17**	34*
AC-1028	3	82**	79*	73**	21**	35*
AC-1022	4	79**	75*	66**	25**	38*
Seafarer	5	76**	72*	65**	9	23*

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
1. Ranking based on yield under drought.

Table 2.8. Significance of differences as percentages of reduction, between non-stressed and drought treatments for water status and water use traits in five genotypes. East Lansing, MI, 1988.

GENOTYPE	R (1)	RELATIVE WATER CONTENT	MOISTURE RETENTION CAPACITY	STOMATAL CONDUCTANCE % (2)
Sierra	1	5*	-68**	-11*
LEF2RB	2	6*	-77**	-11*
AC-1028	3	1	-119*	-6*
AC-1022	4	2	-37**	-14*
Seafarer	5	6*	-131**	-2

Level of Significance: 0.10(*); 0.05(**); 0.01(***)
1. Ranking based on yield under drought.
2. Stomatal conductance above in percentage about the total stomatal conductance.

Table 2.9. Significances of differences, expressed as percentages of reduction, between non-stressed and drought treatments for yield and biomass components, and morphological and physiological characteristics of twenty genotypes. East Lansing, MI, 1990.

GENOTYPE	R (1)	YIELD %	PTN %	SN %	STW %	PW %	TB %	SGR %	LT %	WP %	LS %
LS4	1	53*	49*	57*	51**	48**	52**	39**	-2	-4	-10
LS7	2	50*	45*	52*	43	37	34	30	-2	-10**	18
LEF2RB	3	49*	38*	43*	51	45**	49**	12	-2	-7**	31**
Sierra	4	59*	46*	51*	42	59**	55**	39*	-3	-5	-10
AS3	5	45*	54*	58*	47**	64**	49**	42*	-3	-3	14
LS103	6	56*	49*	54*	44	70**	55**	45*	-4*	3	-3
AS102	7	63*	68*	68*	41	63**	58**	56*	1	3	23**
AS6	8	69*	61*	68*	56**	64**	65**	59*	-7*	-5	31**
LS6	9	60*	46*	60*	37	53**	54**	52*	-6*	-5	32**
LS102	10	29	23	21	40	20	30	-39	-1	0	19
AC-1022	11	72*	69*	72*	51**	71**	67**	66*	-2	-8	8
AS11	12	63*	63*	64*	60**	64**	63**	45*	-5*	1	37**
AS101	13	69*	71*	65*	64**	72**	68**	58*	-2	-2	29**
AC-1028	14	72*	63*	73*	11	72**	56**	68*	-5*	-3	30**
LS11	15	51*	22	43	28	40	44	27	-8*	-9	44**
AS1	16	77*	48	75*	52**	70**	71**	75*	-5*	1	19
LS101	17	74*	60*	73*	55**	49**	66**	63*	-6*	-1	10
AS104	18	72*	63*	66*	60**	69**	66**	62*	0	5	8
LS104	19	78*	0	72*	2	58**	61**	66*	-8*	-6**	21**
AS103	20	34	23	43	17	57	32	24	-3*	-4	23**

Level of significance: 0.10(*); 0.05(**); 0.01(***).

1. Ranking based on yield under drought

PTN: Total number of Pods
SN: Seed Number
STW: Stem Weight
PW: Pod Weight
TB: Total Biomass

SGR: Seed Growht Rate
LT: Leaf Temperature
WP: Water Potential
LS: Leaf Size

and AC1028 (Tables 2.6, 2.7 and 2.8). In 1990, lines LS102, LS11 and AS103 (Table 2.9) had the lowest yield reduction caused by drought and also the lowest susceptibility index. These lines did not show significant genotypic differential responses for most of the variables. In general, the genotypes with the lowest yield reduction in yield also have the lowest increase in leaf temperature

Variability in Yield

The results of both years indicated substantial variability among genotypes both in their yield response to drought and in their yield potential estimated as the yield performance under nonstressed conditions (Figures 1, 2a and 2b, and Tables 2.29 and 2.30).

Yield under drought varied from 23 to 40% of the potential yield in the 1988 experiment and from 22 to 71% in the 1990 experiment. Yield potential was variable, ranging from 27.7 to 55.5 g/plant in 1988 and from 3.2 to 26.9 g/plant in 1990. Differences between treatments were observed in both years.

Significant differential genotypic responses due to drought treatments were detected in both years (Tables 2.6 and 2.9). The best genotypes exhibited the highest yield under drought combined with medium susceptibility index, usually lower than 1.0 but higher than 0.7 (Tables 2.29 and 2.30). Although the lines LS102, LS11 and AS103 did show the lowest susceptibility index, indicating the highest drought resistance, they had from medium to poor yield under drought (Table 2.30).

In both years the genotypes Sierra and LEF2RB showed high yield under drought and also good yield under non stressed conditions. AC1022 and AC1028, two genotypes selected by their favorable response to drought (Acosta-Gallegos, 1988), showed a relative poor yield under drought but a high yield under nonstressed conditions. This behavior affected the value of geometric mean as a combined indicator of yield under stress/non-stress treatments.

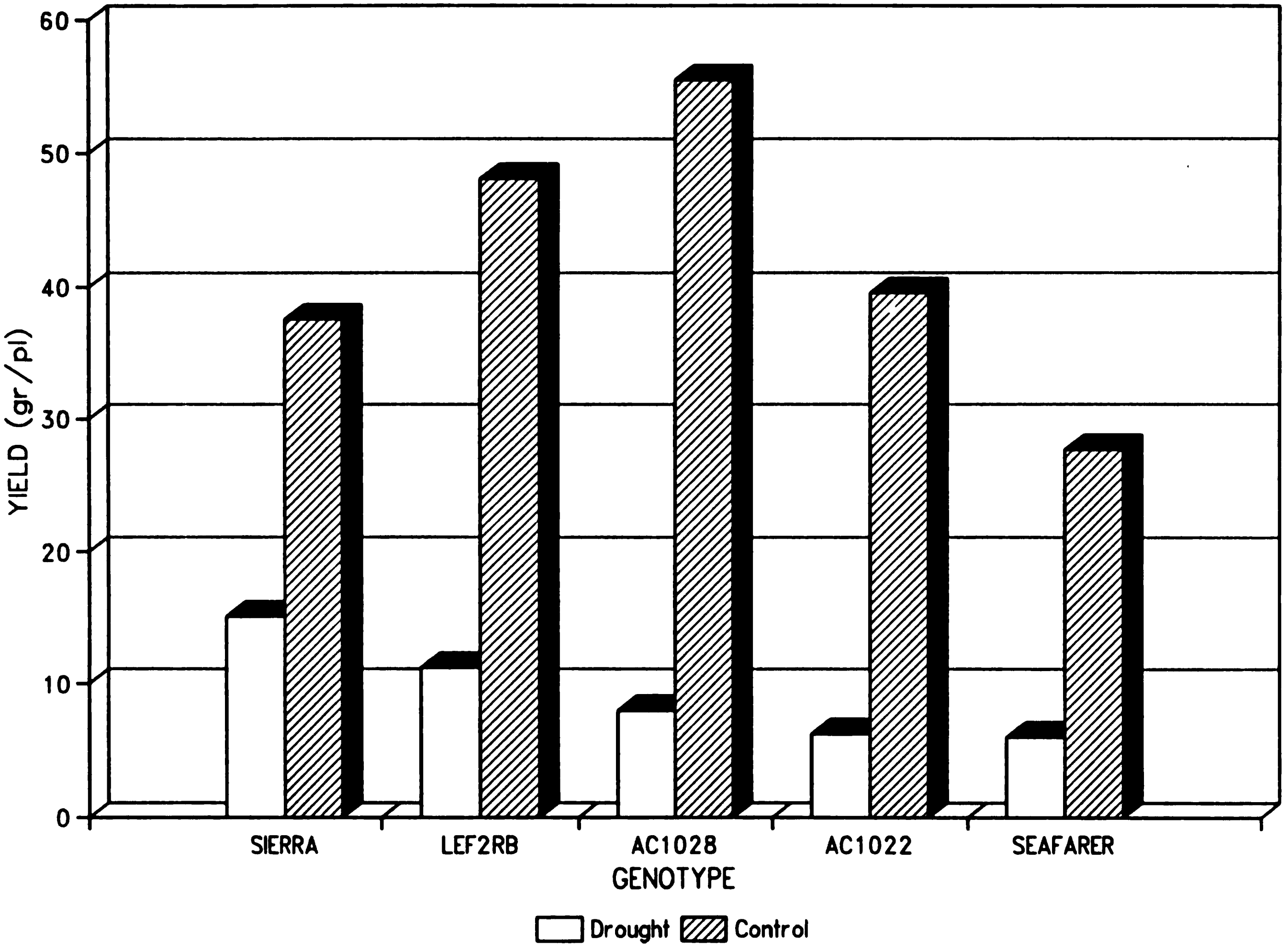

Figure 1. Yield of genotypes grown under drought and non-stress conditions in 1988.

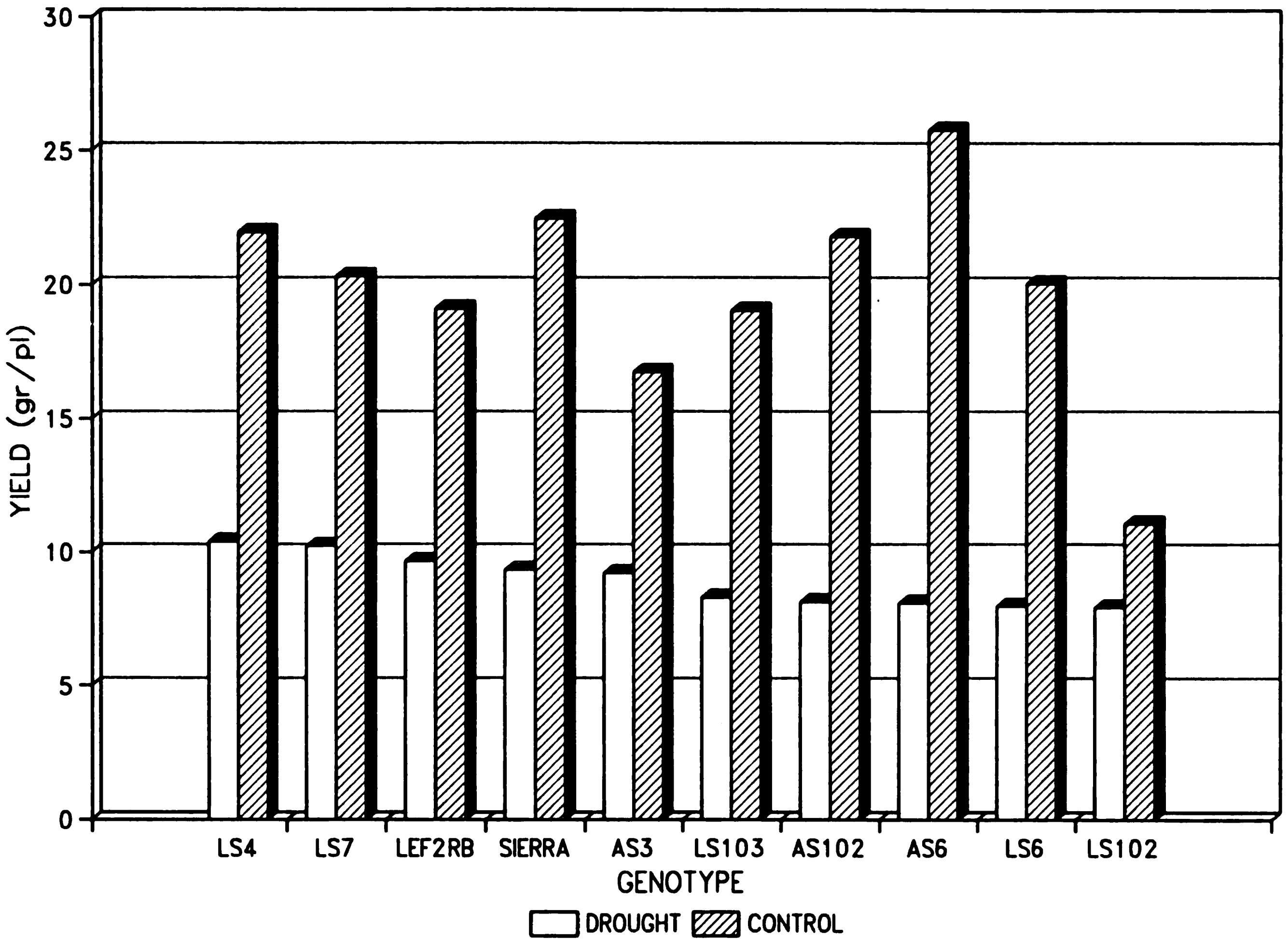

Figure 2a. Yield of genotypes grown under drought and non-stress conditions in 1990.

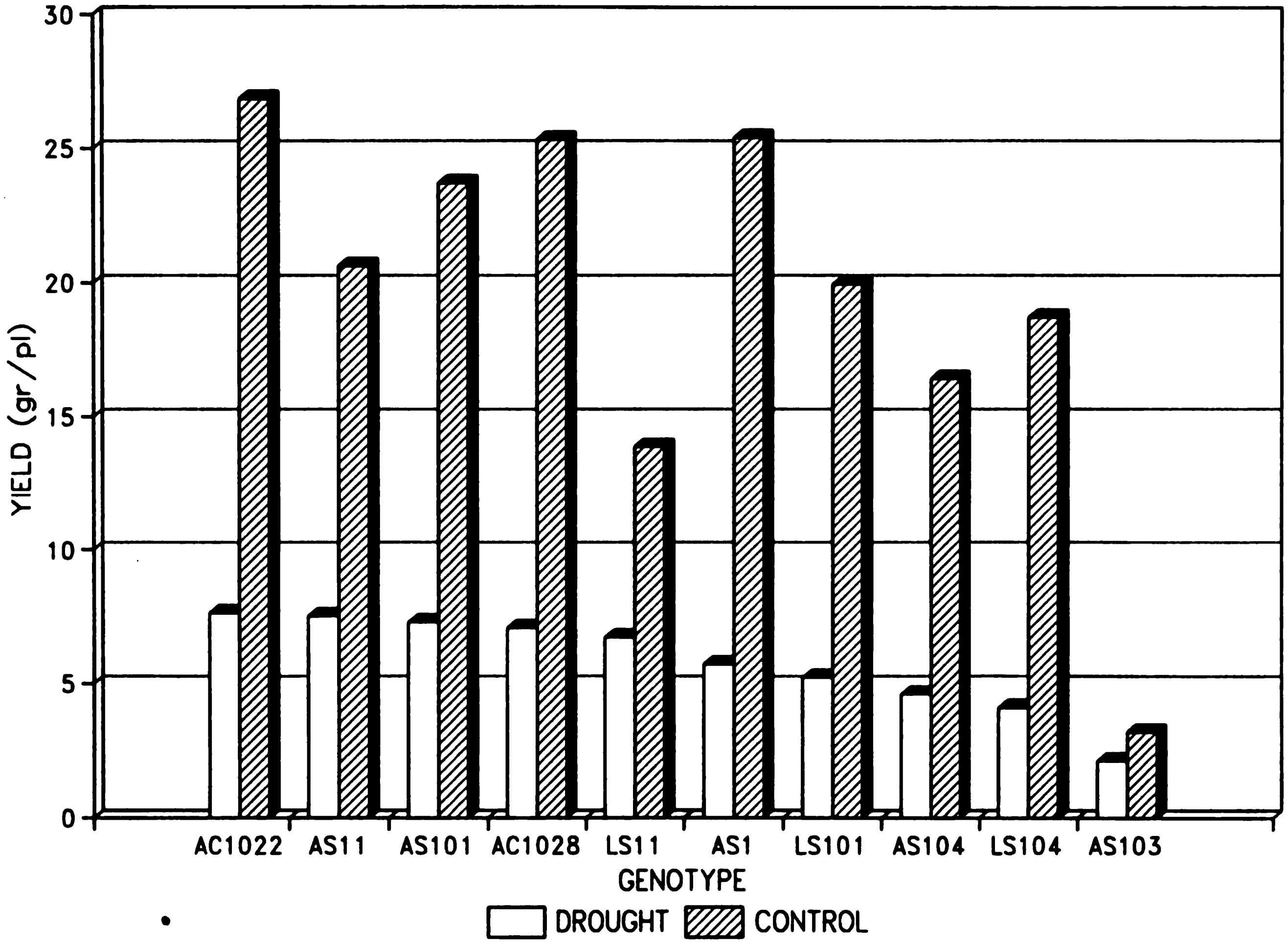

Figure 2b. Yield of genotypes grown under drought and non-stress conditions in 1990.

Variability in Yield Components

Significant differences among genotypes in the number of pods with seed, total number of pods, seed size, and number of seeds per pod were detected in both treatments in the 1988 experiment. Differences among genotypes were only detected in the number of pods without seed and number of seeds under nonstressed conditions (Tables 2.10a and 2.10b).

Significant differences among genotypes in both drought treatments were observed for seed size in the 1990 experiment. Under nonstressed conditions the variables, seed number, seeds per pod, number of pods with seed and total number of pods displayed statistical significances (Tables 2.11 and 2.12). The lowest differences in yield components were observed in genotypes with the lowest yield reduction and these genotypes also had the lowest susceptibility index in both years.

Differential genotypic responses to the drought treatments are shown in Tables 2.6 through 2.9. These responses were detected in the total number of pods and number of seeds in both years, and in the number of pods with seed and number of seeds per pod in 1988.

Variability in Partitioning Indices

Tables 2.13a, 2.13b, 2.14 and 2.15 contain the genotypic responses under drought and nonstressed conditions of partitioning variables such as harvest index, economic growth rate, seed growth rate, relative sink strength and biomass growth rate in 1988 and 1990.

Considerable genotypic variation in all the indices was detected and significant statistical differences were found for most of the indices in both years of evaluation. Only harvest index under drought conditions in 1990 did not show statistical significant differences among genotypes, despite the appreciable numerical differences in this variable, which ranged from 0.36, in the line AC1028,

Table 2.10 a, b. Significance of average yield components measured on five genotypes grown under drought and non-stress treatments. East Lansing, MI, 1988.

(a)

GENOTYPE	PODS WITH SEED+		PODS W/O SEED+		TOTAL NUMBER OF PODS+	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	22.50 A	29.50 C	2.66	1.50 C	25.50 A	30.83 C
LEF2RB	17.50 BC	37.67 BC	5.55	2.00 BC	22.83 AB	39.33 BC
AC-1028	14.00 CD	47.00 A	5.83	5.83 A	19.83 BC	52.33 A
AC-1022	12.67 D	38.50 AB	5.16	4.50 AB	17.83 BC	43.50 AB
Seafarer	18.00 B	44.17 AB	5.50	5.83 A	23.50 AB	49.83 A
Mean (a)	16.90	39.37***	4.93*	3.93	21.29	43.17**
CV (%)	19.8	18.6	59.3	58.6	17.0	17.7
Significance (b)	***	***	NS	***	**	***
LSD 0.05	3.98	8.83	---	2.78	4.42	9.22

Levels of significance: 0.10(*); 0.05 (**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05

LSD (0.05) for genotype x drought treatmentt interaction: pods with seed = 6.34, total number of pods = 6.79.

a. Asterisks indicate significances between drought treatments.

b. Significance among genotypes within drought treatments.

Table 2.10b. (cont'd)...

(b)

GENOTYPE	SEED SIZE (1)$^+$		SEED NUMBER$^+$		SEEDS/POD$^+$	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	34.83 A	44.83 A	42	84 C	1.90 B	2.87 C
LEF2RB	22.56 B	31.33 B	50	158 B	2.87 A	4.19 B
AC-1028	20.50 BC	25.67 C	39	219 A	2.74 A	4.60 AB
AC-1022	16.33 CD	22.00 D	38	181 AB	3.01 A	4.68 A
Seafarer	15.20 D	19.83 D	40	142 B	2.19 B	3.22 C
Mean (a)	21.88	28.73***	41	157***	2.54	3.91***
CV (%)	19.9	6.3	23.5	25.0	14.3	9.7
Significance (b)	***	***	NS	***	***	***
LSD 0.05	5.18	2.17	----	47.20	0.43	0.45

Levels of significance: 0.10(*); 0.05 (**); 0.01(***).
+. In each column any two means with a common letter ane not significantly different by LSD Test at α =0.05.
LSD (0.05) for genotype x drought treatment interaction: seed number = 33.06, seeds per pod = 0.43.
a. Asterisks indicate significances between drought treatments.
b. Significance among genotypes within drought treatments.
(1) Weight of 100 seeds.

Table 2.11. Significance of average pods with seed and total number of pods of twenty dry bean genotypes evaluated under drought and non-stress conditions. East Lansing, MI, 1990.

GENOTYPE		PODS WITH SEED[+]		TOTAL NUMBER OF PODS[+]	
	R(1)	Drought	Non-Stress	Drought	Non-Stress
LS4	1	8.5	21.0 AB	12.5	24.5 AB
LS7	2	8.5	17.0 BCD	10.5	19.0 ABC
LEF2RB	3	9.0	16.5 BCD	11.5	18.5 ABC
Sierra	4	7.5	16.5 BCD	10.0	18.5 ABC
AS3	5	7.0	17.5 ABCD	9.0	19.5 ABC
LS103	6	8.5	19.0 ABCD	11.0	21.5 ABC
AS102	7	6.0	17.5 ABCD	6.0	19.0 ABC
AS6	8	6.0	17.0 BCD	7.0	18.0 BC
LS6	9	6.5	16.0 BCD	9.5	17.5 BC
LS102	10	7.0	10.5 DE	10.0	13.0 CD
AC-1022	11	8.0	26.0 A	8.5	27.5 A
AS11	12	7.0	21.0 AB	8.5	23.0 AB
AS101	13	6.0	22.5 AB	7.0	24.5 AB
AC-1028	14	7.0	24.0 AB	9.5	26.0 AB
LS11	15	6.5	11.5 CDE	10.5	13.5 CD
AS1	16	6.0	19.5 ABC	10.5	20.0 ABC
LS101	17	5.0	16.0 BCD	7.0	17.5 BC
AS104	18	7.5	21.5 AB	8.5	23.0 AB
LS104	19	5.0	17.0 BCD	19.0	19.0 ABC
AS103	20	1.5	4.0 E	5.0	6.5 D
Mean (2)		6.7	17.6***	9.6	19.5**
CV (%)		30.8	23.9	37.0	22.4
SS(3)		NS	**	NS	**
LSD 0.05		-----	8.8	-----	9.2

Level of statistical significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.

LSD (0.10) for genotype x drought treatment interaction : total number of pods = 6.69.

1. Yield under drought ranking.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

Table 2.12. Significance of averages of seed traits of twenty dry bean genotypes grown under drought and non-stress treatments. East Lansing, MI, 1990.

GENOTYPE		SEED NUMBER^{+}		SEED SIZE^{+a}		SEEDS PER POD^{+}	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	38.0	88.0 BCD	27.6 ABCD	25.6 BCDE	4.7	4.2 CDEFG
LS7	2	39.0	81.5 BCD	26.2 ABCDE	24.7 BCDEF	4.6	4.8 ABCDE
LEF2RB	3	45.0	79.0 BCD	21.4 CDEF	24.0 CDEF	5.0	4.8 ABCDE
Sierra	4	32.0	65.5 BCD	28.9 ABC	34.0 A	4.3	4.0 EFGH
AS3	5	31.0	73.0 BCD	29.5 AB	18.8 FG	4.4	4.1 CDEFG
LS103	6	31.5	68.0 BCD	26.8 ABCD	28.6 ABCD	3.7	3.6 GHI
AS102	7	26.0	80.5 BCD	31.1 A	26.7 BCDE	4.7	4.5 BCDE
AS6	8	28.0	88.0 BCD	29.2 ABC	27.7 BCD	4.8	5.2 AB
LS6	9	26.5	65.5 BCD	29.5 AB	30.6 AB	4.1	4.1 DEFGH
LS102	10	33.0	42.0 DE	23.7 ABCDEF	28.2 ABCD	4.8	4.0 EFGH
AC-1022	11	41.5	148.5 A	19.0 EF	17.8 G	5.2	5.6 A

Table 2.12. (cont'd)...

GENOTYPE		SEED NUMBER^{+}		SEED SIZE^{+a}		SEEDS PER POD^{+}	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
AS11	12	24.5	68.5 BCD	30.3 A	30.0 AB	3.5	3.3 HI
AS101	13	26.0	74.0 BCD	28.4 ABC	30.5 AB	4.3	3.4 GHI
AC-1028	14	30.5	112.0 AB	22.4 BCDEF	28.8 DEFG	4.3	4.7 BCDE
LS11	15	32.5	57.5 CDE	20.35 DEF	24.0 CDEF	5.0	5.0 ABC
AS1	16	22.5	91.0 BC	23.7 ABCDEF	28.3 ABCD	3.7	4.6 BCDE
LS101	17	21.0	79.0 BCD	25.3 ABCDEF	26.0 BCDE	4.3	4.9 ABCD
AS104	18	26.0	77.5 BCD	18.3 F	21.0 EFG	3.5	3.6 FGHI
LS104	19	21.0	76.0 BCD	20.8 DEF	23.6 CDEFG	3.4	4.5 BCDEF
AS103	20	6.5	11.5 E	20.8 ABC	29.0 ABC	4.5	2.9 I
Mean (2)		29.1	76.3 **	25.6	26.1 NS	4.3 NS	4.3
CV (%)		32.4	30.0	14.1	10.9	18.0	9.6
SS (3)		NS	**	**	***	NS	***
LSD 0.05		----	48.0	7.5	6.0	----	0.9

Levels of statistical significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.

LSD (0.10) for genotype x drought treatment interaction: seed number 29.5.

1. Yield under drought ranking
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

a. Weight of 100 seeds.

Table 2.13 a, b. Significance of averages of partitioning related traits of five dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

(a)

GENOTYPE	HARVEST INDEX (HI)$^{+}$		ECONOMIC GROWTH RATE (EGR)$^{+a}$		SEED GROWTH RATE (SGR)$^{+a}$	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	0.51 A	0.63 B	0.18 A	0.41 BC	0.38 A	0.77 ABC
LEF2RB	0.49 A	0.68 A	0.14 A	0.52 A	0.34 A	1.01 A
AC-1028	0.35 B	0.55 C	0.08 B	0.44 AB	0.16 B	0.78 AB
AC-1022	0.34 B	0.54 C	0.07 C	0.32 C	0.13 B	0.51 BC
Seafarer	0.42 AB	0.61 B	0.08 B	0.34 C	0.18 B	0.64 BC
Mean	0.42	0.60***	0.11	0.40***	0.24	0.74***
CV %	20.80	4.87	37.34	21.19	40.90	28.46
Significance	***	***	***	***	***	***
LSD 0.05	0.11	0.04	0.05	0.10	0.11	0.25

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.
LSD for genotype x drought treatment interaction: economic growth rate (0.05) = 0.08, seed growth rate (0.10) = 0.15.
1. Asterisks indicate significance between environments.
2. Significance among genotypes within drought treatments.
a. grams/day

Table 2.13b. (cont'd)...

(b)

GENOTYPE	BIOMASS GROWTH RATE (BGR)$^{+a}$		RELATIVE SINK STRENGTH (RSS)$^{+}$	
	Drought	Non-Stress	Drought	Non-Stress
Sierra	0.34 A	0.65 BC	1.08 A	1.18 A
LEF2RB	0.28 AB	0.77 AB	1.15 A	1.30 A
AC-1028	0.22 BC	0.80 A	0.71 B	0.96 B
AC-1022	0.18 C	0.53 C	0.65 C	0.86 B
Seafarer	0.19 C	0.54 C	0.93 AB	1.18 A
Mean	0.24	0.66***	1.00	1.09***
CV %	22.64	18.59	24.23	11.96
Significance	***	***	***	***
LSD 0.05	0.07	0.15	0.26	0.16

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD at $\alpha = 0.05$.

LSD (0.05) for genotype x drought treatment interaction: biomass growth rate = 0.11.

1. Asterisks indicate significance between treatments.
2. Significance among genotypes within drought treatments.

a. Grams/day.

Table 2.14. Partitioning related traits of twenty dry bean genotypes grown under drought and non-stress treatments. East Lansing, MI, 1990.

GENOTYPES		HARVEST INDEX[†]		ECONOMIC GROWTH RATE[†] (g/day)		SEED GROWTH RATE[†] (g/day)	
	R(1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	0.606	0.614 A	0.131 AB	0.252 ABC	0.333 ABC	0.512 AB
LS7	2	0.614	0.649 A	0.125 ABC	0.226 ABC	0.313 ABC	0.449 ABC
LEF2RB	3	0.665	0.668 A	0.133 A	0.209 ABCD	0.358 A	0.408 ABC
Sierra	4	0.588	0.637 A	0.125 ABC	0.257 ABC	0.338 AB	0.528 A
AS3	5	0.559	0.435 BC	0.111 ABCD	0.185 ABCD	0.254 ABCDE	0.436 ABC
LS103	6	0.641	0.661 A	0.109 ABCD	0.230 ABC	0.264 ABCD	0.484 ABC
AS102	7	0.552	0.605 A	0.084 ABCDE	0.210 ABCD	0.184 CDEF	0.417 ABC
AS6	8	0.534	0.568 A	0.084 ABCDE	0.244 ABC	0.180 CDEF	0.436 ABC
LS6	9	0.558	0.650 A	0.096 ABCD	0.230 ABC	0.225 ABCDE	0.472 ABC
LS102	10	0.601	0.569 A	0.102 ABCD	0.106 DE	0.260 ABCD	0.187 DE
AC-1022	11	0.527	0.608 A	0.080 ABCDE	0.261 AB	0.164 DEF	0.476 ABC
AS11	12	0.536	0.560 AB	0.087 ABCDE	0.197 ABCD	0.199 BCDE	0.360 ABCD

Table 2.14. (cont'd)...

GENOTYPES		HARVEST INDEX+		ECONOMIC GROWTH RATE+ (g/day)		SEED GROWTH RATE+ (g/day)	
	R(1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
AS101	13	0.584	0.565 AB	0.080 ABCDE	0.222 ABC	0.180 CDEF	0.425 ABC
AC-1028	14	0.359	0.550 AB	0.073 ABCDE	0.245 ABC	0.156 DEF	0.495 ABC
LS11	15	0.553	0.640 A	0.080 ABCDE	0.143 CDE	0.208 BCDE	0.283 CDE
AS1	16	0.468	0.621 A	0.065 BCDE	0.273 A	0.136 DEF	0.538 A
LS101	17	0.468	0.653 A	0.064 CDE	0.209 ABCD	0.158 DEF	0.422 ABC
AS104	18	0.348	0.401 C	0.049 DE	0.155 BCD	0.111 EF	0.295 BCD
LS104	19	0.308	0.638 A	0.052 DE	0.197 ABCD	0.126 DEF	0.370 ABCD
AS103	20	0.424	0.384 C	0.023 E	0.033 E	0.048 F	0.063 E
MEAN (2)		0.525	0.584 NS	0.087	0.204***	0.209	0.399***
CV %		24.1	11.5	31.9	25.8	34.3	25.7
SS (3)		NS	***	**	**	**	**
LSD 0.05		----	0.132	0.066	0.115	0.148	0.220

Level of statistical significance: 0.10(*); 0.05(**); 0.01(***).
+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.
LSD (0.10) for genopyte x drought treatment interaction: seed growth rate = 0.149.
1. Ranking based on yield under drought
2. Askterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

Table 2.15. Averages and levels of significance of partitioning related traits of twenty dry bean genotypes grown under drought and non-stress treatments. East Lansing, MI, 1990.

GENOTYPE		RELATIVE SINK STRENGTH^{+}		BIOMASS GROWTH RATE^{+a} (g/day)	
	R(1)	Drought	Non-Stress	Drought	Non-Stress
LS4	1	1.499	1.248 ABCD	0.214 A	0.404 A
LS7	2	1.539	1.279 AB	0.201 ABC	0.343 AB
LEF2RB	3	1.781	1.310 AB	0.199 ABC	0.310 ABC
Sierra	4	1.604	1.309 AB	0.210 A	0.401 A
AS3	5	1.278	0.870 EFG	0.196 ABCD	0.357 AB
LS103	6	1.558	1.397 A	0.169 ABCDE	0.345 AB
AS102	7	1.209	1.206 ABCD	0.152 ABCDE	0.339 ABC
AS6	8	1.141	1.014 CDEF	0.155 ABCDE	0.401 A
LS6	9	1.298	1.334 AB	0.170 ABCDE	0.353 AB
LS102	10	1.548	0.993 DEFG	0.168 ABCDE	0.180 CD
AC-1022	11	1.085	1.102 BCDE	0.150 ABCDE	0.422 A
AS11	12	1.231	1.010 CDEFG	0.157 ABCDE	0.355 AB
AS101	13	1.231	1.075 BCDE	0.138 CDE	0.373 AB
AC-1028	14	0.767	1.122 BCDE	0.210 AB	0.440 A
LS11	15	1.428	1.261 ABC	0.140 CDE	0.224 BCD
AS1	16	0.984	1.225 ABCD	0.135 CDE	0.437 A
LS101	17	1.129	1.316 AB	0.124 E	0.322 ABC
AS104	18	0.781	0.767 FG	0.196 BCDE	0.372 AB
LS104	19	0.745	1.197 ABCD	0.132 DE	0.303 ABC
AS103	20	0.891	0.748 G	0.053 F	0.075 D
MEAN (2)		1.240	1.139 NS	0.161	0.338**
CV (%)		27.7	11.2	17.9	22.4
SS (3)		NS	***	***	**
LSD 0.05		----	0.265	0.066	0.162

Levels of statistical significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.

1. Ranking based on yield under drought.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

to 0.69 in the genotype LEF2RB (Table 2.14). The lack of statistical significance can be attributable to the lower number of replications and the high genotypic variability. The highest harvest index and relative sink strength values in the 1988 experiment (Table 2.13a and 2.13b) were displayed by the genotypes Sierra, LEF2RB and Seafarer, in that order while the lowest values were for AC1028 and AC1022 genotypes. A similar pattern was observed in the 1990 experiment.

The harvest index averages for the non-stress treatments were similar in both years of evaluation. Relative sink strength averages for both drought treatments were higher in 1990 than in 1988. The range of variation among genotypes for all the indices was also higher in 1990 than in 1988.

Significant differential genotypic responses to drought treatments were detected for economic growth rate, seed growth rate and biomass growth rate in 1988 (Table 2.7) and in seed growth rate only in 1990 (Table 2.9). These kind of responses were not detected in harvest index and relative sink strength in any of the experiments.

Variability in Biomass Production

The significances of the differences among genotypes for stem weight, pod weight, and total biomass are reported in Table 2.16 and 2.17, for the 1988 and 1990 experiments, respectively. In addition, genotypic differences for leaf retention, leaf size, leaf area index and stem diameter in 1990 are reported in Tables 2.18 and 2.19.

An important variation among genotypes within both treatments for the three biomass variables measured was noted in both years of evaluation. Significant differences among genotypes were detected regardless of the drought treatment and year of evaluation (drought intensity) in all the variables. Significant differential genotypic responses to drought treatments were identified for the variables stem weight and total biomass in both years of evaluation (Tables 2.6

Table 2.16. Significance of averages of biomass related traits measured on five genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

GENOTYPE	STEM WEIGHT^{+} (g/pl)		POD WEIGHT^{+} (g/pl)		TOTAL BIOMASS^{+} (g/pl)	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	7.82 B	12.60 C	5.87 A	9.23 C	28.70 A	59.42 BC
LEF2RB	6.65 BC	12.23 C	4.44 B	10.74 BC	22.27 B	71.17 B
AC-1028	10.15 A	24.87 A	3.57 BC	18.45 A	21.69 B	98.88 A
AC-1022	7.83 B	18.40 B	3.19 C	13.98 B	17.25 BC	71.90 B
Seafarer	5.17 C	9.52 C	3.04 C	7.54 C	14.23 C	44.74 C
Mean (1)	7.52	15.52***	4.02	11.99***	20.83	69.22***
CV (%)	19.9	17.4	22.3	22.0	21.1	21.0
Significance (2)	***	***	***	***	***	***
LSD 0.05	1.78	3.25	1.07	3.32	5.22	17.47

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.

LSD (0.05) for genotype x drought treatment interaction: stem weight = 2.45 g/pl, total biomass = 12.17 g/pl.

1. Asterisks indicate significance between drought treatments.
2. Significance among genotypes within drought treatments.

Table 2.17. Significance and averages of biomass traits of twenty dry bean genotypes grown under drought and non-stress treatments. East Lansing, MI, 1990.

GENOTYPE		STEM WEIGHT^{+} (g/pl)		POD WEIGHT^{+} (g/pl)		TOTAL BIOMASS^{+} (g/pl)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	4.01 BC	8.18 CDEF	2.67	5.17 BCDE	17.05 AB	35.33 ABCD
LS7	2	3.97 BC	6.96 DEFG	2.28	3.64 EFG	20.34 ABC	30.94 BCDE
LEF2RB	3	2.76 C	5.62 FGH	2.01	3.65 EFG	14.44 BCDE	28.37 CDE
Sierra	4	4.15 BC	7.14 DEFG	2.28	5.50 BCDE	15.75 ABCD	35.13 ABCD
AS3	5	4.77 BC	9.08 BCDE	2.30	6.40 ABCD	16.30 ABC	32.18 ABCDE
LS103	6	2.67 C	4.78 GH	1.95	4.87 BCDEF	12.93 BCDE	28.72 BCDE
AS102	7	4.49 BC	7.65 CDEFG	2.15	5.82 BCD	14.75 BCDE	35.27 ABCD
AS6	8	4.79 BC	11.01 BC	2.00	5.58 BCDE	14.87 BCDE	42.38 ABC
LS6	9	4.07 BC	6.41 DEFG	2.10	4.47 DEFG	14.16 BCDE	30.97 BCDE
LS102	10	3.08 C	5.12 FGH	2.12	2.65 GH	13.11 BCDE	18.83 EF
AC-1022	11	4.73 BC	9.64 BCD	2.02	6.91 AB	14.37 BCDE	43.40 AB
AS11	12	3.85 BC	9.59 BCD	2.33	6.56 ABCD	13.71 BCDE	36.79 ABC
AS101	13	3.41 C	9.40 BCDE	1.89	6.76 ABC	12.58 BCDE	39.85 ABC
AC-10128	14	11.02 A	12.44 B	2.26	8.17 A	20.35 A	45.98 A

Table 2.17. (cont'd)...

GENOTYPE	R (1)	STEM WEIGHT+ (g/pl) Drought	STEM WEIGHT+ (g/pl) Non-Stress	POD WEIGHT+ (g/pl) Drought	POD WEIGHT+ (g/pl) Non-Stress	TOTAL BIOMASS+ (g/pl) Drought	TOTAL BIOMASS+ (g/pl) Non-Stress
LS11	15	3.47 BC	4.79 GH	1.81	3.00 FGH	12.01 CDE	21.63 DEF
AS1	16	4.40 BC	9.21 BCDE	1.84	6.22 ABCD	11.97 CDE	40.85 ABC
LS101	17	2.75 C	6.12 EFGH	2.37	4.63 CDEFG	10.34 E	30.72 BCDE
LS104	18	6.76 B	16.83 A	2.02	6.48 ABCD	13.36 BCDE	39.69 ABC
AS104	19	5.36 BC	5.48 FGH	1.92	4.58 DEFG	11.34 DE	28.78 BCDE
AS103	20	2.33 C	2.81 H	0.58	1.36 H	5.01 F	7.36 F
MEAN (2)		4.34	7.91 **	2.04	5.12 **	13.74	32.67 ***
CV%		36.8	20.4	23.1	20.1	16.8	21.9
SS (3)		**	***	NS	***	***	***
LSD 0.05		3.34	3.37	-----	2.16	4.84	14.99

Level of statistical significance: 0.10(*); 0.05(**); 0.01(***).
+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.
LSD (0.05) for genotype x drought treatment interaction: stem weight = 3.24 g/pl, pod weight = 1.62 g/pl, total biomass = 10.76 g/pl
1. Yield under drought ranking.
2. Asterisks indicated significance between drought treatments.
3. Significance among genotypes within drought treatments.

Table 2.18. Leaf retention[a] under drought and non-stress treatments of twenty dry bean genotypes grown in East Lansing, MI, 1990.

GENOTYPE	R(1)	LEAF RETENTION (g/pl)[+] Drought	Non-Stress
LS4	1	0.880 BC	3.835 B
LS7	2	0.590 BC	2.525 BCD
LEF2RB	3	0.485 BC	1.675 CDEFGHI
Sierra	4	0.215 C	0.375 HIJ
AS3	5	0.550 BC	1.545 CDEFGHI
LS103	6	0.695 BC	0.610 GHIJ
AS102	7	1.445 BC	0.330 IJ
AS6	8	1.695 BC	2.255 CDE
LS6	9	0.865 BC	0.895 FGHIJ
LS102	10	0.270 C	1.290 CDEFGHIJ
AC-1022	11	2.270 BC	1.705 CDEFGH
AS11	12	0.770 BC	1.910 CDEFG
AS101	13	1.035 BC	1.550 CDEFGHIJ
AC-1028	14	7.295 A	0.980 EFGHIJ
LS11	15	0.880 BC	2.245 CDEF
AS1	16	2.015 BC	2.255 BC
LS101	17	0.400 BC	1.190 DEFGHIJ
AS104	18	3.695 B	7.435 A
LS104	19	3.350 BC	0.940 EFGHIJ
AS103	20	1.455 BC	0.275 J
Mean (2)		1.615	1.806 NS
CV		97.6	35.8
SS (3)		**	***
LSD 0.05		3.298	1.353

Level of Statistical Significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.

LSD (0.05) for genotype x drought treatment interaction: 2.43 g/pl.

1. Yield under drought ranking.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

a. Weight of dry matter of leaves at physiological maturity.

Table 2.19. Averages and significance of morphological traits of twenty dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1990.

GENOTYPE		LEAF SIZE$^+$ (cm^2)		LEAF AREA INDEX$^+$		STEM DIAMETER$^+$ (mm)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	37.73 A	34.26 CDE	4.45	4.80 BCDEF	4.25 ABCDE	5.40 ABCD
LS7	2	35.10 AB	42.69 ABC	5.93	6.56 ABCDE	4.05 BCDE	4.95 CDEF
LEF2RB	3	25.80 ABC	37.28 ABCD	3.99	5.48 BCDEF	4.00 BCDE	4.45 EFG
Sierra	4	33.01 ABC	30.11 DEF	3.39	5.03 BCDEF	4.75 AB	5.60 ABC
AS3	5	32.19 ABC	37.28 ABCD	3.24	5.49 BCDEF	4.40 ABCD	5.75 ABC
LS103	6	29.06 ABC	28.32 EF	3.19	3.98 DEF	3.60 EF	3.85 GH
AS102	7	32.90 ABC	42.86 ABC	4.23	4.31 CDEF	4.25 ABCDE	5.25 BCDE
AS6	8	30.29 ABC	43.86 AB	3.55	7.16 ABC	4.40 ABCD	5.90 AB
LS6	9	30.13 ABC	44.36 AB	3.41	7.80 AB	4.35 ABCDE	5.25 BCDE
LS102	10	22.97 BC	28.28 EF	3.07	4.75 BCDEF	3.90 CDEF	4.65 DEFG
AC-1022	11	34.83 AB	37.83 ABCD	4.39	5.37 BCDEF	4.65 ABC	5.75 ABC
AS11	12	29.00 ABC	45.90 A	3.72	7.56 AB	4.30 ABCDE	5.65 ABC
AS101	13	25.74 ABC	36.33 BCDE	2.87	3.77 EF	4.10 BCDE	5.30 BCDE

Table 2.19. (cont'd)...

GENOTYPE		LEAF SIZE+ (cm²)		LEAF AREA INDEX+		STEM DIAMETER+ (mm)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
AC-1028	14	32.20 ABC	45.51 A	4.13	9.15 A	4.90 A	5.75 ABC
LS11	15	23.40 BC	41.60 ABC	2.77	7.12 ABCD	3.85 DEF	4.35 FGH
AS1	16	30.30 ABC	37.63 ABCD	3.28	3.24 F	4.10 BCDE	5.60 ABC
LS101	17	21.46 C	23.84 F	3.15	3.72 EF	3.85 DEF	4.95 CDEF
LS104	18	35.32 AB	38.22 ABCD	4.75	3.48 EF	4.65 ABC	6.20 A
AS104	19	30.51 ABC	38.79 ABC	4.08	3.64 EF	3.90 CDEF	4.60 DEFG
AS103	20	30.57 ABC	39.65 ABC	2.43	3.36 F	3.20 F	3.55 H
MEAN (2)		30.11	37.73 *	3.70	5.29 NS	4.17	5.14 **
CV %		13.0	11.0	39.1	28.6	8.9	8.3
SS (3)		**	***	NS	**	**	***
LSD 0.05		12.96	8.66	----	3.17	0.77	0.89

Level of statistical significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.

LSD (0.05) for genotype x drought treatment interaction: leaf size = 8.11 cm^2

1. Yield under drought ranking.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

and 2.9). The genotypes evaluated in 1990 displayed a significant differential genotypic expression for pod weight.

An additional set of four variables associated with biomass production were included in 1990. Leaf retention (a measurement of leaf senescence), leaf size, leaf area index, and stem diameter (Tables 2.18 and 2.19) showed considerable genotypic variation in both drought treatments, although the differences among genotypes were not statistically significant for leaf area index under drought. The genotype AS103 showed the lowest yield but also the lowest leaf area index and stem diameter (Table 2.19). The highest yielding genotypes Sierra, LEF2RB, LS7 and LS4 also showed the lowest leaf retention at physiological maturity meaning that the rate of leaf senescence was higher in these genotypes (Table 2.18). The genotypes AC1022 and AC1028 exhibited the highest values in stem weight while the values for Sierra and LEF2RB were lower (Table 2.16 and 2.17). The response was very similar in both years of evaluation. Differential genotypic responses to water stress were only exhibited by leaf size.

Variability in Phenological Characteristics

The values for days to flowering, physiological maturity and seed fill period obtained in the 1988 and 1990 experiments have been condensed in Tables 2.20 and 2.21, respectively. Statistical significances among genotypes within drought treatments and between drought treatments were obtained for the three characteristics in both years. The results indicate an important genotypic variation, which was clearer in the experiments of 1990. In 1988, the intermediate maturing genotypes Sierra and LEF2RB had the highest yield under drought. These genotypes had higher yield than the late-maturing indeterminate genotypes AC1022 and AC1028, and the early-maturing determinate genotype Seafarer. In 1990, within the range of variation tested, the general tendency was that the genotypes with higher yield under drought were the earliest ones. In this year

Table 2.20. Significance of averages of phenological traits of five dry bean genotypes grown under drought and non-stress treatments. East Lansing, MI, 1988.

GENOTYPES	DAYS TO FLOWER+ (1)		DAYS TO MATURITY+ (1)		DAYS OF SEED FILLING+ (2)	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	45.17 B	42.00 C	86.50 B	91.33 B	41.33 B	49.33 B
LEF2RB	44.67 B	43.33 BC	78.67 C	95.17 B	34.00 C	51.83 B
AC-1028	49.67 A	49.33 A	98.67 A	124.30 A	49.00 A	75.00 A
AC-1022	45.17 B	45.17 B	95.50 A	126.70 A	50.33 A	81.50 A
Seafarer	41.00 C	39.33 D	74.67 C	82.33 B	33.67 C	44.00 B
Mean (3)	45.13*	43.83	86.80	103.96**	41.66	60.13***
CV %	4.6	4.9	6.7	15.5	12.0	28.0
Significance (4)	***	***	***	***	***	***
LSD 0.05	2.45	2.60	6.87	19.39	6.00	20.26

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.

LSD for genotype x drought treatment interaction: days to maturity (0.05) = 12.85, days of seed filling (0.10) = 11.01.

1. Days after planting.
2. Days to physiological maturity - days to flowering.
3. Asterisks indicate significance between drought treatments.
4. Significance among genotypes within drought treatments.

Table 2.21. Averages and levels of significance of phenological related traits of twenty dry bean genotypes evaluated under drought and non-stress treatments. East Lansing, MI, 1990.

GENOTYPE		DAYS TO FLOWERING$^+$ (2)		DAYS TO MATURITY$^+$ (2)		DAYS OF SEED FILLING$^+$ (3)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	47.3 EFGHI	44.5 FGH	79.5 EFGHI	87.5 FG	32.2 CDE	43.0 ABC
LS7	2	49.3 BCDE	44.7 FGH	82.0 DEFGHI	91.0 EFG	32.7 BCDE	46.3 EGF
LEF2RB	3	45.7 IJ	44.6 FGH	73.0 I	91.5 EFG	27.3 E	46.9 EGF
Sierra	4	46.8 FGHIJ	44.9FGH	74.5 HI	87.5 FG	27.7 E	42.6 FG
AS3	5	46.7 GHIJ	46.1 EFGH	83.0 CDEFGHI	89.5 EFG	36.3 ABCDE	44.3 EFG
LS103	6	45.0 J	43.7 H	76.5 GHI	83.0 G	31.5 DE	39.3 G
AS102	7	52.7 A	51.9 AB	97.0 A	104.0 ABCD	44.3 ABC	52.1 ABCDE
AS6	8	50.8 ABCD	46.5 EFGH	95.5 AB	105.5 ABC	44.7 AB	59.0 AB
LS6	9	47.2 EFGHIJ	44.9 FGH	83.0 DEFGHI	87.5 FG	35.8 ABCDE	42.6 FG
LS102	10	47.2 EFGHIJ	45.2 FGH	78.0 FGHI	106.0 ABC	30.8 DE	60.8 A
AC-1022	11	49.1 CDE	46.3 EFGH	95.5 AB	103.5 ABCD	46.4 A	57.2 ABC
AS11	12	49.0 DEF	46.3 EFGH	87.5 ABCDEFG	104.0 ABCD	38.5 ABCDE	57.7 ABC
AS101	13	50.5 ABCD	51.0 ABC	91.0 ABCDE	108.0 A	40.5 ABCD	57.0 ABC

Table 2.21. (cont'd)...

GENOTYPE	R (1)	DAYS TO FLOWER+ (2) Drought	DAYS TO FLOWER+ (2) Non-Stress	DAYS TO MATURITY+ (2) Drought	DAYS TO MATURITY+ (2) Non-Stress	DAYS OF SEED FILLING+ (3) Drought	DAYS OF SEED FILLING+ (3) Non-Stress
AC-1028	14	51.5 AB	53.3 A	97.0 A	104.5 ABCD	45.5 A	51.2 BCDEF
LS11	15	50.6 ABCD	47.5 DEFG	86.0 ABCDEFGH	86.5 CDEF	35.4 ABCDE	49.0 CDEF
AS1	16	46.7 GHIJ	46.1 EFGH	88.5 ABCDEFG	93.5 EF	41.8 ABCD	47.4 DEFG
LS101	17	48.0 EFGH	48.6 BCDE	84.5 BCDEFGHI	96.5 CDEF	36.5 ABCDE	47.9 DEFG
AS104	18	51.3 ABC	50.7 ABCD	92.5 ABCD	106.5 AB	41.2 ABCD	55.8 ABCD
LS104	19	46.1 HIJ	44.4 GH	89.0 ABCDEF	95.0 DEF	42.9 ABCD	50.6 BCDEF
AS103	20	48.7 DEFG	47.8 CDEF	95.0 ABC	98.0 BCDE	46.3 A	50.2 ABC
MEAN (4)		48.51 *	46.91	86.43	96.95 **	37.92	50.1 **
CV %		2.2	3.4	6.8	4.7	15.7	8.3
SS (5)		***	***	***	***	**	**
LSD 0.05		2.26	3.35	12.2	9.57	12.47	8.7

Level of statistical significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.

1. Ranking based on yield under drought.
2. Days after planting
3. Days to physiological maturity - days at flowering.
4. Asterisks indicate significance between drought treatments.
5. Significance among genotypes within treatments.

early-maturing determinate genotypes were not included in the experiments. Days to physiological maturity was reduced while days to flower was delayed. The combined response in both variables caused the reduction in days of pod filling.

Significant differential genotypic responses to drought treatments were found in 1988 for days to maturity and days of seed filling. The genotypes Sierra and Seafarer exhibited the lowest reductions in both characteristics. Sierra was the most stable of both genotypes (Table 2.7).

Variability in Physiological Traits

Water Use Characteristics

The significance of the differences among genotypes is displayed in Tables 2.22, 2.23 and 2.24 for the experiments in 1988 and in Tables 2.25 for the 1990 experiments.

Differences in transpiration rate were clearer under nonstressed conditions since statistical significance were detected only among genotypes growing under these conditions in both years (Table 2.22 and 2.25). Under drought stress statistical differences in transpiration rate required a level of probability of 0.12 in 1990. It is important to note that the coefficients of variation in these variables were relatively low compared to other variables, but they were higher under stress than under non-stress conditions. Greater variability was observed in the 1990 experiments because of the larger genotypic variation.

Likewise, differences in stomatal conductance were significant and clearer under nonstressed conditions in both years. Although statistical differences were detected under drought in 1990, this could be caused by the larger number of genotypes evaluated with different responses to drought and the less severe drought intensity obtained that year.

Table 2.22. Significance of transpiration rates measured on five genotypes grown under drought and non-stress treatments. East Lansing, MI, 1988.

GENOTYPE	TRANSPIRATION RATE (a) Drought	Non-Stress
Sierra	8.23	11.64
LEF2RB	8.90	14.53
AC-1028	8.26	11.58
AC-1022	8.52	11.56
Seafarer	8.70	13.18
Mean (1)	8.72	12.50**
CV (%)	18.65	13.59
Significance (2)	NS	*
LSD 0.05	---	---

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

a. $mgH_2O/cm^2/s$

1. Asterisks indicate significance between drought treatments.
2. Significance among genotypes within drought treatments.

Table 2.23. Significances of water use traits measured on five genotypes grown under drought and non-stress treatments. East Lansing, MI, 1988.

GENOTYPE	STOMATAL CONDUCTANCE (a)					
	ABAXIAL		ADAXIAL		TOTAL	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	0.71	1.67 A	0.28	0.65 AB	0.98	1.81 B
LEF2RB	0.76	1.59 A	0.23	0.68 A	0.99	2.27 A
AC-1028	0.58	1.14 B	0.18	0.41 C	0.77	1.55 B
AC-1022	0.71	1.18 B	0.19	0.48 BC	0.89	1.67 B
Seafarer	0.71	1.31 AB	0.25	0.48 BC	0.96	1.79 B
Mean (1)	0.69	1.28***	0.23	0.54***	0.92	1.82***
CV (%)	21.6	18.2	25.3	20.0	20.7	18.2
Significance (2)	NS	*	NS	**	NS	*
LSD	---	0.29^3	---	0.17	---	0.41^3

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$ or $\alpha = 0.10$ as indicated.

1. Asterisks indicate significance between drought treatments.

3. LSD at 0.10 level of significance.

a. cm/s^1

Table 2.24. Significances of averages of three water use related traits measured on five genotypes grown under drought and non-stress treatments. East Lansing, MI, 1988.

GENOTYPE	ABAXIAL CONDUCTANCE[+a] (%)		ADAXIAL CONDUCTANCE[+b] (%)		LEAF TEMPERATURE[+] (°C)	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	72.62 C	65.21 D	27.38 C	34.79 A	29.39 C	28.65
LEAF2RB	77.20 ABC	69.79 C	22.80 ABC	30.21 B	29.92 BC	28.48
AC-1028	79.30 AB	74.92 A	20.70 AB	25.08 D	31.50 AB	29.54
AC-1022	80.28 A	70.70 BC	19.72 A	29.19 BC	29.96 BC	29.57
Seafarer	74.70 BC	73.24 AB	25.30 BC	26.76 CD	32.38 A	29.39
Mean (1)	76.82***	70.80	23.18	29.20***	30.63***	29.13
CV (%)	4.84	2.84	16.03	7.01	3.81	2.98
Significance (2)	*	***	*	***	**	NS
LSD 0.05	4.61[3]	3.08	4.61[3]	3.08	1.76	---

Levels of Significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$ or $\alpha = 0.10$ as indicated.

LSD (0.10) for genotype x drought treatment interaction: percentage of abaxial and adaxial conductance = 3.43%.

1. Asterisks indicate significance between drought treatments.
2. Significance among genotypes within drought treatments.
3. LSD at 0.10 level of significance.

a. Abaxial conductance/total conductance.

b. Adaxial conductance/total conductance.

Table 2.25. Averages and levels of significance of transpiration rate, stomatal conductance and leaf temperature of twenty dry bean genotypes evaluated under drought and non-stress treatments. East Lansing, MI, 1990.

GENOTYPE		TRANPIRATION RATE^{+} (a)		STOMATAL CONDUCTANCE^{+} (b)		LEAF TEMPERATURE^{+} (c)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	13.18	18.76 A	1.92 ABCD	2.43 A	25.51 D	24.99 CD
LS7	2	12.49	17.33 ABCD	1.70 ABCDEF	2.11 ABCD	25.52 BCD	25.32 BCD
LEF2RB	3	10.82	18.40 ABC	1.70 ABCDEF	2.34 ABC	25.54 CD	24.98 CD
Sierra	4	12.99	16.04 ABCDE	2.11 ABC	1.97 ABCDE	25.52 CD	24.79 D
AS3	5	12.63	18.51 AB	1.85 ABCDE	2.41 AB	25.53 CD	24.82 D
LS103	6	13.29	15.47 BCDE	2.42 A	1.98 ABCDE	25.71 BCD	24.66 D
AS102	7	9.66	13.79 E	1.09 EF	1.38 F	26.27 ABCD	26.49 A
AS6	8	9.52	14.87 DE	1.03 F	1.72 DEF	27.04 A	25.24 BCD
LS6	9	11.30	15.14 DE	1.60 BCDEF	1.82 BCDEF	26.33 ABCD	24.85 D
LS102	10	10.84	17.36 ABCD	1.52 BCDEF	2.18 ABCD	25.53 CD	25.18 BCD
AC-1022	11	14.87	15.34 CDE	2.27 AB	1.87 ABCDEF	25.54 CD	25.16 BCD
AS11	12	8.91	15.56 BCDE	0.98 F	1.90 ABCDEF	26.50 ABCD	25.19 BCD
AS101	13	8.40	15.19 DE	1.01 F	1.89 ABCDEF	25.59 CD	24.98 CD

Table 2.25. (cont'd)...

GENOTYPE	R (1)	TRANSPIRATION RATE+ (a) Drought	TRANSPIRATION RATE+ (a) Non-Stress	STOMATAL CONDUCTANCE+ (b) Drought	STOMATAL CONDUCTANCE+ (b) Non-Stress	LEAF TEMPERATURE+ (c) Drought	LEAF TEMPERATURE+ (c) Non-Stress
AC-1028	14	8.87	18.43 ABC	0.95 F	2.17 ABCD	27.06 A	25.78 ABC
LS11	15	8.87	17.48 ABCD	1.22 DEF	2.32 ABC	26.58 ABCD	24.55 D
AS1	16	12.73	16.51 ABCD	1.70 ABCDEF	2.07 ABCD	26.34 ABCD	24.99 CD
LS101	17	11.61	15.86 ABCDE	1.49 CDEF	1.96 ABCDEF	26.71 AB	25.14 BCD
AS104	18	9.84	13.61 E	1.22 DEF	1.39 EF	25.95 ABCD	26.03 AB
LS104	19	10.12	17.36 ABCD	1.47 CDEF	2.32 ABC	26.77 AB	24.79 D
AS103	20	8.67	15.63 BCDE	1.01 F	1.78 CDEF	26.62 ABC	25.77 ABC
MEAN (2)		10.98	16.33 *	1.51	2.00 NS	26.13	25.19 **
CV %		18.7	9.1	30.0	14.1	2.0	1.7
SS (3)		0.12	**	*	**	**	**
LSD 0.05		4.27	3.10	0.76^4	0.59	1.12	0.92

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.

LSD (0.10) for genotype x drought treatment interaction : leaf temperature = 0.82 °C.

1. Yield under drought ranking.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within treatments.
4. LSD at 0.10 level of significance.

a. mgH_2O/cm^2/s

b. cm/s^1

c. °C

One important finding from these results is the response of the genotypes AC1028 and LEF2RB to drought. AC1028 did have the lowest values of conductance under drought while LEF2RB tended to have the highest values of conductance under drought in both years. The response was clearer in 1988, if the measurements of the abaxial, adaxial and total stomatal conductance are analyzed (Table 2.23). In 1990, the progenies AS102, AS6, AS103, AS11 and AS101 derived from the cross having AC1028 as parent, did have the lowest values of stomatal conductance in both treatments (Table 2.25). In general the lowest values of stomatal conductance were for progenies derived from that cross. The highest values in both treatments were for genotypes involving LEF2RB as a parent.

Leaf temperature also showed a high range of variability among genotypes. Statistical significance for the differences among genotypes was observed for the drought treatment in both years and for the nonstressed treatments in 1990. The coefficients of variation for all the experiments were low (Tables 2.24 and 2.25).

Significant differential genotypic responses to drought were found for the percentage of adaxial stomatal conductance in leaves in the 1988 experiment and for leaf temperature in the 1990 experiment. In Table 2.9 it is shown that the four higher yielding genotypes under drought did not increase their leaf temperature significantly.

Water Relations

In Tables 2.26 and 2.27 the average relative water content, water potential and water content are presented. Significant differences among genotypes were observed in both years and treatments in relative water content and water content, whereas the differences in water potential were significant in both treatments in 1988 and only under nonstressed conditions in 1990.

Table 2.26. Significance of water relations of five genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

GENOTYPE	RELATIVE WATER CONTENT (%)		WATER POTENTIAL (MPa)		WATER CONTENT (%) (1)		MOISTURE RETENTION CAPACITY (%)	
	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
Sierra	73.49 B	77.58 B	-0.78 AB	-0.62 B	80.26 A	80.16 A	24.83 B	14.79
LEF2RB	76.02 A	80.59 A	-0.75 A	-0.56 A	79.72 A	79.84 AB	31.24 A	17.68
AC-1028	75.02 AB	75.54 B	-0.73 A	-0.54 A	82.61 A	80.68 A	23.47 B	10.74
AC-1022	73.26 B	74.66 B	-0.75 A	-0.56 A	79.77 A	80.29 A	24.37 B	17.81
Seafarer	75.73 A	80.67 A	-0.84 B	-0.64 B	76.90 B	78.91 B	32.52 A	14.06
Mean (2)	74.71	77.81**	-0.77***	-0.58	79.45	79.97	27.28**	15.02
CV (%)	1.8	2.6	5.8	5.4	1.3	1.0	14.4	26.7
Significance (3)	**	***	**	***	***	*	**	0.14
LSD 0.05	1.97	3.10	-0.07	-0.05	1.50	1.03[4]	5.92	---

Levels of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD at α = 0.05 or α = 0.10 as indicated.

LSD for genotype x drought treatment interaction: relative water content (0.10) = 2.06%, moisture retention capacity (0.05) = 5.44%.

1. On a fresh weight basis.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.
4. LSD at 0.10 level of significance.

Table 2.27. Averages and levels of significance of water status traits of twenty dry bean genotypes under drought and non-stress conditions. East Lansing, MI, 1990.

GENOTYPE		WATER CONTENT^{+} (%)		RELATIVE WATER CONTENT^{+} (%)		WATER POTENTIAL^{+} (Mpa)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	84.17 ABC	87.78 BCD	78.76 BCDEF	83.33 BC	-0.67	-0.64 ABCD
LS7	2	83.46 ABCD	84.74 BC	77.63 DEF	80.99 BCDEF	-0.68	-0.62 A
LEF2RB	3	81.11 DEF	83.81 BCD	79.28 BCDEF	81.50 BCDEF	-0.67	-0.63 ABCDE
Sierra	4	84.48 ABC	82.53 D	81.00 ABCD	82.93 BCD	-0.68	-0.65 ABCDE
AS3	5	83.57 ABCD	84.16 BCD	76.80 EFG	80.85 BCDEF	-0.67	-0.65 ABCDE
LS103	6	82.22 CDE	83.57 BCD	77.88 CDEF	83.66 BC	-0.67	-0.69 EF
AS102	7	84.84 ABC	83.09 CD	79.40 BCDEF	77.24 F	-0.68	-0.70 F
AS6	8	84.51 ABC	83.84 BCD	78.64 BCDEF	78.83 DEF	-0.66	-0.63 ABC
LS6	9	84.99 AB	85.39 B	81.79 ABC	82.91 BCD	-0.67	-0.64 ABCD
LS102	10	83.15 ABCD	83.46 BCD	83.61 A	84.74 B	-0.64	-0.64 ABCD
AC-1022	11	78.81 F	83.40 BCD	69.86 H	80.53 BCDEF	-0.68	-0.63 ABC
AS11	12	85.47 A	83.65 BCD	81.15 ABCD	81.22 BCDEF	-0.64	-0.64 ABCD
AS101	13	85.28 A	83.61 BCD	78.88 BCDEF	78.43 EF	-0.67	-0.65 BCDE

Table 2.27. (cont'd)...

GENOTYPE		WATER CONTENT^{+} (%)		RELATIVE WATER CONTENT^{+} (%)		WATER POTENTIAL^{+} (MPa)	
	R (1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
AC-1028	14	84.48 BCDE	84.61 BCD	75.84 FG	79.26 CDEF	-0.67	-0.65 ABCD
LS11	15	85.01 AB	84.77 BC	80.38 ABCDE	81.80 BCDE	-0.67	-0.62 AB
AS1	16	84.08 ABC	83.94 BCD	79.39 BCDEF	81.19 BCDEF	-0.66	-0.66 CDEF
LS101	17	85.01 AB	84.12 BCD	82.20 AB	84.58 B	-0.67	-0.67 DEF
AS104	18	85.72 A	84.90 BC	79.65 ABCDEF	79.71 CDEF	-0.64	-0.67 DEF
LS104	19	80.41 EF	84.47 BCD	72.95 GH	78.06 EF	-0.68	-0.64 ABCD
AS103	20	85.17 A	88.17 A	79.15 BCDEF	89.31 A	-0.69	-0.66 DEF
MEAN (2)		83.70	84.18 NS	78.71	81.55 *	-0.67	0.65 NS
CV%		1.5	1.2	2.4	2.6	2.4	3.41
SS (3)		***	**	***	***	0.17	*
LSD 0.05		2.68	2.18	3.97	4.43	0.49	0.04

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05.

LSD (0.05) for genotype x drought treatment interaction: water potential 0.04 MPa.

1. Yield under drought ranking.
2. Asterisks indicate significance between drought treatments.
3. Significance among genotypes within drought treatments.

The averages and statistical significances for leaf moisture retention capacity are shown in Table 2.26 and 2.28 for 1988 and 1990, respectively. Differences among genotypes were statistically significant in the drought treatment in 1988 but not in 1990, while statistical significance was found under non stressed conditions in 1990 but not in 1988. In both years LEF2RB exhibited a high leaf moisture retention capacity under both treatments.

In 1988, relative water content, water content and leaf moisture retention capacity showed significant differential responses. In this year the genotypes Sierra, LEF2RB and Seafarer decreased significantly their relative water content due to drought. The genotypes AC1022 and AC1028 did not exhibit a significant reduction in this variable (Table 2.8). Leaf moisture retention capacity was increased by drought. The highest increases were shown by the genotypes AC1028 and Seafarer. In 1990, water potential (Table 2.9) showed significant differential genotypic responses to drought treatments. This year, LS7 and LS104 genotypes, with LEF2RB genetic background, showed significant reductions in water potential under drought.

Leaf Orientation and Specific Leaf Weight*

Leaf orientation exhibited significant differences among genotypes in both treatments. Sierra exhibited a strong sensitivity for paraheliotropic movements under both stress and non-stress treatments (Table 2.28). The observed response is consistent with field observations in other years. AC1028 showed the opposite response exhibiting the lowest expression of this trait under both treatments.

Significant differences in specific leaf weight among genotypes under conditions of drought, but not under nonstressed treatments, are shown in Table

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* Data for these variables in 1990 are presented in Table 2.26.

Table 2.28. Averages and levels of significance of moisture retention capacity, leaf orientation, and specific leaf weight of twenty dry bean genotypes evaluated under drought and non-stress conditions. East Lansing, MI, 1990.

GENOTYPE		MOISTURE RETENTION CAPACITY[+] (%)		LEAF ORIENTATION[+] (2) (a)		SPECIFIC LEAF WEIGHT[+] (b)	
	R(1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
LS4	1	11.41	7.58 BCD	4.25 ABC	3.25 BCDE	3.92 AB	3.09
LS7	2	7.73	7.57 BCD	4.00 ABC	3.50 BCDE	2.65 ABCD	2.87
LEF2RB	3	13.85	10.15 AB	4.00 ABC	4.00 AB	2.60 ABCDE	2.57
Sierra	4	4.03	6.75 BCD	4.25 ABC	4.88 A	2.16 DEF	3.04
AS3	5	4.80	6.20 BCD	3.13 CD	2.63 DE	2.78 ABC	3.04
LS103	6	12.14	13.66 A	3.13 CD	3.50 BCDE	2.77 ABC	3.57
AS102	7	10.36	8.54 BC	3.25 CD	3.00 BCDE	2.35 CDEF	2.55
AS6	8	9.44	5.34 CD	4.13 ABCD	3.25 BCDE	2.36 CDEF	3.30
LS6	9	5.57	3.94 D	4.63 AB	3.88 ABC	2.56 ABCDE	3.17
LS102	10	8.77	3.89 D	4.88 A	3.50 BCDE	2.48 BCDEF	3.32
AC-1022	11	5.57	6.57 BCD	4.13 ABC	3.75 ABCD	3.04 A	3.55
AS11	12	8.05	5.85 CD	3.25 CD	2.50 E	2.36 CDEF	2.39
AS101	13	13.38	6.05 CD	3.13 CD	2.75 CDE	2.47 BCDEF	3.21

Table 2.28. (cont'd)...

GENOTYPE		MOISTURE RETENTION CAPACITY+ (%)		LEAF ORIENTATION+ (2) (a)		SPECIFIC LEAF WEIGHT+ (b)	
	R(1)	Drought	Non-Stress	Drought	Non-Stress	Drought	Non-Stress
AC-1028	14	9.39	5.57 CD	2.00 D	2.50 E	2.34 CDEF	2.95
LS11	15	9.91	8.71 BC	4.75 A	3.13 BCDE	2.57 ABCDE	3.42
AS1	16	4.13	4.38 D	3.38 BC	3.63 BCDE	1.99 F	2.49
LS101	17	10.39	6.91 BCD	3.88 ABC	3.63 BCDE	2.93 AB	2.72
AS104	18	8.98	4.42 D	3.25 CD	3.00 BCDE	2.24 CDEF	3.75
LS104	19	12.07	7.72 BCD	4.00 ABC	3.88 ABC	2.50 ABCDEF	2.58
AS103	20	7.16	4.19 D	3.38 BC	3.63 BCDE	2.08 EF	1.73
MEAN (3)		8.86 NS	6.70	3.74 NS	3.38	2.51	2.96 NS
CV %		58.50	35.16	16.91	16.16	12.60	17.92
SS (4)		NS	*	**	**	**	0.13
LSD 0.05		----	4.07^5	1.32	1.15	0.56	-----

Level of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at α = 0.05 or α = 0.10 as indicated.

1. Yield under drought ranking.
2. Averages of readings at pre-flowering stage and reproductive stage.
3. Asterisks indicated significance between drought treatments.
4. Significance among genotypes within drought treatments.
5. LSD at 0.10 level fo significance.

a. Scale: 1.0 Horizontal; 5.0 Vertical.

b. mg/cm^2

2.28. The highest values for this variable were observed mostly for LEF2RB genotype and its progeny AC1022, LS4, LS7, LS103, LS6, LS11 and LS 103.

Genotype x Environment Interaction

The results of the analysis of variation for the combined analysis for 1988 are summarized in Tables 5A to 9A and Tables 10A and 11A for 1988 and 1990 season, respectively.

The G x E interaction was not significant in 1988 for the following variables: number of pods without seed, seed size, harvest index, relative sink strength, days to flowering, water content, water potential, abaxial stomatal conductance, total stomatal conductance, transpiration rate and leaf temperature.

In 1990, number of pods without seed, total number of pods, number of seeds per pod, seed size, pod weight, leaf retention, harvest index, economic growth rate, relative sink strength, days to flowering, days to maturity, days of seed filling, stomatal conductance, transpiration rate, leaf moisture retention capacity, leaf orientation, specific leaf weight, leaf area index and stem diameter did not exhibit significant GxE interaction.

In both years the variables, pods without seed, seed size, days to flowering, stomatal conductance, harvest index and relative water content showed non significant GxE interaction. The results indicate that for these variables the effect of the drought treatment is additive.

Biological Significance of Drought Resistance Estimates in Dry Beans

Variability in Drought Resistance Estimates

The data for yield under drought, yield potential, yield differential, percent yield reduction, susceptibility index, geometric and arithmetic means are shown in Tables 2.29 and 2.30 for 1988 and 1990. The drought intensity determined as the yield reduction under drought averaged for all cultivars, was 0.78 and 0.63 in the

Table 2.29. Yield under drought and non-stress conditions and estimates of drought resistance of twenty genotypes grown under drought and non-stressed treatments. East Lansing, MI, 1988.

GENOTYPE		YIELD^{+} (g/pl)		MEAN (g/pl)		DIFF	YR	SI
	R (1)	Drought (Yd)	Non-Stress (Yp)	Arithmetic (2)	Geometric (3)	(g/pl) (4)	(%) (5)	(6)
Sierra	1	15.03 A	37.51 BC	26.27	23.74	22.48	60	0.77
LEF2RB	2	11.18 AB	48.13 AB	29.66	23.20	36.95	77	0.99
AC-1028	3	7.97 BC	55.51 A	31.74	21.03	47.54	86	1.10
AC-1022	4	6.26 C	39.47 B	22.87	15.72	33.21	84	1.08
Seafarer	5	6.02 C	27.65 C	16.84	12.90	21.63	78	1.00
Mean (7)		9.29	41.66***	25.48 NS	19.32	32.17***	78	1.00
CV %		35.5	23.3					
Significance(8)		***	***					
LSD 0.05		1.78	11.70					

Levels of significance: 0.10(*); 0.05(**); 0.01 (***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.

LSD (0.05) for genotype x drought treatment interaction = 8.32 g/pl.

Drought intensity = D = 1 - (Yd/Yp) = 1 - (9.29/41.66) = 0.78.

1. Yield under drought ranking.
2. Average over environments.
3. (Yd x Yp)$^{1/2}$.
4. Yield potential (Yp) - Yield under drought (Yd) = Yield differential.
5. Percentage of reduction; (Yp - Yd)/Yp.
6. Index to drought susceptibility = RI/D.
7. Asterisks indicate significance between drought treatments.
8. Significance among genotypes within drought treatments.

Table 2.30. Yield under drought and non-stress conditions and estimates of drought resistance of twenty genotypes grown under drought and non-stressed treatments. East Lansing, MI, 1990.

GENOTYPE		YIELD (g/pl)		MEAN (g/pl)		DIFF	YR	SI
	R (1)	Drought (Yd)	Non-Stress (Yp)	Arithmetic (2)	Geometric (3)	(g/pl) (4)	(%) (5)	(6)
LS4	1	10.37	21.99 ABC	16.18 AB	15.10	11.62	53	0.84
LS7	2	10.22	20.35 ABCD	15.28 ABCD	14.42	10.13	50	0.79
LEF2RB	3	9.68	19.11 ABCD	14.39 ABCDE	13.60	9.43	49	0.78
Sierra	4	9.31	22.49 ABC	15.90 ABC	14.47	13.18	59	0.94
AS3	5	9.23	16.74 ABCD	12.98 ABCDE	12.43	7.51	45	0.71
LS103	6	8.31	19.08 ABCD	13.69 ABCDE	12.59	10.77	56	0.89
AS102	7	8.12	21.82 ABC	14.97 ABCDE	13.31	13.70	63	1.00
AS6	8	8.09	25.79 AB	16.94 AB	14.44	17.70	69	1.10
LS6	9	7.99	20.09 ABCD	14.04 ABCDE	12.67	12.10	60	0.95
LS102	10	7.91	11.07 DE	9.49 E	9.36	3.16	29	0.46
AC-1022	11	7.62	26.85 A	17.24 A	14.30	19.23	72	1.14

Table 2.30. (cont'd)...

GENOTYPE	R (1)	YIELD (gr/pl) Drought (Yd)	Non-Stress (Yp)	MEAN (gr/pl) Arithmetic (2)	Geometric (3)	DIFF (gr/pl) (4)	YR (%) (5)	SI (6)
AS11	12	7.54	20.65 ABCD	14.09 ABCDE	12.48	13.11	63	1.00
AS101	13	7.29	23.70 ABC	15.49 ABCD	13.14	16.41	69	1.10
AC-1028	14	7.07	25.38 AB	16.23 AB	13.40	18.31	72	1.14
LS11	15	6.74	13.85 CD	10.29 DE	9.66	7.11	51	0.81
AS1	16	5.73	25.42 AB	15.57 ABCD	12.07	19.69	77	1.22
LS101	17	5.23	19.97 ABCD	12.60 ABCDE	10.22	14.74	74	1.17
AS104	18	4.57	16.39 BCD	10.48 CDE	8.65	11.82	72	1.14
LS104	19	4.06	18.73 ABCD	11.40 BCDE	8.72	14.67	78	1.24
AS103	20	2.10	3.19 E	2.64 F	2.59	1.09	34	0.54
Mean (7)		7.36	19.63 ***	13.49	12.02	12.27*	63	1.00
CV %		31.63	25.41					
Significance (8)		0.13	**	*				
LSD 0.05		----	10.44	5.57				

Level of significance: 0.10(*); 0.05(**); 0.01(***).

+. In each column any two means with a common letter are not significantly different by LSD Test at $\alpha = 0.05$.

LSD (0.10) for genotype x drought treatment interaction: 6.55 g/pl.

Drought intensity = D = 1 - (Yd/Yp) = 1 - (7.36/19.63) = 1 - 0.37 = 0.63

1. Yield under drought ranking
2. Average over environments
3. $(Yd \times Yp)^{1/2}$
4. Yield potential (Yp) - Yield under drought (Yd) = Yield differential
5. Percentage of reduction: (Yp - Yd)/Yp
6. Index of drougth susceptibility = Ri/D
7. Asterisks indicate significance between drought treatments.
8. Significance among genotypes within drought treatments.

1988 and 1990 experiments, respectively. The plant water deficits achieved in this research, as indicated by the drought intensity values, was higher than those obtained in previous studies conducted in dry beans by Samper (1984), Elizondo (1987) and Acosta-Gallegos (1988).

The susceptibility index (SI) calculated as proposed by Fisher and Maurer (1978) varied in a set of four genotypes evaluated in both years, from 0.77 to 1.10, with a difference of 0.33, in 1988 (Table 2.29). The range of variation for the same set of genotypes was from 0.78 to 1.14, with a difference of 0.36, in 1990 (Table 2.30). The genotypes Sierra and LEF2RB had susceptibility indices lower than 1.0 in both years. The genotypes AC1022 and AC1028 had susceptibility indices higher than 1.0. The susceptibility indices calculated for LEF2RB, AC1022, and AC1028 agree with the values obtained by Acosta-Gallegos (1988), even though the drought intensity was less in those experiments. A larger number of genotypes were evaluated in 1990. The range of variation for the experiment with twenty genotypes was from 0.54 to 1.24, with a difference of 0.70. The results suggest that a larger genotypic variability was generated in the progenies derived from crosses among selected genotypes.

The best performing genotypes under drought did have susceptibility indices lower than 1.0, e.g. Sierra and LEF2RB in 1988 (Table 2.29) and LS4, LS7, LEF2RB and Sierra in 1990 (Table 2.30). The lowest yields under drought were observed in genotypes with susceptibility indices equal or higher than 1.0, e.g. AC1028 and AC1022 in 1988 (Table 2.29) and AS104 and LS104 in 1990 (Table 2.30). However, an exception to this pattern was observed in the derived lines AS103 and LS11. Both yielded poorly under drought and susceptibility indices were low in these lines. The results indicate the dependency of the susceptibility index on yield potential.

A high arithmetic mean or a high yield potential is not necessarily associated with a low susceptibility index (high drought resistance) as seen in Tables 2.29 and 2.30. On the one hand, derived lines LS11 and AS103 with a low susceptibility index, or a relatively good yielding line LS102 under drought, are not necessarily associated with high yield potential. In addition, a dependency of the arithmetic mean, on yield differential and percentage of reduction on yield potential is observable.

The geometric mean values are expressions of the effect of water stress on the average yield of a genotype. To some extent, the geometric mean appears more associated with yield under drought. Since geometric means are the result of actual values direct comparison among years and locations are not possible, but comparisons should be done by comparing the ranking of the genotypes based on the geometric mean.

Relationships among Drought Resistance Estimates

The correlation coefficients and the levels of statistical significance of the relationships among drought resistance estimates for the 1988 and 1990 experiments are presented in Tables 2.31 and 2.32, respectively. A similar pattern was observed in both years for most of the significant correlation coefficients. The discussion of results will be based mainly on the results of 1990 and the relevant aspects of 1988, because of the larger number of observations used for the estimation of the correlations, the larger number of genotypes included in the evaluation, and the larger genotypic variability evaluated.

Yield under drought was positively correlated to yield potential, arithmetic and geometric mean. Percentage of yield reduction and susceptibility index were negatively related to yield under drought. The response was more evident in 1988 than in 1990. Interestingly yield under drought was significantly associated

Table 2.31. Significance of correlation coefficients (n=5) among drought resistance estimates, on a treatment basis, of five genotypes grown under drought and non-stressed treatments. East Lansing, MI, 1988.

ESTIMATES	YD (1)	YP (2)	AM (3)	GM (4)	DIF (5)	YR(6)
YP	0.139					
AM	0.449	0.947 ***				
GM	0.854 **	0.630	0.845 **			
DIF	-0.216	0.937 ***	0.775	0.319		
YR	-0.857 **	0.381	0.066	-0.466	-0.678	
SI(7)	-0.857 **	0.377	0.063	-0.467	0.675	1.000 ***

Level of Significance: 0.10(*); 0.05(**); 0.01(***)

1. Yield under drought
2. Yield potential
3. Arithmetic Mean
4. Geometric Mean
5. Yield differential (Yp - Yd)
6. Yield Reduction (Yp - Yd)/Yp
7. Susceptibility Index

Table 2.32. Significance of correlation coefficients (n=20) among drought resistance estimates on a treatment basis of twenty genotypes grown under drought and non-stressed conditions. East Lansing, MI, 1990.

TRAIT	YD (1)	YP (2)	AM (3)	GM (4)	DIF (5)
YP	0.448 **				
AM	0.681 ***	0.960 ***			
GM	0.854 ***	0.846 ***	0.961 ***		
DIF	-0.072	0.924 ***	0.780 ***	0.579 ***	
YR (6)	-0.223	0.732 ***	0.530 **	0.296	0.912 ***
SI (7)	-0.225	0.731 ***	0.529 **	0.295	0.912 ***

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

1. Yield under drought
2. Yield Potential
3. Arithmetic Mean
4. Geometric Mean
5. Yield Differential
6. Yield Reduction (%)
7. Susceptibility Index

with geometric mean in both years. The correlation coefficient and level of significance were similar in both years.

The correlation coefficient between susceptibility index and yield under drought was not significant when twenty genotypes were considered in 1990. When the genotypes LS102 and AS103 with susceptibility indices of O.46 and 0.54, respectively, were removed from the calculations due to their low susceptibility index the correlation coefficients became positive and statistically significant ($r=0.80$). Thus, the linear relationship between susceptibility index and yield under drought is maintained when the SI values are higher than 0.60. The results indicated that in genotypes with low drought susceptibility index the linear relationship with yield under drought is not followed, and that a low susceptibility index does not necessarily lead to high yield under drought.

Yield potential was positively and significantly correlated to all the other estimates. The correlation coefficients of this variable with the arithmetic and geometric mean and with yield differential were higher; and lower with yield reduction, susceptibility index and yield under drought, in that order. Arithmetic mean was correlated positively with all the drought resistance estimates, but it showed a larger correlation with yield potential, geometric mean and yield differential. Geometric mean showed a positive high correlation with yield under drought, yield potential and arithmetic mean, but the correlation with yield reduction and susceptibility index was not significant.

In 1988, only the correlation of yield differential with yield potential was significant. Yield differential did not show a significant correlation with yield under drought in both years. A positive significant relationship between yield potential, arithmetic mean and geometric mean was observed in 1990.

Drought Resistance Estimates and Morphological, Phenological and Physiological Characteristics Relationships

The correlation coefficients among susceptibility index, yield reduction, geometric mean and arithmetic mean with morphological, phenological and physiological traits and their levels of significance in 1988 are summarized in Tables 12A and 13A and in Tables 2.33 and 2.34 for the 1990 season. The pattern in the values and directions of the correlation coefficients for most of the variables is similar for both geometric and arithmetic mean in two years of evaluation. The correlations, however, with susceptibility index and yield reduction showed differences between years mostly in the level of significance (e.g. yield under drought and stem weight) and the direction of the relationship (e.g. pods with seed, pod weight and total biomass). The differences could be caused by a larger range of variation in the susceptibility indices of the genotypes included in the 1990 evaluation and by the differences in levels of water stress at which these genotypes were evaluated in both years. This response is similar to that described for the relation between susceptibility index and yield under drought, in which genotypes with different genetic mechanisms of drought resistance do not follow a linear relationship with yield. Then, a linear relationship was not observed in 1990 for the association between susceptibility index and yield nor yield components, such as pods with seed, seed number and seed size, pod weight and total biomass. In 1990, the inclusion of genotypes with lower susceptibility indices caused a reduction in the intensity of the relationship at a less severe drought intensity. Since this condition represents a more generalized and actual situation in a breeding program, the discussion about the relationships among the drought resistance estimates and plant characteristics will be conducted on the results of the 1990 experiments.

In Tables 2.33 and 2.34 the similarity in performance in values between susceptibility index and yield reduction and between geometric mean and

Table 2.33. Significance of correlation coefficients (n=20) of drought resistance estimates with yield components, biomass traits, phenological and morphological characteristics and efficiency and partitioning indexes in twenty genotypes grown under drought conditions. East Lansing, MI, 1990.

TRAIT	SI (1)	YR (2)	GM (3)	AM (4)
YIELD COMPONENTS				
Yield (D)	-0.225	-0.223	0.854 ***	0.681 ***
Pods with Seed	0.018	0.018	0.755 ***	0.649 ***
Seeds/Pod	-0.434 *	-0.425 *	0.225	0.110
Seed Number	-0.113	-0.109	0.726 ***	0.605 ***
Seed Size	-0.044	-0.047	0.506 **	0.417 *
BIOMASS				
Stem Weight	0.459 **	0.460 **	0.188	0.302
Pod Weight	0.258	0.267	0.709 ***	0.680 ***
Total Biomass	0.103	0.105	0.743 ***	0.723 ***
PHENOLOGY				
Days to Maturity	0.447 **	0.449 **	-0.226	-0.051
Days to Seed Filling	0.471 **	0.471 **	-0.283	-0.087
MORPHOLOGY				
Leaf Area Index	0.230	0.235	0.443 **	0.434 *
Stem Diameter	0.449 **	0.456 *	0.617 ***	0.668 ***
PARTITIONING				
Harvest Index	-0.497 **	-0.499 **	0.525 **	0.319 *
Economic Growth Rate	-0.330	-0.329	0.743 ***	0.548 **
Seed Growth Rate	-0.385 *	-0.384 *	0.643 ***	0.439 *
Biomass Growth Rate	0.006	0.009	0.705 ***	0.598 ***
Relative Sink Strength	-0.544 *	-0.544 **	0.451 ***	0.230

Level of Significance: 0.10(*); 0.05(**); 0.01(***)
1. SI = Drought Susceptibility Index
2. YR = Yield Reduction (%)
3. GM = Geometric Mean
4. AM = Arithmetic Mean

Table 2.34. Significance of correlation coefficients (n=20) of drought resistance estimates with physiological traits of twenty genotypes grown under drought. East Lansing, MI, 1990.

TRAIT	SI (1)	YR (2)	GM (3)	AM (4)
Water Potential	0.101	0.100	0.088	0.107
Moisture Retention Capacity	0.065	0.061	-0.001	-0.014
Relative Water Content	-0.370 *	-0.371 *	-0.163	-0.266
Water Content	-0.053	-0.056	-0.182	-0.203
Transpiration Rate	0.001	0.006	0.436 *	0.399 *
Stomatal Conductance	-0.098	-0.096	0.362	0.292
Leaf Temperature	0.387 **	0.384 **	-0.318	-0.171

Level of Significance: 0.10(*); 0.05(**); 0.01(***)

1. Drought Susceptibility Index
2. Yield Reduction (%)
3. Geometric Mean
4. Arithmetic Mean

arithmetic mean is notable. This behavior indicates the high association within both sets of variables. Given the relationships among drought resistance estimates the discussion will be based on susceptibility index and geometric mean but it can be extended to the two other estimates.

In Tables 2.33 and 2.34 it is seen that susceptibility index and geometric mean were differentially related to the same set of variables measured under drought conditions. The differences were found in the values, direction and level of statistical significance of the correlation coefficients. As a result, in most of the variables the susceptibility index is found to be correlated to variables other than those associated with the geometric mean. Thus, geometric mean was associated significantly with yield under drought, number of pods with seed, number of seeds and seed size but not with the number of seeds per pod. However, the negative and significant correlation between susceptibility index with the number of seeds per pod, suggests that higher number of seeds per pod may be associated with a higher ability of the genotype to produce under drought.

Susceptibility index was positively and significantly associated with stem weight but not with pod weight or total biomass. The last variables are positively correlated instead with geometric mean. The phenological characteristics days to maturity and days of seed fill were correlated with susceptibility index but not with geometric mean.

Leaf area index was positively associated with geometric mean but not with susceptibility index. Stem diameter was one of the two variables of all the set of correlated variables that was significantly correlated to both susceptibility index and geometric mean.

All the partitioning variables were positively associated with geometric mean, while harvest index, seed growth rate and relative sink strength were negatively and significantly correlated to the susceptibility index. Thus, an increase in the efficiency of translocation increased the stability of the yield potential under stress.

Among the physiological characteristics (Table 2.34) only relative water content and leaf temperature showed significant correlations, negative and positive, respectively, with susceptibility index but not with the geometric mean. Instead, the geometric mean was found to be positively correlated to transpiration rate and stomatal conductance and negatively with leaf temperature, although the latter two variables were not statistically significant. The result shows the important role of leaf temperature in affecting the susceptibility of a genotype and limiting the expression of yield potential to stress.

The correlations between yield components and phenological, partitioning and physiological responses with susceptibility index showed an opposite sign to that observed for the geometric mean. The negative association of variables with susceptibility index indicates that when a larger expression of the trait under drought occurs there is a low susceptibility index and, therefore, a high drought resistance. Positive associations, however, indicate that an increase in the expression of a trait under drought increases the susceptibility of a genotype to water deficit.

Biological Significance of Shoot-Characteristics for Yield under Drought

Drought resistance is a complex trait determined genotypically by a differential combination of morphological, phenological and physiological individual characteristics of the shoot. In breeding for drought resistance the identification of traits other than yield could facilitate and improve the efficiency of the selection process. Secondary traits could be selected if their biological value, determined by their relationships with yield or other key morpho-physiological traits under drought, is known. In this section results about the relationships among yield with morphological, phenological and physiological shoot responses under drought, based on the estimation of linear correlation coefficients, are presented.

Yield and Shoot-Characteristics Relationships under Drought

The level and type of association for most of the variables was similar in both years of evaluation and few differences were detected between them (Tables 2.35, 2.36 and 2.37 and Tables 2.14A, 2.15A and 2.16A of Appendix A). In the tables the correlation coefficients among yield components and between yield components with morphological, phenological and physiological traits for the 1988 and 1990 experiments are shown. The description of results will be based on the data of 1990 because in this year there were a greater genotypic variability, and a larger number of variables to be correlated. In addition, the results in both years were similar.

Yield and yield components under drought

The correlation coefficients among yield components under drought and their statistical significances are shown in Table 2.35. The yield components, number of pods with seed, number of seeds, number of seeds per pod and seed size displayed a positive and significant association with yield under drought; while number of pods without seed was negatively and significantly associated with yield under drought.

The number of pods without seed was negatively and significantly associated with number of pods with seed, number of seeds and number of seeds per pod. This finding indicates the importance of pod setting in the definition of yield under drought because a larger number of pods without seed corresponds to a reduction in the expression of the other yield components.

Table 2.35. Significance of correlation coefficients (n=40) among yield components of twenty genotypes grown under drought conditions. East Lansing, MI, 1990.

TRAIT	YIELD (D)	PWS	PWOS	PTN	SN	SS
PWS	0.834 ***					
PWOS	-0.501 ***	-0.389 **				
PTN	-0.059	0.157	0.849 ***			
SN	0.872 ***	0.902 ***	-0.428 ***	0.059		
SS	0.299 *	-0.067	-0.288 *	-0.348 **	-0.156	
S/P	0.350 **	0.057	-0.476 ***	-0.478 ***	0.442 ***	-0.125

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
Yield (D) = Yield under drought.
PWS = Pods With Seed.
PWOS = Pods Without Seed.
PTN = Total Number of Pods.
SN = Seed Number.
SS = Seed Size.
S/P = Seeds per Pod.

Table 2.36. Significance of correlation coefficients (n=40) among yield components with morphological and phenological traits and partitioning indexes of twenty genotypes grown under drought conditions. East Lansing, MI, 1990.

TRAIT	YIELD (D)	PWS	PWOS	TP	SN	SS	S/P
STW	-0.192	-0.036	0.259 *	0.257 *	-0.105	-0.318 **	-0.258 *
PW	0.664 ***	0.722 ***	-0.125	0.280 *	0.620 ***	0.037	-0.067
TB	0.738 ***	0.720 ***	-0.235	0.161	0.690 ***	0.029	0.091
DF	-0.110	-0.174	-0.314 **	-0.436 ***	-0.115	0.055	0.179
MAT	-0.478 ***	-0.424 ***	0.155	-0.078	-0.417 ***	-0.114	-0.115
DSF	-0.522 ***	-0.440 ***	0.276 *	0.043	-0.449 ***	-0.150	0.326 **
HI	0.774 ***	0.551 ***	-0.672 ***	-0.404 **	0.634 ***	0.444 ***	0.469 ***
EGR	0.966 ***	0.809 ***	-0.421 ***	0.013	0.846 ***	0.268 *	0.326 **
SGR	0.892 ***	0.734 ***	-0.354 **	0.042	0.785 ***	0.232	0.325 **
RSS	0.732 ***	0.523 ***	-0.537 ***	-0.275 *	0.612 ***	0.360 **	0.434 ***
BGR	0.839 ***	0.795 ***	-0.238	0.202	0.772 ***	0.068	0.130

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
Yield (D) = Yield under drought.
PWS: Pods With Seed
PWOS: Pods Without Seed
TP: Total Number of Pods
SN: Seed Number
SS: Seed Size
S/P: Seeds per Pod
STW: Stem Weight
PW: Pod Weight

TB: Total Biomass
DF: Days to Flower
MAT: Days to Maturity
DSF: Days of Seed Fill
HI: Harvest Index
EGR: Economic Growth Rate
SGR: Seed Growth Rate
RSS: Relative Sink Strength
BGR: Biomass Growth Rate

Yield and morphological characteristics under drought

Since stem weight (SW) was negatively associated to seed size and number of seeds per pod and positively to number of pods without seed, the trait was negatively associated with yield under drought although the association was not significant. Instead, pod wall weight and total biomass were positively correlated to pods with seed and seed number, consequently, both traits showed a positive correlation with yield under drought (Table 2.36). Leaf retention, the dry weight of leaves at physiological maturity, showed a pattern similar to that observed for stem weight. The response could be related to the earliness of the genotypes (Table 2.37).

Morphological traits such as stem diameter displayed a positive correlation with number of pods with seed and seed number, thus, its association with yield was positive and significant (Table 2.37). Leaf orientation showed a positive association with number of seeds per pod (Table 2.37). Leaf area index was positively associated to the number of pods with seed and total number of pods and negatively with number of seeds per pod. The combination of these different associations result in a non-significant linear relationship of LAI with yield under drought (Table 2.37). Leaf size and specific leaf weight did not show any linear relationship with yield components. The response in the latter two variables suggests that the relation between these traits with yield under drought might follow a function other than a linear one.

Yield and phenological characteristics under drought

The importance of the phenological characteristics results from their negative relationships with important yield components such as number of pods with seed and total number of seeds (Table 2.36).

Days to flowering was negatively correlated with pods without seed and total number of pods but not with yield under drought. The negative correlation

Table 2.37. Significance of correlation coefficients (n=40) among yield components with morphological traits of stem and leaf of twenty genotypes grown under drought. East Lansing, MI. 1990.

TRAIT	YIELD (D)	PWS	PWOS	TP	SN	SS	S/P
LR	-0.481 ***	-0.256	0.431 ***	0.316 **	-0.286 *	-0.492 ***	-0.249
SD	0.271 *	0.341 ***	-0.018	0.177	0.281 *	-0.125	-0.122
LO	-0.042	-0.122	0.222	0.173	-0.001	-0.064	0.259 *
LS	0.111	0.160	0.086	0.184	0.090	0.039	0.213
LAI	0.171	0.343 **	0.192	0.403 ***	0.203	-0.100	-0.360 **
SLW	0.112	0.146	0.040	0.127	0.218	-0.202	0.213

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
Yield (D) = Yield under drought.
PWS = Pods With Seed.
PWOS = Pods Without Seed.
TP = Total Number of Pods.
SN = Seed Number.
SS = Seed Size.
S/P = Seeds per Pod.

LR = Leaf Retention.
SD = Stem Diameter.
LO = Leaf Orientation.
LS = Leaf Size.
LAI = Area Index.
SLW = Specific Leaf Weight.

Table 2.38. Significance of correlation coefficients among biomass related traits with phenological and morphological traits of twenty genotypes grown under drought conditions. East Lansing, MI, 1990.

TRAIT	STW	PW	TB	LR
DF	0.325 **	-0.045	0.117	0.343 **
MAT	0.463 ***	-0.148	-0.091	0.593 ***
DSF	0.439 ***	-0.159	-0.141	0.585 ***
SD	0.676 ***	0.460 ***	0.707 ***	0.402 ***
LO	-0.427 ***	-0.057	-0.313 **	-0.331 ***
SLW	-0.187	0.095	-0.020	-0.103
LS	0.439 ***	0.094	0.379 **	0.314 **
LAI	0.475 ***	0.302 **	0.478 ***	0.311**
PW	0.134			
TB	0.512 ***	0.741 ***		
LR	0.888 ***	-0.142	0.179	

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
STW = Stem Weight.
PW = Pod Weight.
TB = Total Biomass.
LR = Leaf Retention.
DF = Days to Flower.
MAT = Days to Maturity.
DSF = Days of Seed Filling.
HI = Harvest Index.
EGR = Economic Growth Rate.
SGR = Seed Growth Rate.
RSS = Relative Sink Strength.
BGR = Biomass Growth Rate.

can be explained by the reduction of the seed filling period when the number of days to flowering is increased, resulting in a larger number of pods without seed when the number of days to flowering is shorter (Table 2.36). Since number of days to physiological maturity and seed filling period were negatively correlated to number of pods with seed and seed number, they were also negatively associated with yield under drought. Days to seed fill was positively associated with number of seeds per pod. Thus, higher yield under drought could be achieved by a combination of early maturity and a relative short seed filling period (Table 2.21).

Yield and partitioning indices under drought

The general pattern observed in the correlations between partitioning traits and yield under drought was the positive association of these traits with the number of pods with seed, number of seeds, seed size and number of seeds per pod and their negative correlation with number of pods without seed (Table 2.36). Harvest index, relative sink strength, economic growth rate and seed growth rate were the characteristics most related to yield and yield components. The ranking of the correlation coefficients with yield were as follows: economic growth rate (0.97), seed growth rate (0.89), biomass growth rate (0.84), harvest index (0.77) and relative sink strength (0.73). The results illustrate the importance of both the period of seed filling and the efficiency in the accumulation of dry matter by day in the seed measured by seed growth rate (Table 2.39). Equally important was the efficiency of photosynthesis measured as the rate of biomass accumulated per day and the assimilation distribution measured by harvest index which (Table 2.36) is a stable parameter.

Table 2.38 shows the correlation coefficients among biomass characteristics and phenological and morphological characteristics. The data showed the positive association of stem weight and leaf retention with days to flower, days to physiological maturity and seed filling period. The responses help explain the negative association of the traits with yield under drought. Stem diameter, leaf size and leaf area index showed a highly significant correlation with biomass components (Table 2.38). Leaf orientation displayed a negative correlation with biomass components. Thus, the ability of paraheliotropic movements is associated with lower dry weight in the stem, leaves and total biomass at maturity.

Table 2.39 shows the negative significant association of stem weight and leaf retention with economic growth rate and relative sink strength. The response indicates that the accumulation of dry matter in leaves and stems affects negatively the accumulation of dry matter into the seed. Days to seed fill and days to maturity showed a significant negative association with harvest index, economic growth rate, seed growth rate, relative sink strength and biomass growth rate. Days to flower showed a negative association with all the five indices but the association was not significant for harvest index and relative sink strength. Thus, lateness seems not to be a favorable phenological adaptation for an efficient dry matter accumulation under drought (Table 2.39). Total biomass showed a positive association with economic growth rate and seed growth rate. This relationship emphasizes the importance of dry matter accumulated before and after anthesis for seed production under drought (Table 2.39). Morphological characteristics such as leaf orientation, leaf area index and leaf size were not correlated with harvest index, economic growth rate and seed growth rate. Only stem diameter and leaf area index were positively correlated with biomass growth rate. All the relationships indicate that individual morphological traits were not linearly related with yield; however, they can be related with the accumulation of dry matter. The analysis of the correlation coefficients showed that yield components were negatively associated to maturity (lateness) whereas biomass

Table 2.39. Significance of correlation coefficients (n=40) among partitioning indexes with biomass and morphological traits of twenty genotypes grown under drought conditions. East Lansing, MI, 1990.

TRAIT	HI	EGR	SGR	RSS	BGR
STW	-0.651 **	-0.277 *	-0.316 **	-0.628 ***	0.273 *
PW	0.231	0.592 ***	0.501 ***	0.198	0.715 ***
TB	0.209	0.647 ***	0.554 ***	0.186	0.920 ***
LR	-0.790 ***	-0.551 ***	-0.564 ***	-0.764 ***	-0.072
DF	-0.164	-0.286 *	-0.319 **	-0.229	-0.491 ***
MAT	-0.607 ***	-0.677 ***	-0.785 ***	-0.787 ***	-0.464 ***
DSF	-0.656 ***	-0.700 ***	-0.816 ***	-0.845 ***	-0.491 ***
SD	-0.240	0.179	0.112	-0.247	0.556 ***
LO	0.146	0.042	0.125	0.245	-0.165
SLW	0.129	0.137	0.132	0.134	0.042
LS	-0.231	0.057	0.006	-0.265 *	0.286 *
LAI	-0.249	0.145	0.131	-0.195	0.411 ***
HI	----	0.796 ***	0.772 ***	0.942 ***	0.406 ***
EGR			0.974 ***	0.819 ***	0.841 ***
SGR				0.802 ***	0.802 ***
RSS					0.429 ***

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

HI = Harvest Index.
EGR = Economic Growth Rate.
SRG = Seed Growth Rate.
RSS = Relative Sink Strength.
BGR = Biomass Growth Rate.
STW = Stem Weight.
PW = Pod Weight.
TB = Total Biomass.
LR = Leaf Retention.

DF = Days to Flower.
MAT = Days to Maturity.
DSF = Days of Seed Filling.
SD = Stem Diameter.
LO = Leaf Orientation.
SLW = Specific Leaf Weight.
LS = Leaf Size.
LAI = Leaf Area Index.

was positively associated with it. The balance between the accumulation of dry matter in the seed and vegetative organs is a key process under drought, explaining the importance of harvest index and relative sink strength under drought. The results agree with the positive correlation between stem weight and leaf retention and days to flowering, days of seed filling and days to maturity (Table 2.38), indicating that both traits are lateness dependent.

Yield and physiological characteristics under drought

The statistical significance of the correlation coefficients among physiological traits with yield and biomass components, and phenological and morphological traits and partitioning indices are summarized in Table 2.40. Correlation coefficients among physiological characteristics are presented in Table 2.41.

The most important physiological characteristics correlated with yield-biomass components, and morphological-phenological traits were transpiration rate, stomatal conductance, leaf temperature and water content, in that order. Traits like water potential, leaf moisture retention capacity and relative water content showed few significant linear correlations with yield under drought.

The negative association between days to flower, physiological maturity and seed filling period with transpiration rate and stomatal conductance, and the positive association of the phenological traits with leaf temperature indicate that a larger stomatal control is exerted in late genotypes, causing the increase in temperature. Additionally, the significant positive association of transpiration rate and stomatal conductance with all the partitioning and efficiency indices, mostly with economic growth rate, seed growth rate and biomass growth rate, indicate the key interactive role of these physiological characteristics under drought in dry beans.

Table 2.40. Significance of correlation coefficients (n=40) among water use and water relation traits with yield components, biomass, phenology, morphology and partitioning traits of twenty genotypes grown under drought. East Lansing, MI, 1990.

TRAIT	WP	MRC	RWC	WC	TR	SC	LT
YIELD COMPONENTS							
Yield (D)	-0.103	-0.183	-0.114	-0.367**	0.475***	0.469***	-0.477***
Pods with Seed	-0.046	-0.115	-0.169	-0.461***	0.503***	0.482***	-0.484***
Pods without Seed	-0.043	0.153	-0.145	-0.117	-0.132	-0.054	0.269*
Total Number of Pods	-0.107	0.071	0.215	-0.417***	0.233	0.297*	-0.047
Seeds/Pod	-0.265*	-0.129	-0.125	-0.185	0.089	0.109	-0.286*
Seed Number	-0.127	-0.170	-0.292*	-0.572***	0.494***	0.497***	-0.518***
Seed Size	-0.003	-0.055	0.320**	0.304**	0.062	0.008	-0.004
BIOMASS							
Stem Weight	-0.248	-0.032	-0.223	-0.059	-0.146	-0.161	0.288*
Pod Weight	-0.035	-0.084	-0.034	-0.233	0.298*	0.226	-0.165
Leaf Retention	0.155	0.096	-0.212	-0.022	-0.294*	-0.284*	-0.366**
Total Biomass	-0.098	-0.179	-0.260*	-0.367**	0.310**	0.281*	-0.183
PHENOLOGY							
Days to Flower	0.057	0.095	-0.043	0.332**	-0.476***	-0.595***	0.280*
Days to Maturity	0.012	0.024	-0.247	0.110	-0.394**	-0.503***	0.436***
Days of Seed Filling	-0.003	-0.003	-0.275*	0.023	-0.309**	-0.400***	0.420***

Table 2.40. (cont'd)...

TRAIT	WP	MRC	RWC	WC	TR	SC	LT
MORPHOLOGY							
Leaf Orientation	-0.144	0.195	0.234	0.011	0.016	0.002	-0.053
Specific Leaf Weight	-0.261*	0.261*	-0.212	-0.262*	0.273*	0.252	-0.272*
Leaf Size	-0.054	-0.357**	-0.313*	-0.121	0.360**	0.272*	0.055
Leaf Area Index	0.231	-0.160	-0.164	-0.181	0.278*	0.213	0.029
Stem Diameter	0.221	-0.221	-0.223	-0.070	0.202	0.154	-0.083
PARTITIONING							
Harvest Index	-0.146	-0.033	0.135	-0.109	0.355**	0.340**	-0.461***
Economic Growth Rate	-0.020	-0.162	0.046	-0.286*	0.476***	0.514***	-0.482***
Seed Growth Rate	-0.028	-0.114	0.098	-0.256	0.441***	0.500***	-0.478***
Biomass Growth Rate	0.124	-0.207	-0.044	-0.289*	0.412***	0.434***	-0.313**
Relative Sink Strenght	-0.060	-0.025	0.187	-0.092	0.069	0.346**	-0.459***

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
WP = Water Potential.
MRC = Moisture Retention Capacity.
RWC = Relative Water Content.
WC = Water Content.
TR = Transpiration Rate.
SC = Stomatal Conductance.
LT = Leaf Temperature.

Table 2.41. Significance of correlation coefficients (n=40) among water use and water relations related traits of twenty genotypes grown under drought. East Lansing, MI, 1990.

TRAIT	WP	MRC	RWC	WC	TR	SC
MRC	-0.026					
RWC	0.298*	0.033				
WC	0.337**	0.043	0.668***			
TR	-0.099	-0.590***	-0.179	-0.401***		
SC	-0.087	-0.509***	-0.196	-0.444***	0.936***	
LT	0.011	0.150	0.062	0.186	-0.470***	-0.567***

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
WP = Water Potential.
MRC = Moisture Retention Capacity.
RWC = Relative Water Content.
WC = Water Content.
TR = Transpiration Rate.
SC = Stomatal Conductance.
LT = Leaf Temperature.

The morphological traits, specific leaf weight and leaf size showed the greater number of correlations with physiological traits. Specific leaf weight displayed a negative association with water potential, relative water content, water content and leaf temperature, suggesting that the increase in specific leaf weight is associated with a reduction in the values of these variables (Table 2.40). At the same time, specific leaf weight showed a positive relationship with transpiration rate and a negative association with leaf moisture retention capacity (Table 2.40). As expected, an increase in specific leaf weight could result in an increase in transpiration rate and a reduction in leaf temperature, making specific leaf weight a useful and easy trait to measure.

Increases in leaf size were related to reductions in leaf moisture retention capacity and relative water content; and an increase in transpiration rate and stomatal conductance. Due to the positive association with transpiration rate and stomatal conductance, leaf size could be a useful trait to measure. Leaf area index showed only a positive relationship with transpiration rate, indicating that larger leaf area indices correspond to higher rates of transpiration. Leaf orientation and stem diameter did not show any relationship with the physiological traits.

Water content was negatively associated with yield, number of pods with seed, total number of pods, number of seeds and total biomass, suggesting that a high water content was accompanied by a reduction in the expression of the yield components and in the final accumulation of dry matter. This finding agrees with the response described for transpiration.

The importance of leaf temperature is based on the negative relationships with yield, biomass and partitioning indices and its positive association with phenological traits. The responses indicate the negative effect of the increase in temperature on the physiological growth process, occurring mainly in late maturing genotypes in which both transpiration and stomatal conductance were low (Table 2.40).

Yield and Shoot-Characteristics Relationships under Non-Limiting and Drought Conditions

Additional evidence about the biological significance of morpho-physiological traits for yield under drought results from the comparison of the correlation coefficients of the association of yield with yield components, biomass components, phenological traits, partitioning and efficiency indices, morphological traits and physiological characteristics under both drought and non-stress conditions. The correlation coefficients of yield components with yield under drought and with yield under non-stress conditions are shown in Tables 2.35 and 17A, respectively. Correlation coefficients of the relationship between biomass, phenological and partitioning traits with yield under drought and nonstressed conditions are described in Tables 2.36 and 18A, respectively. Correlation coefficients showing the association of morphological traits with yield under drought and non-stress conditions are shown in Tables 2.37 and 19A, respectively. In Tables 2.40 and 22A the correlation coefficients of the association between physiological traits with yield under drought and non-stress conditions, respectively, are described.

The comparison indicated that number of pods with seed, number of pods without seed, total number of seeds, number of seeds per pod, pod weight, total biomass, harvest index, economic growth rate, seed growth rate, relative sink strength, biological growth rate, stem diameter and water content did exhibit similar values and levels of statistical significance of the correlation coefficients in both drought treatments. The expression of this "yield-biomass" set of traits under drought was positively associated with the geometric mean. In addition to the "yield-biomass" set of traits, total number of pods and relative water content were negatively and significantly associated with yield, limiting its expression under non-stress conditions.

An additional set of specific yield related characteristics was detected only under drought. The association of these "drought expressed" traits with yield was enhanced and the correlation coefficients were larger and statistically significant under drought but not under the non-stress treatment. Thus, pods without seed, seed size, days to maturity and days of seed fill, harvest index, relative sink strength, leaf retention, transpiration rate, stomatal conductance and leaf temperature had larger correlation coefficient values and were significantly associated with the expression of yield under drought. Among these traits, seed size, stem diameter, transpiration rate, stomatal conductance, harvest index and relative sink strength were additionally associated with geometric mean, indicating their role in the enhancement of the expression of yield under drought. On the other hand, pods without seed, days to physiological maturity, days of seed fill and leaf temperature were negatively associated with yield under drought but positively associated with susceptibility index, suggesting the important role of these traits in the determination of the susceptibility of a genotype to drought.

A third set of "non-yield related" variables integrated by morphological (leaf orientation, leaf size, leaf area index and specific leaf weight) and physiological (water potential, leaf moisture retention capacity and relative water content) variables did not show a direct linear relationship with yield under either treatment. However, leaf size, leaf area index and specific leaf weight were positively associated with the average expression of yield potential since they were correlated to the geometric mean. Interestingly, days to flowering did not show any relationship with yield under drought and yield potential, contrasting with the behavior of maturity and days to seed fill which were significantly associated with yield under drought and susceptibility index. Even though the morphological and physiological traits included in this set did not exhibit a linear relationship with yield under both treatments, they were related to transpiration and stomatal conductance. Both physiological processes were significantly associated with yield under drought.

DISCUSSION

The Effects of Drought

In drought prone environments, the inter-annual and location-to-location variation in rainfall is large (Blum, 1988). Given this variation, drought is normally an uncertain condition varying in incidence, severity and timing (Edmeades *et al.*, 1989). Thus, under normal rainfall conditions it is difficult to obtain a consistent response by exposing large plant populations to conditions which either simulate or represent a realistic drought condition in the field (McWilliam, 1989; Ludlow and Muchow, 1990). As a result, the lack of repeatability in time and intensity of drought is one of the most frequent methodological constrains limiting the progress in breeding for drought resistance in dry beans and other crops.

The experiments reported herein were grown in two contrasting treatments, drought and non-stress. The drought condition was obtained by using a rain-out shelter where rainfall and dew were excluded during the reproductive stage of development. In both years of evaluation the system was effective in reducing the soil water content (Tables 2A and 3A) and causing a severe water stress in the crop. The levels of drought intensity reached in 1988 and 1990 were 0.78 and 0.63, respectively. These levels of drought intensity are the highest reported for experiments conducted in dry beans under drought until now. Drought intensities of 0.08 and 0.29 were reported by Samper (1984) for experiments conducted under normal rainfall in Mexico. Elizondo (1987) achieved a drought intensity of 0.17 in a set of experiments grown in Michigan by using plastic sheets to exclude rainfall under field conditions. Acosta-Gallegos

(1988) had drought indices of 0.48 and 0.59 in two sets of experiments, where the highest drought intensity was obtained in a rain-out shelter. The combined effect of a long season and the effective reduction of the expression of yield potential due to water stress resulted in the high levels of drought intensity observed.

Thus, the results reported now could be considered representative of the effects of drought during the reproductive stage of development in dry bean cultivars grown in Michigan because the severe levels of drought intensity registered in both years were due to the effective reduction in the soil water content. In 1988, the soil water content after flowering in the drought treatment was 63, 50 and 37% less than in the non-stress treatment, at the depths 0 - 15, 16 - 30 and 31 - 45 cm, respectively (Table 2A). In 1990, for the same growth period, the reduction in water content in the drought treatments about the non-stress treatment was 50 and 20% at depths of 0 - 30 and 31 - 60 cm (Table 3A). The soil water content in both years was slightly higher in the drought treatment than in the non-stress treatment in the deepest sampled soil layers, at 46 - 60 cm in 1988 and 90 cm in 1990.

The measurement of soil water content is a common means of describing the levels of drought reached in a specific study. However, the determination of these measurements either is labor intensive or requires specific instrumentation. In addition, the comparison among experiments is difficult because of differences in precision and methodology of estimation and soil characteristics.

Instead, drought intensity based on yield, which is the final integrated response of a genotype to water stress and the final goal in plant breeding may be more useful. The parameter is easy to estimate and does not require additional instrumentation or training. Drought intensity can be a useful index to compare different experiments because it is based on the average performance of a set of genotypes rather than on individual responses. The use of drought intensity does not exclude the estimation of soil parameters for more precise physiological studies. For these reasons drought intensity is a useful parameter for the characterization of water stress between experiments and evaluating genotypes in a breeding program.

Despite the differences in the water stress observed in both years, most of the variables responded similarly to the drought condition. The response in most of the variables was more intense when the drought intensity was higher, regardless of the number and class of genotypes evaluated. The correlation coefficient of the relationship between the responses observed in both years was 0.88. The range of drought intensity observed in the experiments was between 0.63 and 0.78 (Tables 2.4 and 2.5). The generalized response of the dry bean plant is the reduction in the expression of traits with positive effects on yield and the increase of the expression of traits with a negative impact on yield and biomass accumulation. The response was intensified when water stress was increased.

Biological Significance of Drought Resistance Estimates

The result of drought is the reduction in the accumulation of biomass and economic yield. Yield reduction occurs as a result of the reduction in the expression of characteristics with positive effect on yield. Since drought resistance or susceptibility to drought in terms of yield is a function of yield reduction, yield under drought would be the residual expression of yield potential (Blum, 1988) as affected by water stress. In this study, drought resistance is defined as the minimal reduction on yield potential due to drought.

Yield under drought depends on the yield potential and the reduction of yield due to drought. For this reason yield potential correlates positively with yield under drought, as observed by Fisher and Maurer (1978). A similar positive relationship between yield potential and yield under drought of dry bean genotypes occurred in both years of the study. The correlation between variables was significant only in 1990. Thus, the linear relationship was significant at the lowest (0.63) but not at the highest drought intensity (0.78). The result suggests that severe water stress limits severely the expression of yield potential in dry beans and disrupts the linear relationship between yield potential and yield under drought in this crop. As a result, the degree of correlation depends on the severity of the stress. At severe levels of drought it is possible that traits not related with yield potential may be more influential in the expression of yield under drought allowing survival traits to modulate the expression of yield potential under severe water stress.

Yield potential and yield under drought in dry beans are poor estimates of drought resistance. Even though both yields can be positive and significantly correlated, as was demonstrated in this study, the best yielding genotypes under non-stress conditions were not the best under drought. AC-1028 and AC-1022 genotypes, in 1988 and 1990, respectively, are a good illustration of the response. On the other hand, the best yielding genotypes under drought were not the best under non-stress conditions. The observation can be explained by the differential genotypic response to the effects of the environment resulting from the combination of specific sets of traits in each genotype. The significant treatment differences (Table 2.9) in the different plant characteristics support the argument.

Results reported agree with the observation that yield under stress is a poor estimate of drought resistance (Blum, 1982). Since the association between yield and SI is only significant under severe levels of water stress. In addition, under mild stress the relationship between Yd and SI is not observed in highly drought resistant genotypes because they may have either low or high yield under drought. The dependency of yield under drought on yield potential, susceptibility index and maturity (Edmeades *et al.*, 1989); the low genetic variation of yield under drought compared with the environmental component (Frey, 1964); and the lower heritability of yield under stress (Blum, 1988), are factors that may contribute to the poor estimation of drought tolerance. Thus, yield under drought should not be equated to drought resistance *per-se*.

Differential yield reduction due to stress has commonly been used as criteria for selecting cultivars with resistance to water stress. However, the strategy can be counterproductive because of the likelihood of selecting low yielding cultivars whose yield differential (Yp - Yd) is small (Samper, 1984). The present results did not show any correlation between the differential yield reduction and yield under drought in both years. They suggest that differential yield reduction is not a useful drought resistance estimate in dry beans.

The inability to identify specific parameters that represent the key traits which collectively confer survival and productivity has limited breeding for drought resistance (Simpson, 1981). The development of an index representing in a single value the effect of water stress on yield and the components of yield under drought is necessary. Fisher and Maurer (1978) and Samper (1984) used the susceptibility index (SI) and the geometric mean (GM), respectively, to characterize drought resistance in dry bean genotypes. However, the biological significance of both estimates in relation to yield and other significant plant traits has not been demonstrated in dry beans. In addition, the practical usefulness of both estimates in a breeding program has not been validated in dry beans until now. In an early study, Samper (1984) suggested the utilization of the geometric mean rather than the yield differential or the susceptibility index for the selection of genotypes for drought resistance. This recommendation can only be applied to conditions of low water stress because the results were obtained when the drought intensity was only 0.08.

Genotypic variation for susceptibility index was detected in both experimental years. The drought susceptibility index ranged from 0.46 to 1.24 and the variability was higher in 1990 than in 1988. Similar values were reported in wheat by Fisher and Maurer (1978) and in dry beans by Acosta-Gallegos (1988). The increase in variability suggests that new variation for drought susceptibility may be generated when parents differing in the ability to resist water stress are combined. Thus, the recombination of morphological and physiological traits may create new genotypic combinations with a differential response to drought. For example, the proportion of genotypes with susceptibility indices lower than 1.0 was higher (3:1) in the LS population than in the AS population (1:3). The averages of the susceptibility index for the progenitors of the population LS were 0.88 and 0.86, respectively, in 1988 and 1990, while the averages of the susceptibility index for the progenitors of the AS population were 0.94 and 1.04, in 1988 and 1990, respectively. The results suggest that the likelihood of obtaining genotypes with low susceptibility indices is higher in crosses where the progenitors have inherently lower drought susceptibility indices. Since both populations have Sierra as common parent, the two other parents must have contrasting levels of drought resistance. The average of two years of drought susceptibility index in LEF2RB was 0.88 while in AC1028 was 0.99. Thus, when LEF2RB was crossed with Sierra the proportion of progenies with low SI values to progenies with high values was 3:1, whereas, the proportion in the AS population was 1:3. The results indicate that in the cross with LEF2RB the opportunity to identify progenies with more capacity to resist water stress was greater than with the AC1028 parent. The finding supports the need to emphasize the selection of parents and critically evaluate progenies for drought resistance using the susceptibility index estimate as selection criteria.

The correlation between susceptibility index (SI) and yield potential (Yp) was positive in both years of evaluation and significant in 1990. The lack of statistical significance in 1988 could be due to drought intensity, genotypic variability, and a larger sampling error associated with a reduced number of observations. Samper (1984) observed no correlation between SI and yield potential under lower drought intensities. The positive significant association between SI and Yp found in 1990 shows that the level of drought susceptibility, measured as percentage of yield reduction in dry beans under severe water stress at the reproductive phase, depends on the level of yield potential. Therefore, high yielding genotypes could have high indices of susceptibility and are more vulnerable to the effect of water stress due to a larger yield reduction. This relationship limits practically the attainment of high yielding genotypes with the ability to resist the effect of water stress. Yield potential alone therefore is not a useful selection criteria in a breeding program; although, it must be considered in the breeding process.

The association between SI and Yd was negative in both years and significant only in 1988. The results suggest that under severe water stress in 1988 the susceptibility index was better associated with yield under drought than with yield potential. Under less severe stress in 1990 yield and susceptibility index were independent of each other, so a low susceptibility index does not necessarily leads to the attainment of high yield under drought. This is supported by the behavior of the genotypes LS102 and AS103 (Table 2.30) which showed a very low susceptibility index but the lowest yield under normal conditions. The linear relationship between yield under drought and susceptibility index is disrupted in genotypes with an extremely low susceptibility index ($SI < 0.60$). The observation might explain the low yielding ability of genotypes with drought resistance mechanism which could depend on earliness to escape drought at the expense of yield potential. Clarke (1987) argued that highly drought resistant genotypes may not be desirable, given that such genotypes are often unresponsive to favorable moisture conditions. The lower yielding genotypes LS102 and AS103 did not show significant responses to improved environments in the expression of traits such as stem weight, pod weight, total biomass, seed growth rate, leaf temperature, water potential and leaf size. The differential genotypic responses to the environment in the expression of yield and related traits were non-significant in both genotypes (Table 2.9). The result showed that these genotypes are phenotypically stable over environments. The most stable genotypes, in an ecological sense, would be those with minimum variation in yield and minimum variation in morphological and phenological traits. The response however is agronomically undesirable, if the genetic potential for yield is low.

The consistency of susceptibility index values for a given cultivar grown in different experiments despite differences in drought intensity, as suggested by Fisher and Maurer (1978), was observed in the present study (Tables 2.29 and 2.30). AC1022 and AC1028 had SI values higher than 1.0, while LEF2RB and Sierra had values lower than 1.0 in both years, when there were differences in drought intensity.

The level of water stress influenced the relative importance of both components of yield under drought, yield potential and susceptibility index. Two contrasting observations were detected in the results of 1988 (Table 2.31) and 1990 (Table 2.32). Yield under drought was more strongly associated with susceptibility index than with yield potential, under severe water stress (DI = 0.78), while yield under drought was more strongly associated with yield potential than with susceptibility index under less severe stress (DI=0.63). Thus, susceptibility index is a more important index than yield potential for yield under drought, in a severe water stress. The high association of yield under drought with drought resistance may lead to selection for lower yield potential. Combining yield potential with drought resistance may be difficult physiologically because of the trade-off between yield potential and yield resistance to stress (Fisher and Wood, 1979), whereas, moderate levels of susceptibility index may allow the attainment of a high yield potential (Tables 2.29 and 2.30). Selection of dry beans for low SI could be useful when crop production is dependent on sporadic rainfall. This kind of selection could be efficient for the subsistence farmer for whom plant survival in the worst years may be the major objective to ensure some seed production (Richards, 1982).

The geometric mean (GM), however, combines yield potential and yield reduction estimates. Since geometric mean includes the deviation of the average yield potential due to water stress, the estimate is a direct measurement of the effect of water stress on average yield performance. The geometric mean approaches the arithmetic mean only when the yield potential is equal to yield under drought. When this occurs the differences between yield potential and yield under drought tends towards zero. Genotypes with this response will be more drought resistant since the yield reduction due to drought is near zero. A high geometric mean results from the combination of high yield potential and minimal yield reduction. However, in some cases a high geometric mean may also result when yield potential is high and not environmentally limited. In this manner a low yield under drought may be masked in a high geometric mean by yield potential. The performance of AC1028 in both years and AC1022 in 1990 are good examples of this response. Acosta-Gallegos (1988) selected both lines based primarily on their geometric means. However, in the present study both genotypes exhibited poor yield performance under drought in both years of evaluation, even though the yield of both genotypes was superior under non-stress conditions. In both years the weather allowed long season maturity and high yield potential was expressed. In contrast, in 1989 both genotypes were unable to express full yield potential because an early frost which occurred during the last week of September drastically affected the seed production while Sierra and LEF2RB were less affected. The experimental evidence showed that selection for geometric mean could be risky in environments like Michigan where environmental factors, such as low temperatures or photo-period sensitivity or both, limit the growth season of the crop. Thus, GM may be a useful selection criteria for environments without constraints in temperature and photoperiod that could limit the expression of yield potential. A selection approach based on geometric mean could be useful for those farmers for whom the major objective is high yield in the best years since they contribute the most to long-term yields where there is no environmental restrictions on yield potential. Under these conditions it is unlikely that factors contributing to an increase in drought resistance and plant survival in the most extreme dry environments could contribute to high yield in more favorable environments (Richards, 1982).

Geometric mean showed a positive association with Yd and Yp but did not show a significant correlation with SI. Since SI and GM are unrelated, it is possible that they are indicators of different biological responses. SI may be more associated with plant characteristics related with yield stability while geometric mean may be more associated with yield potential traits. The results of this research support positively this assumption. The correlations between yield components, phenological, partitioning and physiological responses with susceptibility index were in direct contrast to those observed for the geometric mean (Table 2.33 and 2.34). At the same time, both estimates appear to be related to different sets of plant traits.

The negative association of plant traits with the susceptibility index suggests that when a larger expression of the trait under drought occurs, there is a low susceptibility index. Thus, larger values of number of seed per pod, harvest index, seed growth rate, relative sink strength and relative water content are related to the resistance of a genotype to water stress. Instead, positive associations imply the increase in the expression of a trait under drought and the susceptibility of the genotype to drought. Thus, increases in stem weight at physiological maturity (lower efficiency in translocation), days to maturity (longer exposure to stress), days of seed filling (lower efficiency in the allocation of dry matter in the seed) and leaf temperature (less physiological efficiency) are associated with the drought susceptibility of a genotype.

The number of pods with seed, number of seeds, seed size, pod wall weight, total biomass, leaf area index, stem diameter, harvest index, economic growth rate, seed growth rate, biomass growth rate, relative sink strength, transpiration rate and stomatal conductance under drought were associated with a larger expression of yield under drought increasing the value of the geometric mean. Negative relationships leading to the reduction in the expression of the geometric mean occurred with days to maturity, days of seed filling period and leaf temperature. All were associated with the reduction of yield under drought.

The differential association of geometric mean and susceptibility index to different sets of plant characteristics implies a biological complementation between both drought resistance estimates. Thus, the geometric mean was associated with traits related to the expression of yield potential and the susceptibility index was associated with characteristics that enhanced the expression of yield related traits under drought. In this way, genotypic drought endurance and yield stability was increased. GM could be more useful than yield potential itself in the breeding process, since GM is unrelated to SI and expresses the yield potential under two different treatments rather than the yield potential in a non-stress environment. These characteristics make GM a useful estimate in combination with SI. Geometric mean by itself does not give any information about the level of drought susceptibility of a genotype expressed as the reduction of the potential of yield. Thus, the estimate should be used in combination with the arithmetic mean or with the susceptibility index. The combined use of geometric mean and susceptibility index could allow an integration of improved performance under both environments into a single drought resistance genotype. Such genotypes would have a high yield under non-stressed conditions and a minimum reduction due to drought.

GM and SI represent integrative estimates of drought resistance in several ways. Both estimates consider the components of yield under drought in their calculations and represent the integrated response of a set of specific morphological, phenological and physiological traits. The susceptibility index and the geometric mean are integrative indices complementary to each other and associated to different morphological, physiological and phenological traits, exhibiting adequate genotypic variability. Since yield under drought in dry beans depends on yield potential and the percentage of yield reduction (drought susceptibility), the selection for drought resistance must consider both components.

A drought resistance genotype can be agronomically characterized by: a large geometric mean (high yield potential) and intermediate level of SI, probably in a range between 0.75 and 0.95. The characteristics of the genotypes Sierra and LEF2RB in 1988 (Table 2.29) and LS4, LS7, LEF2RB, and Sierra in 1990 (Table 2.30) are a good illustration of this combination. The results of two years of evaluation of dry bean genotypes grown under drought and non-stress treatments showed that the attainment of such combinations is feasible in this crop. Similar results were obtained in sunflower (Fereres *et al.*, 1986), where the lack of association between drought susceptibility and yield potential were combined into improved cultivars as a high yield under both drought and nonstressed environments. The lack of correlation between geometric mean and susceptibility index observed in this study will allow the same combination of traits to be attained in dry beans.

Biological Significance of Shoot Characteristics for Yield under Drought

In this study the relative importance of plant traits for the expression of yield was established by comparing the correlation coefficients between yield and plant traits under drought and non-limiting conditions. From the comparisons, three sets of traits were identified. They were called "yield-biomass", "drought expressed" and "non-yield related" traits.

Traits classified in the "yield-biomass" set were mainly yield components (pods with seed, pods without seed, total number of seeds and seeds per pod), biomass components (pod weight, stem diameter and total biomass) and efficiency indices (harvest index, economic growth, seed growth rate, relative sink strength and biological growth rate). The correlation coefficients of this set of traits showed similar values and statistical significances in both environments. The similarity of the correlation coefficients suggests the association of these traits with the expression of yield regardless of the level of water stress. The results discussed agree with reports of studies conducted separately in dry beans, either under non-stress or drought conditions; the reports showed the relationships between these traits with yield expression. For example, Laing *et al.* (1983), Acquaah *et al.* (1991) and Scully and Wallace (1990) reported the relationships of yield with total biomass, stem diameter and efficiency index under non-limiting environments, respectively, while, Elizondo (1987), Acosta-Gallegos (1988) and Passioura (1977) indicated the importance of the relationships of yield with total biomass, stem diameter and harvest index in drought conditions, respectively. The results of the present research indicate that this set of "yield-biomass" traits are equally important in the expression of yield despite the intensity of water stress. The range of drought at which the relationships between the plant traits and yield have been reported, in present and former studies, support the assumption that this relationship holds for both non-limiting conditions up to drought intensities as high as 0.78.

The similarity in the correlation coefficients between the "yield-biomass" traits with yield expression in both treatments could explain the positive association between non-drought yield and yield under drought. Acosta-Gallegos (1988) in dry beans, Fisher and Maurer (1978) in wheat reported similar positive associations between both yields. It is possible that high yield and yield components as well as high harvest index represent a strategy of the plant for the allocation of resources to minimize investment in organs, tissues or tissue reserves of any kind, and to buffer yield and yield components against the effect of water stress (Fisher and Wood, 1979). Plants with such characteristics will show higher susceptibility indices under drought conditions because the yield reduction would be higher, yet the residual yield expression would be higher. The argument is particularly important for the present research because harvest index and relative sink strength were more intensively associated with yield under drought than with non-drought yield, and differential genotypic responses were not observed in both partitioning indices. Thus, the partitioning processes were more important for the expression of yield under drought than in absence of stress. Similar results were reported previously by Samper (1984).

The positive association of yield under drought with non-drought yield contribute to increase drought susceptibility, since the gap between yield under drought and normal conditions is increased. Thus, direct selection for yield in absence of drought, or selection via most of the non-drought traits, increases susceptibility and, depending on drought level may increase or decrease yield under drought as in wheat (Fisher and Wood, 1979). The argument could explain partially the observation in dry beans that SI is associated positively to non-drought yield; although the association was more pronounced at the least severe level of stress observed in the present study. Additional observations in dry beans and wheat support the point. For example, Ibarra (1985) attributed genotypic differences in drought response to the genetic potential for adaptation rather than to drought-resistance capabilities of dry beans. Sojka *et al.* (1981) suggested that traits conditioning high yield potential are likely to be expressed over a large range of environments, conferring to the genotypes a high baseline yield under drought; however, the author indicated that the baseline must not be confused with drought resistance. The "yield-biomass" set of traits found in the present research in dry bean derived lines may contribute to this baseline such that the baseline being expressed is the residual of the yield potential.

The existence of a "yield-biomass" set of traits responsible of the yield expression under any condition verifies the importance of yield potential in the improvement of the expression of yield under drought. Although there is a dependency between the expression in both environmental conditions, the dependency is not total since the association is reduced under higher levels of drought intensity. Thus, the correlation coefficients between yield potential and yield under drought in the present study were only 0.14 and 0.45 in 1988 and 1990, respectively, and 0.43 in the study of Acosta-Gallegos (1988). It seems therefore that other factors affect the level of association between yield potential and yield under drought. The final yield will depend on the characteristics associated with the expression of yield under drought. Both sets of traits may contribute to define specific genotypic responses to the water stress (Tables 2.6, 2.7, 2.8 and 2.9).

Non-drought yield correlated positively with yield under drought and SI (Tables 2.31 and 2.32); the association with SI was more intense under the least severe level of water stress observed in this research. The observations can be explained by the fact that some characteristics associated with the expression of yield under non-limiting conditions may have some influence on the resistance to drought, particularly those characteristics associated with changes in the source-sink relationships that result in the improvement of yield potential. Additionally, during the process of breeding for yield under non-limiting conditions some traits could have been carried forward due to linkage or because some pleiotropic relationships are enhanced by water stress. However, the presence of such traits is not detected if the genotypes are not tested under the limiting conditions. A good illustration of this point is the cultivar Sierra in which the characteristics of drought resistance were known only when the genotype was tested under drought. The observation could be particularly important because it is possible that variability for drought resistance remains hidden and unexploited in genotypes developed for high potential under non-drought conditions.

It is not biologically possible to separate the effect of both yield potential and susceptibility index on the expression of yield under drought. However, it is conceptually and methodologically possible and necessary to improve yield under drought. The discussion suggests that drought resistance could be improved if yield potential and yield under drought were improved. The improvement of the expression of yield under drought can be done through the incorporation or selection for specific traits to enhance the expression of yield under stress.

A second set of traits was called "drought expressed" traits because the association of these traits with the expression of yield was enhanced by drought. The correlation coefficients of these traits with yield were higher under limiting conditions. The significance of the correlations was clearer in drought conditions for these set of traits. Phenological characteristics (days to maturity and days of seed filling) and water use traits (transpiration rate, stomatal conductance and leaf temperature) were the most important components of this set of traits. Additionally, other traits involving yield components (seed size), biomass components (leaf retention) and partitioning indices (harvest index and relative sink strength) were included in this category. Seed size, stem diameter, transpiration rate, stomatal conductance, harvest index and relative sink strength were positively correlated with yield under drought and geometric mean. The latter association shows the role of these traits in the enhancement of the expression of yield potential under drought. Pods without seed, days to physiological maturity, days of seed fill and leaf temperature were negatively associated with yield under drought and positively associated with susceptibility index. The association suggests that these traits limit the expression of yield and define the susceptibility of a genotype to water stress.

Thus, there is a basic set of variables determining the expression of potential for yield in any environmental condition. However, the specific differential genotypic response will be modulated by other set of traits. The additional set of traits may be specific for each type of stress. For drought the set of traits plays a role reducing the susceptibility and increasing the expression of yield potential under water stress. Thus, genotypes with high yield potential buffered with a few drought resistance traits will be able to yield well under favorable conditions and not substantially less than highly drought resistance genotypes under drought (Clarke, 1987). The challenge under this situation is to improve the success of selecting genotypes with high and stable yield under water stress.

This set of variables was principally integrated by phenological and physiological characteristics. The strongest association of these "drought expressed" variables with yield under drought shows that the dry bean plant responds to water stress by increasing the efficiency of accumulation of dry matter in the following manner. There is a reduction in the amount of leaf area due to the reduction in leaf growth and the increase in leaf senescence as the remobilization of reserves from the leaf to the reproductive organs occurs. The reduction in leaf area index (LAI) and leaf area duration (LAD) leads to the reduction of dry matter accumulation. The plant produces and accumulates less dry matter and less resources are available for growth and development. As a result, the plant responds by reducing the time of exposure to stress reducing the growing cycle and seed filling period. The plant compensates for less available time and the smaller photosynthetic apparatus by increasing the positive association and relative importance of transpiration rate, stomatal conductance, harvest index and relative sink strength. Thus, the general strategy of the plant facing the negative effects of drought is to increase its physiological efficiency. Thus, resistance to drought is conferred by the ability of the plant to manage its morphological and physiological characteristics to take advantage of the physical resources available in a reduced growing cycle. This is a type of developmental plasticity. So, water use traits (biomass accumulation) and efficiency indices (partitioning and remobilization) become critical under drought conditions for the accumulation of dry matter in the seed. In this drought situation the accumulation of dry matter in stems and leaves has a negative relationship with yield (Samper, 1984) (Tables 2.36 and 2.37) and with harvest index (Table 2.39). The accumulation of reserves and the increase in temperature, probably due to stomatal closure, are indicative of decreased efficiency in dry matter accumulation and partitioning. Thus, the plant is forced to maximize seed production with fewer physical resources and time, when the water stress is continuous, gradual and prolonged as in this study.

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A third set of variables which were not linearly correlated with yield expression in both drought treatments will be identified as "non-yield related" traits. This set of traits involved physiological and morphological traits. Morphological traits were leaf orientation, leaf size, leaf area index and specific leaf weight, while physiological traits included water potential, moisture retention capacity and relative water content. The lack of correlation with yield under drought can be explained in two different ways. One explanation is that the relationships are non-linear. Another explanation is that since yield is a very complex trait resulting from the expression of many individual characteristics and their interactions, it is very difficult to detect any relationship with individual traits controlled by a single or reduced number of genes. It is more probable that these type of characteristics are more related to less complex traits in the scale of the organization of the plant. It is interesting that some of the same traits such as leaf orientation, leaf size, LAI, specific leaf weight, water potential and leaf moisture retention capacity have been suggested by Ludlow and Muchow (1990) as selection criteria in breeding for drought resistance in plants.

Yield and Shoot-Characteristics Relationships under Drought

The following discussion will focus on the analysis of individual characteristics related either directly or indirectly with yield under drought.

Yield components

The analysis of the linear correlations between yield and yield components suggested the importance of pod setting in the definition of yield under drought. The results did not differ from former studies in dry bean and other large seeded legumes. In former studies yield reduction was a function of a lower number of pods and, to a lesser extent, changes in the number of seeds per pod and seed size. The observation has been demonstrated in dry beans by the results reported herein (Tables 2.4 and 2.5). In dry bean, the reductions in yield components, regarding the average response of two years of evaluation, were in the following order: seed number> pods with seed> total number of pods> seeds per pod> seed size. The number of pods with seed was the most severely affected yield component (60% of average reduction in two years). The most stable yield components were number of seeds per pod and seed size, because they showed an average reduction of 18% and 13% in two years. The only trait showing a positive response to drought as an average of two years was number of pods without seed. The highest reductions can be explained because in dry bean the most sensitive phase of development to water stress is from flowering to early pod set (Dubetz and Mahalle, 1969; Laing *et al.*,1983; Laing *et al.*,1984; Halterlein, 1983). In addition, prolonged stress before flowering restricts canopy development which in turn limits yield (Laing *et al.*,1984). In this study, pods without seed was negatively correlated with other yield components. The response indicates that an excessive number of pods could have a negative effect on yield probably because the sink (flowers and developing pods) exceeded the source, and assimilates were diverted to increase reproductive processes instead of being accumulated in the seed.

Seed size was shown to be associated with yield under drought, at the range of seed size and genotypic variability tested in this study, since genotypes with higher yield produced larger seed size under drought conditions. In 1988, the response was clearer when Sierra and LEF2RB produced the largest seed size in both drought and non-limiting conditions (Table 2.10b). In 1990, Sierra and three derived lines showed the best yield under drought and the largest seed size (Table 2.12). The positive association between seed size and yield under drought could be explained by the compensation mechanism among yield components. In this study this compensatory mechanism was supported by the negative relationship of seed size with total number of pods. This mechanism of compensation may be part of the whole strategy adopted by the plant to increase its efficiency of production under water stress, since the plant is able to allocate into the seed assimilates that under non stress should be used for pod development. Since seed size is a very stable yield component and less affected by water stress (Robins and Domingo, 1956; Stocker, 1974; Muchow, 1985a) the trait may compensate for the reduction in yield due to a lower number of pods, which is a very drought sensitive trait in dry bean, as has been demonstrated in this research (Table 2.4 and 2.5). In addition, in this study, the dependency of seed size on the efficiency of partitioning and reallocation of assimilates of the plant under drought was indicated by the positive correlation between seed size and harvest index and relative sink strength, and the negative correlation of seed size with stem weight and leaf retention. From this perspective, it is the capacity of compensation between seed number and seed size which confers upon a genotype the ability to produce a high yield under drought and to maintain a stable yield performance over environments rather than seed size by itself. Thus genotypes with an inherent high compensation capability and highest efficiency of production under drought will show larger seed size and, therefore, high yield under drought. In some way heavier seed weight seems to stabilize performance over diverse and, particularly, unfavorable environments as it has been showed by Heinrich *et al*. (1983) who found that seed size was markedly higher in stable genotypes in sorghum. Finally, in both years of evaluation, the G x E interaction was not significant, which indicates the additive effect of the environment on the expression of seed size and likely a high genetic control.

Biomass components and morphological characteristics

The analysis of the correlations between morphological traits and yield (Table 2.36) showed the positive association of yield with total biomass and stem diameter and the inverse association with leaf retention (Table 2.37).

The positive association between total biomass and yield under drought was also reported by Elizondo (1987), Acosta-Gallegos and Kohashi-Shibata (1989). In non-limiting conditions the importance of biomass in the determination of yield has been indicated by Scully and Wallace (1990) and Scully *et al.* (1991). In this research, total biomass at physiological maturity was significantly associated with yield in both conditions; although the association between both variables was stronger under non-limiting conditions than under drought (Tables 2.18A and 2.36). The association of biomass with yield could result from the positive relationship of this trait with pods containing seed and seed number. Higher biomass may be the consequence of thicker stem diameter, larger leaf size and greater LAI. So, total biomass at maturity is the integration of dry matter accumulated during the growing cycle of the crop by the canopy before and after flowering. The importance of total biomass in the production process results from the accumulation of assimilates before anthesis and its remobilization after anthesis, demonstrated by the positive association between total biomass and both economic and seed growth rates (Table 2.39). In Tables 2.6 and 2.9, genotypes with lower SI values exhibited the lowest percentages of reduction in total biomass, which indicates that the stability of the trait is important in the determination of yield under drought. The results of this research confirm the theory that total biomass at maturity could be useful as a secondary trait to assist in breeding dry bean for drought resistance (Elizondo, 1987; Acosta-Gallegos, 1988). Genotypic variability was also evident in both years of evaluation (Tables 2.16 and 2.17). Although the measurement of the trait does not require special training nor special equipment, its use could be restricted by the time of measurement because during the cycle destructive sampling techniques would be required. The possibility of indirect estimation of biomass will be discussed later.

Leaf retention (LR), the dry weight of the leaves retained on the shoot at physiological maturity, measures indirectly the level of leaf senescence. In this study LR was negatively and significantly related with yield under drought. The inverse relation suggests that yield under drought is lower when the amount of dry matter retained by the leaves is large. The fact can be explained in two different ways. First, competition between source and sink due to a continuous vegetative growth may exist since the vegetative and reproductive stages overlap in indeterminate genotypes. The argument is supported by the positive correlation between leaf retention and days to flower (DF), days to maturity (MAT) and days of seed fill (DSF) (Table 2.38), resulting in a larger leaf retention in late maturing genotypes. Secondly, lower translocation and remobilization rates that reduce the rate of senescence, which is supported by the negative associations of LR with harvest index (HI), economic growth rate (EGR), seed growth rate (SGR) and relative sink strength (RSS) observed in this study. The later point could be the consequence of either poor pod set or seed set reducing the sink strength, as has been observed in non-senescent dry bean genotypes. Delayed senescence may also involve problems of photoperiod-temperature adaptations as has been indicated by White and Izquierdo (1989). Thus, it seems from both explanations that larger LR associated with late genotypes is detrimental to yield under drought for Michigan's climatic and soil conditions because of its negative influence on remobilization, translocation and dry matter accumulation. The trait could be useful for other environments, where longer growing cycle beans are less affected by declining or freezing temperatures. Under these circumstances, the reduction in the rate of senescence and the increase in leaf area duration do not seem to be a practical approach for Michigan. However, Boyer (1983) has suggested that the prevention of premature shedding under drought and the maintenance of the rate of senescence observed in non-limiting environments may be important. The estimation of LR is easy and does not require special training or specific equipment but it is labor and time consuming, requiring more than two replications to ensure a valid estimate of the trait.

Stem diameter (SD) was significantly and positively associated with the expression of yield under drought which may result from the association of SD with pods with seed (PWS) and seed number (SN). In addition, SD was more strongly associated with biomass characteristics such as stem weight, pod wall weight, total biomass and leaf retention than with yield characteristics (Tables 2.37 and 2.38). The relationship indicates the important biological value of the trait for its direct and indirect influence on yield. The thickness of stem may have a dual biological function, depending on the stage of development. Before anthesis, during the vegetative stage, the stem may provide enough water and mechanical support for higher levels of photosynthesis, canopy development and biomass accumulation, and a site for storage of photosynthates. After anthesis, during the seed filling period, the stem may be a source of assimilates that are remobilized because of the impairment of the leaf area due to water stress. Thus, under drought conditions the expression of yield may depend on the remobilization of assimilates. The mechanism of remobilization has been shown by Sheriff and Muchow (1984), Samper(1984) and White and Izquierdo (1989) to be hastened by water stress. When water stress occurs during the seed filling period an increased proportion of the assimilates is transferred to the seed, so pre-anthesis photosynthesis becomes more important provided that a source limitation exists (Hsiao *et al.*, 1976; Turner, 1979). In dry beans photosynthates from the leaves are primarily accumulated in the root and stem, so, the stored dry matter is subsequently translocated to the reproductive organs, first from the root and then from the stem (D'Souza and Coulson, 1988). The process is possible because the ray tissue in stems and roots is a primary site of the deposition of starch, which may be remobilized later and used elsewhere in the plant (Adams and Pipoly, 1980). The relationship between stem weight and yield under drought was not significant in the present study. In addition, a negative relationship between stem weight and harvest index, relative sink strength, seed growth rate and economic growth rate was observed. Thus, genotypes exhibiting higher stem weight showed also lower efficiency for the allocation of assimilates in the seed.

Stem diameter was also positively correlated with non-drought yield, susceptibility index and geometric mean. Stem diameter is probably associated with both yield potential and with yield stability, through its association with biomass and ultimately with seed yield. Stem diameter may be used as an indirect estimator of biomass as has been shown by Lehman and Clark (1989) in *Amaranthus* and suggested by Acosta-Gallegos (1988) in dry bean. The results of this research support the use of stem diameter for the estimation of total biomass and yield under drought. Stem diameter represents a very useful characteristic to utilize in the selection of drought resistance because it is easy to measure, non-destructive, displayed by the plant at flowering, able to be measured with different levels of precision, genotypically variable and affected additively by the environment (non significant G x E interaction). The last characteristic suggests that selection for stem diameter under non-drought conditions could be beneficial for the expression of yield under drought. Since a thicker diameter is suggested as an important component of the dry bean ideotype for Michigan (Adams, 1982; Acquaah *et al,,* 1991), it is possible that the character is associated with baseline yield under drought. When using this trait special attention should be paid to inter-plant competition, since a differential expression in stem diameter may be attained by differences in competition due to the effect of the environment. Thus, for selection purposes a uniform stand with plants under full competition and uniform management is required to avoid environmental effects.

Leaf size (LS) and leaf area index (LAI) were not associated with yield under drought but were positively correlated with total biomass (Table 2.38). Although both characteristics did not show a significant linear relationship with yield, they were related indirectly with the expression of yield through the increase of total biomass. LAI was associated positively with PWS and total number of pods (PTN) which is supported by the significant correlation of both characteristics with stem weight, total biomass and leaf retention. Hence, both traits contribute to the accumulation of dry matter before flowering, which eventually may be remobilized later to the seed. LAI has been recognized as an important determinant for both yield under non-drought conditions (Laing *et al.*, 1983; Laing *et al.*,1984) and under drought in indeterminate dry bean cultivars (Acosta-Gallegos and Kohashi-Shibata, 1989) because water stress affects leaf area significantly and also total dry matter (D'Souza and Coulson, 1988). Since changes in total leaf are due to modifications in both leaf number (senescence) and leaf size (leaf expansion), high LAI or larger leaf size could be indicative of the ability of the genotype to retain its photosynthetic apparatus longer.

In comparing both traits, leaf size seems to be a more practical trait in terms of time, labor, level of destruction and repetitive sampling. Genotypic variability was evident in both drought treatments. In Table 2.9 it is seen that four of the best genotypes under drought (LS4, LS7, Sierra and AS3) showed non-statistical significance between environments for this trait. Consequently, it is possible to assume that leaf size within genotypes was unaffected by the drought treatment and that the stability of leaf size over environments contribute to the good performance of these genotypes under drought. The trait could be particularly important because Bonnano and Mack (1983) found that the main cause of the reduction of total leaf area under water stress in snap beans was leaf size.

Specific leaf weight (SLW), the mass of tissue per unit of leaf area, was positively correlated with leaf photosynthesis in several legume species and suggested as a potentially useful selection criteria in soybean (Nelson and Schweitzer, 1988). Drought reduces leaf area and increases specific leaf weight (Fisher and Turner, 1978). *Triticum* species with high SLW also have a thicker leaf and a higher photosynthesis rate per unit of area (Austin *et al*., 1977). Hence, if transpiration is dependent on area, SLW could be associated with improved water use efficiency (WUE) (Passioura, 1977; Richards, 1982). In dry beans, Bonnano and Mack (1983) reported that the increase in SLW could be due to an increase in epicuticular wax, more cell wall material per unit of area, and/or an increase in solute and/or starch accumulation in the cells; Burga (1978) demonstrated a positive linear regression of CO_2 uptake upon SLW under non-drought treatment; and Adams (1982) suggested that the ideotype for non-limiting conditions in dry beans should consider a higher SLW. In this research there were no significant differences in SLW between non-limiting and drought conditions (Table 2.5). Since water potential is more negative in leaves of stressed plants, it is possible that solute accumulation contributes to the increase in SLW. In cowpea, SLW has been reported as a measure of the long term water status of plants due to its correlation with leaf water potential (Turk and Hall, 1980). An inverse correlation between SLW and leaf water potential was detected (Table 2.40); which suggests that a higher water stress (lower WP) corresponds to a higher SLW in dry beans.

Therefore, the characteristic may be considered in a breeding program since SLW reflects directly the effect of water stress and the response of the plant.

The non-significant linear relationships between SLW and yield (Table 2.37), biomass components (Table 2.38), partitioning and efficiency indices (Table 2.39) showed that SLW was not associated directly with either the expression of yield or biomass accumulation under drought. However, SLW was correlated with physiological traits. This aspect suggests the importance of SLW at a lower level of plant organization. Since SLW was positively correlated with transpiration rate (TR) and stomatal conductance (SC) and these traits are directly involved with CO_2 assimilation and water use efficiency, the results agree with the observations reported by Burga (1978), Richards (1982) and Nelson and Schweitzer (1988). Hence, SLW could be a useful trait because it is related with the production of biomass and accumulation of dry matter in the seed under drought, at the physiological level. Additionally, SLW was inversely correlated with WC and LT, relationships that reaffirm that SLW is associated with stomatal conductance because both higher water content and higher leaf temperature are a consequence of stomatal closure mechanisms. Significant differences among genotypes were more evident under the drought treatment (Table 2.28). The lack of a significant G x E interaction suggests the possibility of selection under non-drought conditions, for the additive effect of the environment on genotypes. It was interesting that the highest SLW values were obtained by genotypes with LEF2RB genetic background such as the AC1022, LS4, LS7, LS103, LS11 and LS101. Since SLW is easy to measure, not time and labor consuming, non destructive, displayed by the plant throughout the growing cycle, genotypically variable and additively affected by the environment, the trait can be used in the detection of genotypes that promote transpiration and stomatal conductance and through them the improvement of water use efficiency.

Leaf movements (paraheliotropism) in dry bean genotypes were also analyzed. The interest in this trait arises from the fact that leaf movements have been shown to be related with leaf water potential and stomatal resistance in soybean (Oosterhuis *et al.*, 1983), dry bean (Dubetz, 1969; Berg and Hsiao, 1986) and cowpea (Lawn, 1982a). Paraheliotropic movements have been associated with drought resistance in soybean (Lawn, 1982a), tepary bean (Parsons and Davis, 1978) and cowpea (Shakel and Hall, 1979; Lawn, 1982a). Paraheliotropism may contribute to increased light penetration and a reduction of transpiration, leaf temperature and water loss, resulting in enhanced carbon balance. Genotypic differences within species are rare because most of the studies have been physiologically oriented towards species differences. However, differences within species have been reported by Lawn (1982a). The trait may contribute to the stability of yield in intermittent stress but have little direct effect on yield components because leaf movements are essentially survival traits (Ludlow and Muchow, 1990).

Leaf movement or leaf orientation (LO) was evaluated by using a visual scale from 1.0 to 5.0. In this scale 1.0 corresponded to a minimum sensitivity for leaf movements, with leaves oriented perpendicular to the sunshine. Genotypes with an intense sensitivity, with leaves oriented parallel to the sunshine, had a value of 5.0. The genotype Sierra was considered the standard because it showed a consistent and intense paraheliotropic movements at different stages of development. In this study, LO showed a positive correlation with seeds per pod but an inverse association with stem weight, total biomass and leaf retention. The relationship suggests that higher LO values were associated with a smaller biomass accumulation in the stem and leaves, which could be related with genotypic earliness and/or remobilization efficiency. It is evident in Table 2.28 that the best four genotypes under drought exhibited levels of leaf orientation similar to Sierra. Genotypes with low susceptibility index such as LS102 and LS11 showed the highest LO values, 4.88 and 4.75, respectively. Since LO showed a negative non-significant correlation with SI, the relationship could indicate the tendency of the genotypes with low SI to have a higher LO ability, which confers yield stability (Ludlow and Muchow, 1990), but not necessarily more yield, as the inverse correlation between LO and total biomass indicated. This relationship and the lack of significant linear correlations with yield components and efficiency indices support the argument that the trait has little effect on yield and is related more to survival than to productivity (Ludlow and Muchow, 1990). The analysis of variation detected genotypic differences in both drought and non-limiting conditions, but neither differences between drought treatments nor the G x E interaction were significant. This response suggests that the trait is expressed regardless of the level of water stress. The insensitivity and the positive correlation between environments ($r=0.57$) suggest an additive effect of the drought treatments on the expression of LO and the possibility of selection in non-drought conditions. LO is easy to estimate, displayed throughout the growing cycle, genotypically variable and measured without special equipment or training.

Since little research has been done to assess the range of genetic variability of LO in dry bean the present study represents one of the first attempts to compare LO among genotypes and show the potential variability of the trait in dry bean. Since LO apparently does not mean any cost for crop productivity and does confer yield stability, it may be a useful trait in breeding dry bean for drought resistance. As a first step in evaluating the potential of selection for LO, more research is necessary to establish a standard scale of evaluation; determine relations of LO with physiological traits at different stages of development, particularly with photosynthesis and leaf temperature; and assess the genotypic variation in segregating populations.

Phenological characteristics

Data on days to maturity (MAT), days to flowering (DF) and days of seed fill (DSF) presented in the Tables 2.4 and 2.5 showed that MAT and DSF were reduced under drought conditions. The reduction was more drastic at more severe levels of drought stress. In contrast, DF was increased in both years of evaluation. Thus, the time of floral initiation and seed development was affected by drought. The changes in phenology may result from the interaction between the level of stress and the stage of development at which the stress was applied (Dubetz and Mahalle, 1969). The reduction in MAT and DSF, in response to drought, agree with results of previous studies reported by Acosta-Gallegos (1988) and CIAT (1987) in dry beans and Lawn (1982b) in four other species of legumes. However, the percent of reduction reported exceed those previously reported. The higher levels of drought intensity reached in this research probably contributed to intensify the response.

MAT and DSF were negatively correlated with yield and yield components while DSF was more intensively associated with yield than MAT. Similar results were reported by Samper (1984). DSF was also positively correlated with pods without seed and seeds per pod (Table 2.36). DF, MAT and DSF were positively correlated with stem weight and leaf retention (Table 2.38). As expected, these phenological traits correlated negatively with harvest index and others efficiency indices (Table 2.39). The experimental evidence suggests that lateness has negative implications for yield under drought for the environmental conditions of Michigan. Lateness under drought conditions results in less physiological efficiency. Since a late genotype requires more days to flower, the plant accumulates more dry matter in vegetative tissues (stem and leaves). In addition, if the water stress is applied before flowering the vegetative stage is extended even more. Thus, when the late genotype reaches flowering, the level of water stress is more intense and the effect on flowering and pod setting more drastic. In this way the total number of pods is reduced more in genotypes with longer DF, as the inverse correlation between number of pods and DF ($r=-0.436^{***}$) showed. Furthermore, late genotypes require more days to complete the seed filling process. At this point, the transpiration rate and conductance could have been reduced (Table 2.40), so both photosynthesis and dry matter production and accumulation are lowered. The lowest transpiration rate and conductance may be a mechanism of compensation in late genotypes to reduce water loss in a bigger canopy with larger LAI and longer LAD, in the absence of other mechanism of adjustment to water stress, such as osmotic adjustment. A late maturing genotype, under drought will have less resources to complete its growing cycle. Given the negative correlation between stem weight and leaf retention with yield and the positive association between MAT and DSF with stem weight and leaf retention, it is possible to think that the sink strength is reduced because there is a lower number of pods and seeds to fill. In late genotypes, it is possible that a smaller sink due to a deficiency in pod setting could contribute to lower remobilization and translocation of assimilates for being allocated in the seed. All these factors contribute to produce a less efficient plant and therefore a lower yield under drought. The process may explain why pods without seed and seed size were more strongly associated with yield under drought because both characteristics are important to maintain a sink strength as high as possible. Therefore, larger seed size may compensate for the reduced number of pods, enhancing translocation and remobilization while maintaining a reproductive demand in the plant. The assumption may be supported by the relative sink strength (RSS) values of the best and worst yielding genotypes in both years. Thus, Sierra and LEF2RB did have larger RSS values than AC1028 and AC1022 in both years of evaluation (Table 2.13b and 2.15) while in 1990 the four best yielding genotypes under drought also had the largest RSS values. Therefore, in late genotypes a limited sink relative to source may limit yield under drought. An important restriction related with seed size is that the level of compensation is not endless because the size of the seed is limited by the genetic background of the genotype, which determine ultimately the maximum seed size attainable by the plant.

The results of this study showed that the most productive genotypes in both years of evaluation displayed the lowest number of days of seed fill under water stress applied before flowering. These genotypes were able to adjust their growing cycle more efficiently to the drought conditions, delaying flowering and reducing days to maturity and days of seed fill. The fact that the best yielding genotypes under drought displayed the shortest growing cycle (days to maturity) in both normal and drought treatments (Tables 2.20 and 2.21) emphasizes the importance of lateness and indeterminacy on the performance of Type II and Type III genotypes under drought. Genotypes with phenological characteristics similar to Sierra and LEF2RB rather than earlier or later genotypes are desirable. Thus, matching crop development to environmental factors and the pattern of soil availability is one important criterion for improving yield of dry bean under drought. A pattern of development adapted to the maximum growing season in terms of water and low temperatures may have greater long-term profitability, for conditions of a modern agriculture, like Michigan. Earlier genotypes than Sierra and LEF2RB have lower yield potential, developmental plasticity to adjust their growing cycle and drought resistance. On the other hand, later genotypes than Sierra and LEF2RB have undesirable characteristics even for non-drought conditions, due mainly to the potential risk of low temperatures during the seed fill period. Indeterminancy determine development plasticity and higher yield potential. Thus, fitting plant's growing cycle to environmental constraints may improve yield capabilities. A breeding strategy should begin from the adjustment of the growing cycle to normal conditions, and then test for developmental plasticity, based on the lowest reduction in the seed fill period under stress (Table 2.20). The strategy is supported by the correlation between drought treatments. Such correlation coefficients between drought treatments over genotypes for DF, MAT, and DSF were 0.95 **, 0.93 ** and 0.92 **, respectively in 1988; and 0.82 ***, 0.68 *** and 0.51 **, respectively, in 1990. The intensity of association was as follow: DF>MAT>DSF. The sequence shows that the intensity of correlation is lower for MAT than for DF in both years, indicating that a larger variation due to differential genotypic developmental plasticity reduces the intensity of association between drought treatments. The lowest association intensity was observed in DSF which was likely due to a larger effect of water stress since maximum intensity of water stress occurred in that period.

Partitioning and efficiency indices

Since productivity under drought is a matter of efficiency in terms of biomass accumulation and duration of growing cycle, the harvest index, relative sink strength, biomass growth rate, economic growth rate and seed growth rate were analyzed and their relationships with other plant variables evaluated in this study (Table 2.36).

The results showed that all the indices were affected negatively by water stress (Tables 2.4 and 2.5). The percent of reduction was more evident in the year with the stronger water stress. The reductions in the indices, regarding the average response of two years of evaluation, were in the following order: EGR>BGR and EGR>HI>RSS. Thus, the rate of dry matter accumulation in the seed filling period (EGR) was the most affected index (65% as an average of two years). HI and RSS were the most stable indices because they showed an average reduction of only 20% and 4%, respectively, in two years. RSS was the only index with a positive response to drought (9%). There is no previous information about all the indices, but results in dry beans (Samper, 1984; Acosta-Gallegos, 1988; White and Izquierdo, 1989), wheat (Fisher and Maurer, 1978) and sunflower (Fereres *et al.*, 1986) showed reductions in HI due to drought. Samper (1984) and Acosta-Gallegos (1968) reported reductions in crop growth rate (BGR) and seed growth rate (SGR), respectively, in dry beans.

All the indices behaved similarly in their relationships with the other plant characteristics and correlated positively with yield and yield components. The intensity of correlation with yield is shown in the following order: EGR>SGR>BGR>HI>RSS. All the indices did have correlation coefficients greater than 0.7 and were highly significant. The intensity of association between EGR and SGR with the expression of yield under drought showed that the efficiency in the accumulation of dry matter in the seed is a key process for productivity under water stress. Similar conclusions were reported by Samper (1984).

HI, EGR, SGR and RSS were negatively associated with stem weight and leaf retention, and positively related to total biomass (Table 2.39). These relationships show that the accumulation of dry matter in the stem and leaves is in competition with the accumulation of dry matter in the seed as suggested by White and Izquierdo (1989) and that total biomass is a key factor for yield under drought as suggested by Samper (1984), Elizondo (1987) and Acosta-Gallegos (1989).

All the indices showed a negative correlation with DF, MAT and DSF. The relationships indicate that lateness was not favorable for the accumulation of dry matter under water stress, under the environmental conditions of this study, but, earlier flowering and shorter duration of the seed fill period designed to match phenology does necessarily not mean higher yields, as Muchow (1985a) indicated.

BGR, HI and RSS seem to be the most useful traits in a breeding program directed to the selection of yield drought resistance because they supply information about the efficiency in biomass accumulation and remobilization and partitioning of assimilates. Under drought it has been suggested that a rapid initial growth before the onset of water stress could be beneficial for yield. Rapid establishment in the field could help avoid evaporation, increase transpiration, to promote a rapid root development and to accumulate biomass in vegetative organs for future remobilization (Fisher and Turner, 1978; Fisher and Wood, 1979). As photosynthesis is impaired physiologically and morphologically during water stress, dry matter accumulated before anthesis in roots, stems and leaves becomes the main source of dry matter for seed production. In dry bean Samper (1984), Elizondo (1987), Acosta-Gallegos (1988), D'Souza and Coulson (1988) and White and Castillo (1989) have emphasized the importance of both dry matter accumulation and remobilization in seed production.

In breeding dry bean for drought resistance BGR and RSS may be useful indicators of the speed of dry matter accumulation (as an indirect measurement of early vigor) and the intensity of dry matter remobilization, respectively. In this study the highest rates of biomass accumulated were observed in the best yielding genotypes under drought. Sierra showed the highest rates of biomass accumulation in both years of evaluation. The results were confirmed in field observations where the rapid development and establishment of this variety showed the advantage of this developmental mechanism for seed production under water stress.

RSS, which is the ratio between SGR and BGR, expresses the relative proportion of the dry matter produced that is used for the production of seed.

Thus, if all the seed growth can be explained by the current photosynthesis, BGR (net accumulation of dry matter) should be greater than SGR, and RSS will be lower than 1.0. If not, it is possible to assume that seed growth is exceeding the rate of biomass production and that seed growth is sustained, in part, by other sources of dry matter, such as roots, stems and leaves (D'Souza and Coulson, 1988; Hoogenboom *et al.*, 1988). When RSS is larger or equal to 1.0 it is possible to assume good translocation ability, strong sink strength, and/or that assimilates were remobilized during the generative phase (Scully and Wallace, 1990). Thus, treatment and cultivar differences in partitioning and efficiency abilities can be detected, as this study showed (Tables 2.13b and 2.15), in which the best genotypes under drought showed high RSS values. Austin *et al.* (1977) reported a similar variation among wheat cultivars in ability to fill grain from pre-anthesis assimilates under water-limiting conditions. The response may indicate that in these genotypes more dry matter is remobilized from vegetative organs to the seed, due to an insufficient production of dry matter by the canopy via current photosynthesis. The response may be associated with short duration of the growing cycle and seed filling period because in late genotypes the RSS is lower. This likely results from a lower number of pods and seeds to fill and/or from competition between vegetative and reproductive organs due to the overlapping of both growth phases in indeterminate cultivars. In addition, high RSS may be associated with low SI values because of the negative correlation between both indices, which means more drought resistance. Scully and Wallace (1990) have demonstrated the usefulness of RSS in the improvement of yield in non-limiting conditions and the presence of genotypic variability for the trait in dry bean, suggesting that genotypes with RSS values equal or higher than 1.0 would be useful in the improvement of productivity in dry beans. Genotypic variability for RSS was observed in both years of evaluation under both non-limiting and drought conditions (Table 2.13b and 2.15). Furthermore, the positive and significant correlation of responses between non-drought and drought treatments in both years of evaluation and the lack of statistical significance in the G x E interaction indicate the additive effect of the environment. Thus, it is expected that the improvement of RSS under non-limiting conditions may improve the yield expression under drought. From this evidence, it is possible to assume that RSS is related to the baseline of yield potential that is expressed under drought. RSS, like HI, may be a very useful index for the improvement of yield expression under both conditions, in combination with absolute yield.

Harvest index (HI) has been the main cause of the improvement of productivity in cereals (Donald and Hamblin, 1976) and possibly in grain legumes such as soybean and groundnut (Lawn, 1989) under non-limiting conditions. However, in dry bean it has been shown that the improvement of yield through HI is not feasible because the species already posses a high HI and there is not enough variability for the trait within current cultivars (White, 1987). HI has been considered as being the main component in the analysis of yield under drought in wheat (Passioura, 1977). In the present study the significance of HI was supported by the positive correlations with yield, yield components and geometric mean and the negative correlation with SI. Drought reduced the HI (20% in averages of two years) (Tables 2.4 and 2.5), increasing the proportion of yield potential that is not realized due to water stress. Thus, the relative importance of HI in the expression of yield under drought is greater. The positive association between HI and yield components agree with the results reported by Acosta-Gallegos (1988). Differences among genotypes as those observed in the present research were observed also by Samper (1984), Elizondo (1987), Acosta-Gallegos (1988) and White and Castillo (1989). Those differences suggest enough genotypic variability in the harvest index expressed under the environmental conditions of Michigan. The genotypic variability observed in all studies suggests that improvement through selection for high HI is possible. These findings disagree with those reported by White (1987) under tropical conditions.

The lack of significance in the G x E interaction and the positive correlation between drought treatments observed in 1988 (r=0.92) and 1990 (r=0.43) are indicative of the additive effect of the drought treatment on this characteristic and the lack of significant differential genotypic responses to the drought treatment. Since the best yielding genotypes in both years of evaluation showed high HI values under both drought treatments, it seems that the improvement of HI may be beneficial for both non-limiting and drought conditions. Current results from two contrasting drought treatments verify that HI depends on the relative duration of the vegetative and reproductive phases and on the relative partitioning and remobilization of stored assimilates to the reproductive organs, as confirmed by the positive strong correlation between HI and RSS (Table 2.39). Thus, HI in dry bean may be enhanced when a rapid early dry matter accumulation occurs (large BGR), when the duration of the reproductive growth is large enough to maximize yield and to avoid environmental constrains (developmental plasticity), where most of the assimilation after flowering is partitioned into pods (high SGR), and where there is a substantial remobilization of assimilates from vegetative tissues into pods and seeds (high RSS).

In breeding dry beans for drought resistance the balance in the accumulation of dry matter between seed and vegetative organs is a key process that must be considered. In order to avoid some of the negative consequences of the improvements for HI such as earliness, reduction of yield potential, alternation of indeterminancy (Lawn, 1989) coupled with weak and spindly stems which are susceptible to lodging (Morgan, 1989), it will be necessary to follow the simultaneous improvement of total biomass and HI. Under this framework, selection for stem diameter and for HI are complementary. The approach can be carried out under normal non-limiting conditions. The experimental evidence supports the assumption that HI is related with the yield potential baseline that will be expressed under drought conditions.

Physiological traits

Seven physiological traits were analyzed for their relationships with yield components, phenological traits and interrelationships. The traits classified as water use variables were transpiration rate (TR), stomatal conductance (SC) and leaf temperature (LT) while water relation variables were water content (WC), relative water content (RWC), water potential (WP) and leaf moisture retention capacity (MRC). TR, SC, LT, RWC and WC appear to be the most important traits based on their relationships with other variables in the study of the drought physiology of dry bean. In general, water use characteristics were more important than water relations traits.

Water use characteristics

The positive association of TR and SC with yield components, total biomass, partitioning and efficiency indices, mainly with EGR, SGR and BGR, suggests a key role of these physiological processes in the accumulation of dry matter in dry bean under drought. Thus, any reduction in SC and TR is negative for biomass accumulation and seed production. The results of this study showed a parallel reduction in net photosynthesis and transpiration due to drought which indicates that stomatal closure is the principal cause of water mediated reduction of net photosynthesis (O'Toole *et al.*, 1977; Velasquez-Mendoza, 1986). Stomatal closure is the primary mechanism by which water stress reduces net photosynthesis under natural conditions, directly by impeding CO_2 supply and indirectly by increasing leaf temperature (Slatyer, 1969). Thus, high stomatal sensitivity leading to stomatal closure and lower TR is undesirable because of its negative effects on yield. Then, in breeding dry bean for drought resistance the best traits would be those which cause no sacrifice in growth and yield (Boyer and McPherson, 1975). Experimental evidence obtained in the present study indicates that for the environmental conditions of Michigan, selection for SC should be oriented to the selection of genotypes with higher levels of SC and TR under drought, as indicated by Ludlow and Muchow (1990). The best prospect for the improvement of yield under drought appears to be increasing the amount of water transpirated and maintaining harvest index not restricting transpiration. The importance of transpiration for yield under drought has been stressed by Passioura (1977) suggesting a model for the analysis of yield under drought. The model has three main components, one of which is transpiration or water use. The model has been considered suitable for the analysis of yield under drought and has been validated in several crops (Richards, 1982; Blum 1989; Ludlow and Muchow, 1990). In dry bean the analysis of the results of the present research supports the use of the model in the analysis of yield under drought, to help in selecting drought related traits.

Since diffusive conductance is directly proportional to transpiration rate (Sheriff and Muchow, 1984) and is more responsive to plant water stress, it should be useful for monitoring the day-to-day relative plant stresses (Bonnano and Mack, 1983) and detecting genotypic differences. In this study genotypes differed in SC and TR capacities. The differences were more evident in 1990 than in 1988 when the drought intensity was less severe; the lower level of drought intensity allowed the detection of larger genotypic variability. In 1988 when the drought intensity was stronger (0.78), statistical genotypic differences were found in the non-drought treatment but not in the drought treatment (Table 2.23) while in 1990, genotypic differences were significant under both treatments (Table 2.25).

Both facts suggest that severe water stress may have caused stomatal closure in all genotypes at the highest drought intensity while stomatal closure prevented the detection of genotypic differences. Perhaps, under these conditions the level of water stress was so intense that all the genotypes reached a threshold at which the average stomatal resistance in both surfaces of the leaf acts as an on-off switch to prevent further decline in leaf water potential (Kanemasu and Tanner, 1969). Other evidence supporting the assumption is that even though significant differences were not found the genotypic tendencies were maintained (Table 2.23).

The observations have some methodological implications. Thus, it is possible that under strong water stress, genotypic differences are not able to be detected, even though a relative large number of replications (four) and sampling (five) were used. However, genotypic differences may be observed, even with a minimum number of replications (two), when the stress is less severe at mild drought intensity. Therefore, the chances of detecting genotypic differences at mild drought intensities, around 0.5, seem to be higher than at more severe drought intensities. It appears that two replications and three samplings per plot, each in three plants could be enough for the estimation of these variables.

Differences in SC among genotypes in dry bean were reported by Laing *et al.* (1983), Laing *et al.* (1984), Bascur *et al.* (1985) and Ehleringer (1990), but Mkandawire (1987), Elizondo (1987) and Acosta-Gallegos (1988) did not observe genotypic differences. This contradictory experimental evidence and the results of the present study suggest that in measuring stomatal conductance attention must be paid to methodological aspects involving sampling technique, levels of drought intensity, number of samples, time of the day for sampling and stage of development in which the sample is taken.

The identification of a link between phenological adaptations and physiological mechanisms was a major finding in this study. The performances of the genotypes AC1028 and LEF2RB are a suitable example of this association. AC1028 tended to have the lowest SC values under drought while LEF2RB did have the highest values in both years of evaluation. The behavior was clearer in 1988 when abaxial, adaxial and total SC were measured (Table 2.23). In 1990, the progenies AS102, AS6, AS103, AS11 and AS 101 derived from a cross possessing AC1028 germplasm had the lowest values of SC in both drought treatments. In general, the lowest values of SC were found in progenies derived from that cross. On the other hand, the highest SC values in both drought treatments were detected in genotypes possessing the LEF2RB genetic background. The negative association between days to flower, physiological maturity and seed fill period with TR and SC and the positive association of these phenological traits with leaf temperature (Table 2.40) indicate that a strong stomatal control is exerted by late genotypes. Thus, late genotypes, such as AC1028, exhibited the lowest SC and TR values and in consequence they did produce lower yields under drought. A possible explanation is that in late genotypes stomatal closure is a mechanism used by the plant to survive water stress, even though the productivity is affected (Slatyer, 1969). However, as late genotypes have inherently a higher yield potential, conferred by a large LAI and longer LAD, the reductions caused by a temporal stomatal closure may be compensated for when the plant is released from drought. Perhaps, short periods of stomatal closure occurring under intermittent drought may compensate with a relatively low cost in final productivity. In these genotypes the persistence of drought and stomatal closure may be extremely detrimental for biomass and crop productivity unless the release from water stress occurs. Thus, stomatal closure is a very conservative mechanisms directed to the maintenance of water content, reducing water loss, related to survival rather than to productivity. In late maturing genotypes, a strategy of the plant directed to maintain high SC and TR is more dangerous for the plant because it could exhaust soil water and cause the dehydration and death of the plant. Under these conditions it is not possible to take advantage of the higher productivity of late maturing genotypes unless water stress is intermittent. Similarly, Markhart (1985) observed that tepary bean closed its stomata completely at lower levels of water stress than did dry bean cultivars. The response observed in late genotypes could explain the good performance of Type III genotypes under intermittent drought, as suggested by Acosta-Gallegos and Kohashi-Shibata (1990) and Ludlow Muchow (1990). In this way when the water stress in continuous, prolonged and progressive late genotypes are ecologically but not agronomically drought resistant. In contrast, in early genotypes stomatal closure may be detrimental for yield because they have a shorter growing season, so, they do not have enough time, for LAI and LAD to compensate for the reduction in productivity. The only possible way available for these genotypes to compensate the effects of drought is either to increase or maintain their efficiency in dry matter accumulation. Thus, in earlier indeterminate genotypes a different strategy to stomatal closure may be necessary to maintain maximum productivity with minimal resources. Under these circumstances, developmental plasticity to reduce minimally maturity and seed fill period may be a very powerful mechanism for adaptation to drought.

The importance of LT resulted from its negative relationships with yield and yield components, biomass components, and partitioning indices, and its positive association with phenological traits. The responses indicate the negative effect of the increase in temperature in the production process, mainly in late genotypes in which both low TR and SC were evident (Table 2.40). In addition, leaf temperature was correlated negatively with SC, TR (Table 2.41) and SI. The inverse relationship between LT and SC under drought has been also observed in cowpea, soybean (Lawn, 1982a) and dry bean (Bascur *et al.*, 1985; Laing *et al.*, 1983; Laing *et al.*,1984); and the inverse relationship between canopy temperature and yield has been reported in soybean (Harris *et al.*, 1984), wheat (Blum *et al.*, 1989) and dry bean (Bascur *et al.*, 1985). The negative association between LT and yield under drought confirms indirectly the dependency of biomass and seed production on SC and TR. So, a low temperature under drought reflects high SC and TR; therefore, higher plant photosynthesis and dry matter accumulation. The association between LT and SC, TR and yield make LT a very practical characteristic with a high potential for use in breeding for drought resistance, provided that enough genotypic variability exits in the population to be selected.

In this study, as in soybean (Harris *et al.*, 1984), *Brassica* sp. (Singh *et al.*, 1985), wheat (Blum *et al.*, 1989) and dry bean (Mkandawire, 1984) genotypic differences in leaf temperature were found. Genotypic differences in leaf temperature were detected under drought in both years of evaluation despite the level of drought intensity (Tables 2.24 and 2.25). In the non-drought treatment in 1988 significant differences were not detected, but differences were found in 1990. This additional evidence confirm the importance of TR and SC under drought. Both the lack of significant differences under non-drought in 1988 and the significant differential genotypic response observed in 1990 suggest that selection for the trait must be done under drought conditions. Thus, selection for low LT under drought would be a selection approach for higher SC and TR, which in turn will lead to higher photosynthesis, high dry matter accumulation and high seed yield in dry bean. The results of this study confirm the assumption because in both years of evaluation the lowest temperatures were obtained by the best yielding genotypes under drought (Tables 2.24 and 2.25), whereas the highest temperatures were obtained by low yielding genotypes. In 1990 the four highest yielding genotypes did not increase their temperature significantly due to drought (Table 2.9). The response suggests that SC and TR were adjusted by the plant to maintain temperature, through the maintenance of stomatal conductance and transpiration. Bonnano and Mack (1983) explained a similar response, suggesting that water potential at which stomata close is environmentally dependent and can be increased by moisture stress hardening due to osmotic adjustment. It is possible that stomatal adaptation to moisture stress may have occurred under the dry treatment in these experiments.

This suggestion may explain the consistent higher stomatal conductance observed in LEF2RB in different field observations and experiments probably because in leaves with osmotic adjustment, stomata remain partially open to progressively lower water potentials (Ludlow and Muchow, 1990). This stomatal adjustment has the opposite effect to both low conductance and higher sensitivity to leaf water status because it promotes continued water loss and a progressive decline in leaf water potential. Thus, in LEF2RB and Sierra, the resistance to drought may be conferred by lower stomatal sensitivity and lower stomatal closure threshold, possibly due to osmotic adjustment. On the other hand, genotypes such as AC1028 are very susceptible to water stress, as a result the plant respond by closing the stomata at lower levels of water stress than do LEF2RB and Sierra.

Since leaf and canopy temperature have been found to be related to physiological and morphological responses of the plant to water stress and yield, it appears possible to use them as selection criteria. Bascur *et al.* (1985), Laing *et al.* (1983), Laing *et al.* (1984) and Blum *et al.* (1989) suggested the use of this plant response as a selection criterion. The experimental evidence reported here support the use of this characteristic in breeding dry beans for yield resistance and yield under drought. Leaf temperature represents one of the most important plant responses from the plant breeding perspective, because the response represents the output of a very complex net of physiological and morphological characteristics and responses that result from the specific strategy and mechanisms adopted by the crop to resist the effects of drought.

It is possible to assume that the contrasting morphological and physiological differences observed in LEF2RB and Sierra as compared with AC1028 and AC1022 are the expression of two different drought resistance mechanisms: stomatal adjustment to maintain high transpiration rate and reduction of water loss (stomatal closure). Each mechanism is related to specific levels of expression of morphological and physiological characteristics and phenological adaptations. Thus, LEF2RB, Sierra, AC1028 and AC1022 possess some kind of drought resistance, conferred by either one or other mechanism; however, only those genotypes with the ability to maintain stomatal conductance, and hence photosynthesis and transpiration under the drought pattern applied, have demonstrated to be satisfactory for the growing conditions of the experiments, which are characterized by water stored in the soil, a very well defined growing cycle and a modern agriculture. In addition to these findings, the results have shown that each mechanism is related to specific levels of expression of morphological, physiological and phenological characteristics; that each mechanisms fits better to specific environmental constrains and productivity requirements; that each mechanism confers a specific level of drought resistance for a particular environment and system of production; and that both mechanisms are mutually exclusive in a single genotype.

Water relations

Among the water relations evaluated, water content in a fresh weight basis (WC) and leaf moisture retention capacity (MRC) were more significantly related with other plant characteristics.

The negative association between MRC and TR and SC was evident (Table 2.41). The association showed that increases in MRC are detrimental for TR and SC. In this way increases in MRC negatively affect yield. These relationships suggest the conservative nature of the trait and its closer relation with survival rather than with productivity. MRC may enable the leaf to remain physiologically functional and therefore contributing to a return to normal photosynthesis when conditions of water availability improve. The relationships between TR and SC with processes related with dry matter accumulation (Table 2.40) and the lack of a significant relationship between MRC with those traits indicate that stomata control, or gas exchange through stomata, plays a more important role than the cuticular control in water balance that enhances the expression of yield under drought. However, high MRC could lead to a reduction in the amount of transpiration rate. The value of the trait as a secondary selection criteria would be for the indirect selection for transpiration.

The negative relationship between WC and TR and SC indicates that the reduction in SC and TR leads to a larger conservation of water. In addition, water content was negatively associated with yield, number of pods, number of seeds and total biomass, suggesting that high WC results from lower SC and TR. In this research the associations between WC with TR and SC were significant and inversely proportional. A larger conservation of water results in less TR and SC, which in turn affects the expression of yield components, mainly in late genotypes derived from AC1028. The response was clearer in late genotypes because SC and TR were negatively associated with lateness. The conservative nature of water content and stomatal closure is also supported by the negative association of WC with SLW and partitioning indices. The lack of correlation between yield and MRC agree with observations reported by Mkandawire (1987) in dry bean landraces. However, Acosta-Gallegos (1988) found a positive significant correlation between MRC and yield and yield components. MRC in wheat showed a low correlation with yield and tended to be negative in high yield environments and positive under drought (Clarke, 1987).

Both traits, MRC and WC, are relatively easy to measure; are genotypically variable; do not require special training and/or special equipment; can be measured before maturity if necessary; and are non-destructive. All these characteristics make the traits potentially useful as secondary characteristics in breeding dry beans for drought resistance.

General Aspects

The improvement of drought resistance should involve breeding for both yield potential and yield under drought and should seek to reduce the gap between the expression of yield under both environmental conditions. The discussion showed that the improvement of inherent yield potential may increase the baseline of yield potential expressed under drought because there are plant characteristics important for yield expression regardless of the level of water stress and favorable for the expression of yield in both conditions. The fact that Sierra, a Type II genotype, did have a consistently good performance under drought and a susceptibility index lower than 1.0 suggests that genotypes with the same characteristics would be suitable for the conditions of Michigan, confirming results of previous studies (Acosta-Gallegos, 1988). The type II cultivars are well adapted and exhibit high yield potential in Michigan (Kelly *et al.*, 1987). Interestingly, some of the traits with positive effects on yield under drought in this research were considered by Adams (1982) as desirable in the dry bean ideotype or archetype for Michigan. Such characteristics are: indeterminate growth, large overall plant size (large biomass), but not with extended vine growth; thick stem diameter; leaf orientation; higher specific leaf weight; stem and root starch storage and remobilization during pod and seed filling (high RSS); and high seed filling rate. If a genotype possess these characteristics a good performance under drought and non-limiting conditions would be expected, as occurs with Sierra. Thus, the improvement for yield potential may extend to an increase of yield under drought due to the improvement of the yield baseline that is expressed under drought.

The improvement of yield potential may be one important factor in the improvement of yield under drought; however, the approach is not always effective given the differential genotypic responses to drought, and because the expression of yield potential under drought is modulated by specific drought resistance mechanisms. Those mechanisms result in a differential level of expression of morphological and phenological characteristics under drought.

The improvement of yield under drought could be possible if specific traits and/or plant responses related positively to the expression of yield under drought are identified and enhanced. However, this is not always possible since yield is a very complex trait. The selection of specific characteristics could be achieved more easily if yield under drought is analyzed as a function of its main components under drought. Passioura's (1977) model may be a suitable approach for such a task in dry beans. Under this framework, it is possible to group the individual traits and plant responses studied in this research to improve yield under drought in dry bean as follows: amount of water used by a crop can be increased by the improvement of TR, SC and early vigor by mean of a higher BGR to decrease soil surface water loss. The most useful characteristics for the improvement of water use efficiency in dry bean may be leaf size, specific leaf weight, leaf orientation and water content. Harvest index could be improved through traits such as: yield components, specially seed size, leaf retention, stem weight, leaf size, LAI, days to maturity, days of seed fill, harvest index, RSS, EGR and SGR. Based on this model the improvement of any component should improve yield and indiscriminate recommendation of selection criteria is avoided because the model focuses directly on the processes that affect productivity in dry environments (Richards, 1987). In addition to the three main components suggested by Passioura, in the present study, phenology was shown to be a very important determinant of the expression of yield under drought in dry beans. This fact suggests the inclusion of phenological characteristics in the analysis of yield under drought. In Figure 3 the main processes determining the expression of yield under drought in dry bean are shown. In this model, yield under drought has four main components: phenology; photosynthesis, involving transpiration and stomatal conductance; biomass accumulation; and partitioning and remobilization. In this study developmental plasticity represented by the adjustment of maturity and days of seed fill was an important phenological aspect in the determination of yield. The maintenance of leaf stomatal conductance, leading to the maintenance of transpiration and photosynthesis, helped to maintain water use and improved water use efficiency. Early biomass accumulation, through high biomass growth rate, in combination with partitioning and remobilization mechanisms contributed to the higher expression of yield of dry bean under drought. Related to every component of this model there are different plant traits and responses. Thus, the analysis of yield under drought is not possible without regarding phenological adaptations which condition yield potential, developmental plasticity and indeterminacy, and physiological attributes related with drought resistance, principally water use efficiency and partitioning and remobilization. All the components need to be regarded in breeding dry

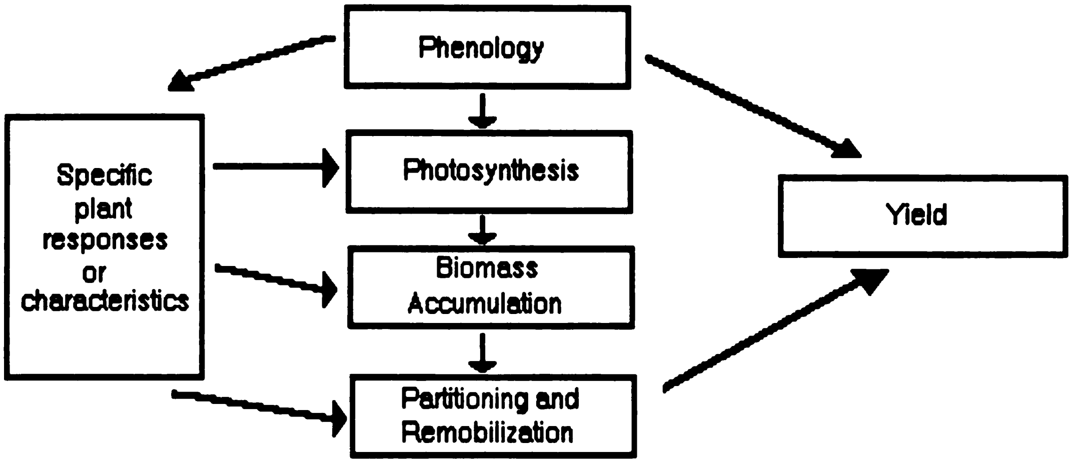

Figure 3. Components of yield under drought at the reproductive phase in dry beans.

beans for drought resistance. Following this scheme the analysis of yield under drought for the identification of plant characteristics to be included in a breeding program could be made easier, mainly if the relationships between individual characteristics or plant responses with yield and yield components of this model under drought are known. The model could be particularly useful since yield under drought is determined by all the attributes of the plant, and the identification of individual traits directly correlated to it is difficult. The chances of success using a trait as substitute for yield under stress are greater if such trait is closer to yield in the scale of organization of the plant. However, such single traits or integrated whole plant traits or responses, although possibly more reliable, are subject to environmental effects, are usually measured on mature plants and are difficult to use in early generations. In the short term, they tend to be the most reliable approach and are proving to be successful (ICSU,1989). In the present study, leaf temperature, specific leaf weight, stem diameter, water content, transpiration rate and stomatal conductance are examples of integrated traits because they are the expression of many individual plant characteristics. Additionally, these traits are expressed throughout the growing crop cycle and can be estimated before maturity.

In the present study, morphological, physiological and phenological traits and measurements of partitioning, remobilization and efficiency were analyzed. All these traits were studied to get a better understanding at the whole plant level of the effects of drought, to study the relationships between all these characteristics at different levels of organization and to study the interactions between characteristics at different levels of complexity since each characteristic does not function in isolation, but is part of a complete system. Agronomically, the analysis of a number of characteristics could be a valuable approach to identify morphological and physiological characteristics related to specific mechanisms of drought resistance required to satisfy specific environmental constrains and productivity needs, since every agroecosystem requires specific mechanisms of drought resistance.

It was evident from the discussion that the evaluation of germplasm in a rain-out shelter, to develop a progressive reduction of soil water content was useful to detect two of the most important mechanisms associated with drought resistance: stomatal adjustment leading to the maintenance of high transpiration rate and reduction of water loss through stomatal closure. The suitability of this technique for the identification of drought resistance mechanisms and the levels of drought intensity that are possible to be reached with such a system make this technique suitable for selection of parents and screening of progenies. The initial investment in equipment and limitations in space may restrict its use.

In the discussion, most of the morphological and phenological characteristics under study were shown to be directly or indirectly related to yield under drought. However, seed size, total biomass, stem diameter, leaf size, specific leaf weight, leaf orientation, days of seed fill, harvest index, relative sink strength, seed growth rate, biological growth rate, stomatal conductance, leaf temperature and water content appear to be the most promising traits in breeding dry bean for drought resistance. Most of the traits are relatively easy to estimate and have shown enough genotypic variability. Only the measurement of stomatal conductance and leaf temperature require special equipment and training. The final value of every trait for breeding purposes will be determined by the heritability of such characteristics.

Finally, the results of this research confirm the reports of previous studies that indicate the complexity of yield under drought and drought resistance in dry bean and the lack of a single trait that by itself could improve the productivity of dry beans under drought. Therefore, the best approach in breeding yield under drought will be a combination of traits, which should be integrated by incorporating traits representing each of the main mechanisms determining yield under drought in dry bean.

CONCLUSIONS

I. Effects of Drought.

1. The rain-out shelter screening technique proved to be efficient for the evaluation of dry bean genotypes under drought. The system was effective in reducing the soil water content, causing a severe water stress in the crop in both years of evaluation and producing repeatable and controllable levels of drought intensity. Both initial cost and dimensions of the structure may limit its use.
2. Drought intensity is a useful parameter for the characterization of water stress between experiments and evaluating genotypes in a breeding program. The parameter is easily estimated and the estimation does not require either additional instrumentation or equipment.
3. The results from this research are representative of the effects of drought occurring during the reproductive stage of development in dry bean cultivars because of the severe drought intensities obtained in both years of evaluation.
4. Most of the plant traits and responses under study responded similarly to water stress despite differences in water stress intensity in both years of evaluation. The response was more intense at higher drought intensities, regardless of the class and number of genotypes included in the evaluation. The generalized response of the dry bean plant to drought was the reduction in the expression of traits with positive effects on yield and the increase in the expression of traits with negative impact on yield and biomass accumulation. The response was observed even at levels of drought intensity as severe as 0.78 and intensified by water stress increments.

II. Biological Significance of Drought Resistance Estimates.

1. The results showed that there is a linear positive correlation between yield potential and yield under drought; that severe water stress limits severely the expression of yield potential and disrupts the linear association between yield potential and yield under drought; and that the degree of association between both expressions of yield depends on the severity of stress.
2. Experimental evidence indicated that yield potential, yield under drought and differential of yield reduction are not useful estimates of drought resistance in dry beans. However, yield under drought and yield potential must be considered in a breeding program.
3. In this study, genotypic variation for susceptibility index was detected. Additionally, it was demonstrated that the likelihood of obtaining genotypes with low susceptibility index is higher when the parents have inherently lower susceptibility indices. Thus, the selection of parents becomes critical and evaluation of progenies for yield resistance may be improved using this estimate as one of the selection criteria.
4. Genotypes with a very low susceptibility index (highly drought resistant) showed the lowest yield under normal conditions, which could be attributable to an inherent low yielding capacity. These genotypes were shown to be phenotypically and ecologically stable over environments. The most ecologically stable genotypes therefore are those with minimal variation in yield and morphological and phenological traits. However, the response is agronomically undesirable, if the genetic potential for yield is low.
5. Since susceptibility index and geometric mean were shown to be unrelated, it is possible that they are indicators of different biological responses. Thus, susceptibility index may be more associated with plant characteristics related with the yield stability, while geometric mean may be more associated with yield

potential. Increases in stem weight at physiological maturity (lower efficiency in translocation), days to maturity (longer exposure to stress), days of seed filling (lower efficiency in the allocation of dry matter in the seed) and leaf temperature (lower physiological efficiency) increased the drought susceptibility of a genotype. Increases in the number of pods with seed, number of seeds, seed size, pod wall weight, total biomass, leaf area index, stem diameter, harvest index, economic growth rate, seed growth rate, biomass growth rate, relative sink strength, transpiration rate and stomatal conductance were associated with a larger expression of yield under drought, increasing the value of the geometric mean.

6. Geometric mean and susceptibility index are integrative estimates of drought resistance. Both estimates consider the components of yield under drought and represents the integrated response of a set of specific morphological, phenological and physiological traits. They are integrative indices complementary to each other, exhibiting adequate genotypic variability. For all their characteristics these indices are easily estimated and suitable estimates of drought resistance to utilize in breeding dry bean for drought resistance.
7. Since yield under drought in dry bean depends on yield potential and the percentage of yield reduction (drought susceptibility), the selection for drought resistance must consider both components.
8. The differential association of geometric mean and susceptibility index with different sets of plant characteristics implies a biological complementation between both drought resistance estimates. Thus, the use of geometric mean and susceptibility index could allow integrate good performance under both environments into a single drought resistance genotype. Such genotypes would have a high yield under non-stressed conditions and a minimum yield reduction under drought.

9. A drought resistance dry bean genotype can be characterized agronomically by a large geometric mean (high yield potential) and an intermediate susceptibility index, probably at the range between 0.75 and 0.95. The results showed that the attainment of such combinations is biologically feasible in this crop.

III. Biological Significance of Shoot Characteristics for Yield under Drought.

1. Three patterns of relationships between yield and the expression of morphological, physiological and phenological traits under non-stress and drought conditions were observed. In the first pattern, a set of "yield-biomass traits" shown to be related to the expression of yield regardless of water stress. In a second pattern, a set of "drought expressed traits" were only associated with yield under drought. The third pattern was characterized by the non-significant linear relationships between a set of "non-yield-related traits" with yield; although, they may be related linearly with any of the main processes determining yield under drought. Thus, a set of traits was responsible for the expression of yield in any environmental condition while other set of characteristics or responses modulated that expression under stress. The modulating set of traits may be specific for each type of stress. In water stress conditions those traits may define the susceptibility to drought and assist in the expression of yield potential under drought.
2. The study showed that number of pods with seed is as highly sensitive to water stress as yield. Number of seeds per pod and seed size are the two most stable yield components of dry bean under drought, because they are little affected by water stress.
3. The results demonstrated that transpiration and stomatal closure are critical physiological processes for the accumulation of total dry matter and seed yield under drought in this crop, and that the strategies and mechanisms adopted by

the crop to resist drought are based on the functional characteristics of stomata. Within the range of genotypic variability explored, dehydration avoidance or postponement was the main strategy identified. Within this strategy reduction of water loss via stomatal closure, and stomatal adjustment for the maintenance of high transpiration rate and stomatal conductance, the latter mechanism possibly based on osmotic adjustment, could be the most important mechanisms adopted by the dry bean plant to resist drought. Each mechanism was shown to be related to specific levels of expression of morphological and physiological characteristics and phenological adaptations. Each mechanism confers specific levels of drought resistance in specific environments and fits better to specific environmental constrains and productivity requirements. The two mechanisms seem to be mutually exclusive and highly heritable.

4. In this crop phenological adaptations are critical for yield drought resistance and yield under drought because they condition potential for yield and biomass accumulation, via LAI and LAD; indeterminacy and developmental plasticity capabilities; and the physiological strategies adopted by the genotype to face the effects of drought to optimize plant productivity. The strong connection between duration of growing cycle and the physiological mechanisms adopted by the crop to resist drought suggests that phenological adaptations either determine or limit the short and long-term strategies related with stomatal sensitivity to optimize plant productivity and survival under drought. Thus, for Michigan where Type II indeterminate growth habit dry bean genotypes are adapted to a environmentally well defined crop growth cycle and to a modern agriculture production system utilizing stored moisture in the soil, the best physiological strategy to resist drought seems to be the maintenance of transpiration via high levels of stomatal conductance and transpiration rate. The strategy seems suitable to resist either intermittent periods of drought or

prolonged, continued and gradual water stress similar to that applied in this study with a minimal productivity cost. Under this set of conditions the combination of a long crop growth cycle and high stomatal sensitivity and low stomatal conductance to avoid water loss seems to be counterproductive. Reduction of water loss via stomatal closure seems to be a more suitable strategy for locations where late indeterminate genotypes, like Type III dry bean genotypes, are adapted to environmental conditions allowing a long crop growth cycle, without low temperature and/or photoperiod restrictions, short intermittent periods of water stress, and a less developed agriculture systems where uniform flowering is not required. The results suggest that the processes of domestication and selection for high productivity in dry bean have been oriented to the attainment of high rates of leaf gas exchange, which involve sustained stomatal opening in varying environments. In general, It seems that dehydration avoidance strategies based on high stomatal sensitivity, low stomatal conductance and reduced transpiration, although ecologically desirable, are opposite to the maintenance of high yield potential, and agronomically undesirable in dry bean.

5. The importance of other physiological processes such as biomass accumulation before and after anthesis, and partitioning and remobilization of stored assimilates from roots, stems and leaves after anthesis for yield under drought in this crop was demonstrated. At the same time, the significance of biological growth rate, harvest index and relative sink strength in the characterization of the differential genotypic efficiency relative to these processes under drought was established. Thus, the expression of yield under drought will be enhanced under the following conditions: when an early rapid dry matter accumulation occurs (high biological growth rate); when the duration of the reproductive growth is long enough to maximize yield and to avoid

environmental constrains (developmental plasticity leading to a high seed growth rate); where most of the assimilation after flowering is partitioned into pods (high harvest index); and where there is a substantial remobilization of assimilates from vegetative tissues into pods (high relative sink strength).

6. The complexity of yield under drought and yield drought resistance and the lack of a single trait or response that by itself could improve the productivity of dry bean under drought make necessary the analysis of yield under drought as a function of its main determining components. The results indicated that the main processes determining the expression of yield under drought are phenological adaptations, transpiration (photosynthesis), biomass accumulation before and after anthesis, and partitioning and remobilization after anthesis. The analysis of yield under drought is not feasible without regarding phenological adaptations which condition yield potential, indeterminacy and developmental plasticity, and physiological attributes associated with drought resistance, principally transpiration, water use efficiency and partitioning and remobilization. Different plant traits and responses are related to these processes. In breeding for drought resistance all the components need to be considered.
7. Plant traits and responses potentially suitable for being implemented in a breeding program were identified. The traits and responses shown to be associated with drought resistance were related either with yield under drought or with major physiological processes determining yield under drought, practical and easy to measure, stable in their expression, and genotypically variable. Such traits are: seed size, total biomass, stem diameter, leaf size, specific leaf weight, leaf orientation, days of seed fill, harvest index, relative sink strength, biological growth rate, seed growth rate, stomatal conductance, leaf temperature and water content. The importance of these traits is supported by

the fact that traits such as stem diameter, Type II growth habit, specific leaf weight, leaf orientation, harvest index, relative sink strength and seed growth rate have been associated with the expression of yield in non-limiting conditions. However, the final value of every trait for breeding purposes ultimately will be determined by the heritability and genetic variability of each characteristic.

8. Stomatal conductance and leaf temperature have important biological and practical implications in breeding for drought resistance. The characterization of stomatal conductance is a key factor for the determination of strategies and mechanisms adopted by the crop to resist drought, and it may be an important tool in the identification and selection of parents. Leaf temperature may have important implications for the breeding process because it represents the integrated output of a highly complex network of individual physiological and morphological responses and characteristics, which results from the basic physiological strategy and mechanism of drought resistance adopted by the crop. Differences in leaf temperature can be detected in environmental conditions where differences in stomatal conductance and transpiration are not detectable; thus, the trait can be very useful in screening progenies under field conditions as indirect selection criteria for stomatal conductance. Leaf temperature is highly expressed even at high levels of drought stress, contrasting with other plant traits and responses in which the expression is reduced and highly variable. In addition, both the drought resistance strategy and the mechanism adopted by the crop to resist water stress affect the temperature of the leaf. Leaf temperature arises as one of the most suitable and practical physiological responses to select in breeding for drought resistance in dry bean. However, its use would depend on its genetic characteristics of heritability and variability.

9. This research showed that in the process of identification of mechanisms and strategies, and individual responses and characteristics associated to them, it is critical to take into account the methodological aspects. Aspects to be considered are: type and pattern of drought intensity; genotypic variation under study; experimental and sampling techniques; and number and type of variables under study.

10. The results of this research confirm reports of previous studies about the complexity of yield under drought and drought resistance in dry bean and the lack of a single trait that by itself could improve dry bean productivity under drought. Consequently, the best approach in breeding yield under drought will be the integration of multiple selection criteria. The indices must be integrated by both plant characteristics and responses associated with each of the main processes determining yield under drought, within the basic physiological strategy and mechanisms conditioning the response of the plant to drought that fits a specific agroecosystem better.

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IDENTIFICATION AND ESTIMATION OF HERITABILITIES OF DROUGHT RELATED RESISTANCE TRAITS IN DRY BEAN (*Phaseolus vulgaris* L.)

VOLUME II

By

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A DISSERTATION

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CHAPTER 3

VARIANCE COMPONENTS AND HERITABILITY OF MORPHOLOGICAL, PHENOLOGICAL AND PHYSIOLOGICAL DROUGHT RESISTANCE RELATED TRAITS IN DRY BEAN (*Phaseolus vulgaris* L.).

INTRODUCTION

The main goal in a breeding program for drought resistance is the improvement of yield under water stress. However, the efficiency of selection under environmental stress based solely on yield has been shown to be low (Rosielle and Hamblin, 1981; Rumbaugh *et al.*, 1984; Atlin and Frey, 1989). Generally, yield under stress has a lower genetic variance component as compared to the environmental component of variation (Johnson and Frey, 1967; Rumbaugh *et al.*, 1984) which results in lower heritability estimates for stress as compared to nonstress yield (Frey, 1964; Johnson and Frey, 1967; Blum, 1988; Atlin and Frey, 1989). Furthermore, yield *per se* under drought is a poor estimate of drought resistance because of its failure to accurately estimate yield potential, as has been demonstrated for dry bean in this study.

Breeding procedures to increase yield under drought may be facilitated and improved if morphological, phenological and physiological criteria for the identification of high yield families are utilized. In order to facilitate this purpose a suitable trait or response has to be causally related with yield, easy and rapid to assess and higher in heritability than yield itself. From a plant breeding perspective the value of a trait is determined not only by its relationships either with yield or with yield related physiological processes or with other useful agronomic attributes, but also by the genetic properties and practicability of measuring that trait. Hence, traits showing strong relationships with yield or yield-related physiological processes will have a minimum value in breeding dry bean for drought resistance if they are shown to have low heritability.

Estimates of heritability are important in plant breeding to both define the best method to improve a population, and predict the expected response due to selection. Heritability in the broad sense is the ratio of genetic variance to the phenotypic variance, and measures the extent to which trait variability in a field is due to genetic rather than environmental causes (Atlin and Frey, 1989). The estimate expresses the reliability of the phenotypic values as a guide to the breeding values, or the degree of correspondence between phenotypic values and breeding values. Heritability enters into almost every formula connected with breeding methods and many practical decisions about procedure depends on its magnitude (Falconer, 1960). Heritability values can be expressed on a progeny mean basis when the breeder is concerned with average performance for a population over locations and years. Heritability expressed on a single plot or single plant basis can be used to characterize a particular trait. Comparing estimates of heritability from experiments differing in the number of replications, locations and years is simpler when estimates are expressed on a single plot basis (Hanson *et al.*, 1956). Heritability is a property not only of a character but also of the population and the environmental circumstances to which the individuals are subjected. Since heritability values depend on the magnitude of all components of variance, a change in one of these will affect the estimate (Falconer, 1960). Stansfield (1983) has indicated that the concept of high or low heritability is not rigidly defined, but the following values are generally accepted: high heritability (>50%), medium heritability (between 20 and 50%) and low heritability (< 20%).

As heritability values are determined by the proportion of the environmental variance, changes in environmental factors will lead to changes in heritability values. Environmental conditions of stress that limit plant productivity or the expression of plant traits dramatically affect heritability. Stress can be caused by many factors, i.e. drought, fertility, diseases, etc. The severity of stress can vary along a continuous scale of intensity producing a reciprocal variation in the level of productivity or trait expression. Limiting conditions are particularly important for the estimation of heritability, since an increase in the productivity or the expression of the trait indicates generally a decrease in stress, and vice-versa. Decreased stress permits greater genotypic expression, increasing genotypic variances among lines (Johnson and Frey, 1967). As a result, it is normal to find lower genotypic variances and heritabilities for yield under stress conditions (Frey, 1964; Johnson and Frey, 1967; Rosielle and Hamblin, 1981; Blum, 1988; Atlin and Frey, 1989). For instance, Frey (1964) showed that heritability for oat grain yield varied from 45% to 32% under non-stress and stress conditions, respectively; and Rumbaugh *et al.* (1984) found that heritability values for stand density and shoot dry weight of alfalfa and wheatgrass seedlings were reduced when stress increased. In the latter study, most of the phenotypic variance in the drier treatments was environmental. Heritabilities for yield often decrease under stress because genetic variance falls more rapidly with increasing stress than do environmental variances (Blum, 1988). However, the decline may not be great until yield levels are severely reduced by the stress. Accordingly, Edmeades *et al.* (1989) have shown in corn that mean broad sense heritabilities for yield were 57, 54 and 43% under nonstress, stress during grain filling, and stress during both flowering and grain filling, respectively. In general, heritability values were lower under stress.

However, heritability for all plant traits is not consistently increased by reducing stress, because the reduction of stress may increase the heritability of one character while decreases heritability in others, as Johnson and Frey (1967) showed in oat. Hall *et al.* (1990) found genotypic differences in carbon isotope discrimination, which is a trait related to drought resistance in cowpea. In the same study, broad sense heritability under dry conditions was similar to that observed under non-stress conditions. In this way the same level of stress may cause changes in heritability and trait expression, but the magnitude and direction of those changes will vary accordingly with the trait. Thus, it seems that the best environment for selection of all plant traits is not always in the absence of stress. In agreement with this observation, a differential response in various plant traits of dry bean genotypes to the effects of drought was demonstrated in this study.

In dry bean, broad sense heritabilities (H) under non-limiting conditions have been reported for yield ranging from 9 to 94% (Coyne, 1968; Chung and Goulden, 1971; Davis and Evans, 1977; Mutschler and Bliss, 1981; Scully *et al.*, 1991). Narrow sense heritabilities (h^2) for this trait are usually lower varying from 1 to 29% (Paniagua and Pinchinat,1976; Chung and Stevenson, 1973; Nienhuis and Singh, 1988). Low heritability estimates were reported for number of pods with H values of 43% (Davis and Evans, 1977) and h^2 values ranging from 20 to 41% (Sarafi, 1978; Paniagua and Pinchinat, 1976; Nienhuis and Singh, 1988). Intermediate heritabilities were found for seeds per pod, which has H values of 64% (Davis and Evans, 1977) and h^2 values from 53 to 76% (Paniagua and Pinchinat, 1976; Conti, 1985; Nienhuis and Singh, 1988). High heritabilities have been reported for seed size with h^2 ranging from 63 to 74% (Paniagua and Pinchinat, 1976; Motto *et al.*, 1978; Nienhuis and Singh, 1988). Thus, heritabilities for yield and number of pods are low, while heritabilities for number of seeds per pod and seed size are higher than for yield. Motto *et al.* (1978) emphasized the role of the high heritability of seed size on the stability of the trait over environments.

Nienhuis and Singh (1988) reported that growth habit, maturity and seed size are controlled by major genes and are highly heritable in dry bean. In agreement with this observation, high H values ranging from 79 to 98% were reported for days to flower (Conti, 1985; Scully *et al.*, 1991), days to maturity (96%) and days of seed fill (94%) (Davis and Evans, 1977; Scully *et al.*,1991). In soybean, Brim (1973) reported average heritability values of 80 and 84% for days to flower and days to maturity, respectively.

Estimates of heritability for several morphological traits in dry bean have been reported. Davis and Evans (1977) and Acquaah *et al.* (1991) reported H values ranging from 31 to 41% for hypocotyl diameter while Paniagua and Pinchinat (1976) reported h^2 values ranging from 39 to 65% for the same trait. For total biomass Scully *et al.* (1991) reported a H of 93% in dry bean and Mahon (1983) reported a H of 94% in pea. Mahon (1983) reported a H of 93% for specific leaf weight in pea; and Nelson and Schweitzer (1988) found repeatability values of 48% for the same trait in soybean. Davis and Evans (1977) reported high H values for main stem length (88%), number of nodes in the main stem (92%) and total number of nodes (86%) in navy beans. Acquaah *et al.* (1991) reported H values ranging from 10 to 80% for plant height and 51 to 64% for branch angle. Harrison *et al.* (1981) reported heritability values for plant height from 67 to 90%.

Fewer studies have been conducted in legumes to estimate physiological trait heritabilities. In dry bean Scully *at al.* (1991) reported high H values for harvest index (92%), seed growth rate (87%), economic growth rate (86%) and biomass growth rate (87%). In pea Mahon (1983) found high H (90%) for harvest index and seed growth rate; and low H (14%) for relative growth rate. Photosynthesis heritabilities were reported for dry bean and soybean. Wallace *et al.* (1976) reported a H of 60% and a h^2 of 7% for photosynthesis in dry bean. In addition, Izhar and Wallace (1967) indicated that the genetic mechanisms controlling varietal differences in photosynthetic efficiency are quantitative in nature; that there may be relatively few genes involved in the determination of the trait; and that there is some dominance for low photosynthetic efficiency. Mahon (1983) reported high H (85%) for photosynthesis in pea.

Heritability estimates of specific drought related traits determined under conditions of water stress are scarce in the literature. Schonfeld *et al.* (1988) found that differences in relative water content in wheat were due predominantly to genes with additive effects; that narrow sense heritability reached a maximum value of 64%; and that heritability values were increased when drought stress was intensified. Clarke and Townley-Smith (1986) reported narrow sense heritabilities for moisture retention capacity ranging from 11% to 49% in a F_4/F_6 comparison and from 10 to 38% in a F_6/F_8 comparison, under drought stress in field conditions. In cotton, Roark and Quisenberry (1977) reported heritabilities for total leaf stomatal resistance of 25 and 37% for narrow sense and broad sense heritabilities, respectively. In the same study most of the genetic variance was additive and the largest genetic variances and heritabilities were observed during the driest period of the day. Hubick *et al.* (1988) found a broad sense heritability of 81% under field drought conditions and non-significance for the genotype x environment interaction for carbon isotope discrimination in peanut. Hall *et al.* (1990) described genotypic differences in carbon isotope discrimination by cowpea under wet and dry conditions in field conditions. In the same study the authors found a broad sense heritability, on entry mean basis, of 76% in leaf determinations and similar heritabilities under both wet and dry conditions. The complexity of the genetic control in drought resistance related traits was emphasized by Singh (1989). This author suggested that osmotic adjustment and transpirational cooling are controlled by a single gene; and their component characters (water potential, osmotic potential, relative water content and stomatal conductance) by two or more genes. He suggested alternatively that osmotic adjustment and transpirational cooling may be governed by a block of interlinked genes, which may be behaving as if they were controlled by a single gene.

There are not many studies comparing heritability values of morphological, phenological and physiological traits. However, Hallauer and Miranda (1988) compared yield and its components, and morphological and phenological traits in corn. The authors showed that yield had low heritability (<30%) and that the dominant component of variation contributed a large proportion of the total genetic variance of this trait. Yield components had heritability about twice as large as that for yield, with values between 30 and 50%. Morphological and phenological traits showed heritabilities between 50 and 70% or even larger. Thus, ranking of traits based on heritability in corn is shown: morphological and phenological traits > yield components> seed yield. The authors did not specify if some level of environmental stress was involved in the estimations of heritability.

The objective of this research was directed at the estimation of heritabilities of morphological, phenological and physiological traits of dry bean genotypes grown under two contrasting water stress regimes: drought and non-stress conditions. The estimation of heritability is a key step to assess the merit of plant traits as secondary selection criteria.

The main hypothesis tested in this study was that morphological, phenological and physiological traits related with yield under drought and/or yield drought resistance in dry bean (*Phaseolus vulgaris* L.) are more highly heritable than yield and less affected by water stress.

MATERIALS AND METHODS

Experimental aspects related with experimental location, environmental conditions, germplasm evaluated, cultural practices, experimental design, variables under study and data recording have been described in the Chapter 2.

Estimation of Variance Components

Variance components were obtained from the combined analysis of genotypes over drought conditions for the years 1988 (Tables 7A to 11A) and 1990 (Table 12A and 13A). A third estimation was done from the combined analysis of the performance of four genotypes (Sierra, LEF2RB, AC1022 and AC1028) over two drought conditions and two years (Table 3B). A random model was assumed for genotypes, drought conditions and years in all the analysis (Steel and Torrie, 1980; Wricke and Weber, 1986; Fehr, 1987). F test for the models used in this study were done following McIntosh (1983).

The following variance components were estimated for the combined analysis over years:

σ_g^2 = line (genotype) component due to genetic differences among lines.

σ_{gl}^2 = component arising from interaction of lines and locations (drought conditions).

σ_{gy}^2 = component arising from interaction of lines and years.

σ_{gly}^2 = component arising from interaction of lines, locations (drought conditions) and years.

σ_e^2 = component arising from a composite of remaining effects including the plot effects, error due to sampling within plot and errors of measurement.

The components arising from interactions with years were not calculated for the combined analysis over drought conditions for each year.

Estimates of variance components were substituted in the equations given below to obtain estimates of heritability, genetic coefficients of variation and a factor of response to selection.

The phenotypic variance on entry mean basis was estimated by the following general formula (Hanson *et al.*, 1956; Rasmusson and Glass, 1967; Fehr, 1987):

$$\sigma_{ph}^2 = \sigma_g^2 + (\sigma_{gl}^2/l) + (\sigma_{gy}^2/y) + (\sigma_{gly}^2/ly) + (\sigma_e^2/rly)$$

where r, l and y are the number of replications, locations and years.

The phenotypic variance on a plot basis was estimated by the following general formula (Hanson *et al.*, 1956; Fehr, 1987):

$$\sigma_{ph}^2 = \sigma_g^2 + \sigma_{gl}^2 + \sigma_{gy}^2 + \sigma_{gly}^2 + \sigma_e^2$$

In computing phenotypic variances, negative estimates of components were assumed to be zero (Hanson *et al.*, 1956; Rassmuson and Glass, 1967). Estimates of heritability (H) were obtained from the general formula:

$$H = \sigma_g^2/\sigma_{ph}^2$$

Genetic coefficient of variation (GCV) as used by Johnson et al. (1955) and Hanson et al. (1956) was estimated by the equation:

$$GCV = (\sigma_g/\bar{X}) \times 100$$

where σ_g is the genetic standard deviation and $\bar{x}$ is the population mean.

A factor of response to selection was calculated as the product of the square root of heritability and the genetic coefficient of variation.

RESULTS

Estimates of variance components, phenotypic variances, heritabilities and genetic coefficients of variation for yield and its components, and morphological, phenological and physiological traits of dry bean genotypes grown under drought and non-limiting conditions in 1988 and 1990 are presented in Tables 3.1, 3.2., 3.3 and 3.4.

In 1988 the level of drought intensity was 78%. In this year the overall estimates of the genetic variances (Table 3.1) were smaller than the variances of the error for most of the traits under study. However, traits such as seeds per pod, seed size, stem weight, days to flower, days to maturity, water content and water potential showed larger genetic variances than the variance of the error. Under these environmental conditions, the genetic variance for yield was nine times smaller than the variance of the error and the GxE interaction variance. The genetic variances for pods with seed, number of pods and total seed number were negative. The negative variances resulted from the high values of the mean squares of the GE interaction above the mean square of the error. The genetic variances were larger than the GE variance for pods without seed, seeds per pod, seed size, stem weight, harvest index, economic growth rate, seed growth rate, relative sink strength, days to flower, days to maturity, days of seed fill, water content, water potential and all the water use traits under study. The phenotypic variances on an entry mean basis were smaller than those estimated on a plot basis for all the traits.

Heritabilities on an entry mean basis were larger than the estimates based on a single plot. Estimates of heritability for 1988 were low for yield, pods with seed, total number of pods and pod weight; medium heritability for total biomass and moisture retention capacity; and high heritability for seeds per pod, seed size, stem weight, harvest index, economic growth rate, seed growth rate, relative sink strength, biomass growth rate, days to flower, days to maturity, days of seed fill, water content, relative water content, water potential, stomatal conductances, transpiration rate and leaf temperature. Heritability estimates were not calculated for pods with seed, pods total number and pod weight because the negative genetic variances for these traits were equated to zero.

Table 3.1. Estimates of variance components and phenotypic variances for morphological, phenological and physiological characteristics of dry bean genotypes grown under drought and non-limiting conditions. East Lansing, MI, 1988.

TRAIT	VARIANCES[1] GENETIC	 GXE	 ERROR	PHENOTYPIC VARIANCES ENTRY MEAN	 SINGLE PLOT
YIELD	5.6225	49.5750	51.3700	34.6908	106.5675
YIELD COMPONENTS					
Pods with Seed	0.0000	42.5933	29.8300	23.7825	72.4233
Pods w/o Seed	1.8333	0.0467	6.6100	2.3575	8.4900
Pods Total Number	0.0000	50.2733	34.2200	27.9884	84.4933
Seed Number	0.0000	1195.1000	811.3800	665.1600	2006.4800
Seeds/pod	0.3758	0.0533	0.1400	0.4141	0.5692
Seed Size	76.9192	1.1233	11.2900	78.4217	89.3325
BIOMASS					
Stem Weight	10.3883	9.3783	4.4400	15.4475	24.2067
Pod Weight	0.0000	10.7867	4.1100	5.7358	14.8967
Total Biomass	30.2925	163.9283	109.8400	121.4100	304.0608
PARTITIONING					
Harvest Index	0.0039	0.0000	0.0040	0.0042	0.0079
Economic Growth Rate	0.0023	0.0013	0.0050	0.0034	0.0086
Seed Growth Rate	0.0148	0.0048	0.0250	0.0193	0.0446
Relative Sink Strength	0.0328	0.0000	0.0330	0.0356	0.0658
Biomass Growth Rate	0.0037	0.0047	0.0090	0.0068	0.0173

Table 3.1. (cont'd)...

TRAIT	VARIANCES[1] GENETIC	 GXE	 ERROR	PHENOTYPIC VARIANCES ENTRY MEAN	 SINGLE PLOT
PHENOLOGY					
Days to Flower	10.9375	0.0633	4.3000	11.3275	15.3008
Days to Maturity	194.2558	43.4717	122.4600	226.1966	360.1875
Days of Seed Fill	124.6250	29.8883	129.2300	150.3383	283.7433
WATER RELATIONS					
Water Content	0.9363	0.1700	0.8000	1.1213	1.9063
Relative Water Content	2.6830	1.2650	2.9600	3.6855	6.9080
Water Potential	0.0018	0.0000	0.0010	0.0019	0.0028
Moisture Retention Capacity	3.5663	6.1625	14.1900	8.4213	23.9188
WATER USE					
Abaxial Stomatal Conductance	0.0075	0.0025	0.0400	0.0138	0.0500
Adaxial Stomatal Conductance	0.0031	0.0030	0.0070	0.0055	0.0131
Total Stomatal Conductance	0.0200	0.0050	0.0700	0.0313	0.0950
Abaxial Stomatal Conductance%	7.2238	2.5725	8.1900	9.5338	17.9862
Adaxial Stomatal Conductance%	7.2238	2.5725	8.1900	9.5338	17.9862
Transpiration Rate	0.5200	0.0000	2.6700	0.8538	3.1900
Leaf temperature	0.3950	0.2550	1.0900	0.6587	1.7400

G x E = Genotype x Drought Environmental Condition Interaction.

[1] The best estimator of negative variances is zero.

In 1988 the genetic coefficients of variation (GCV) (Table 3.2) ranged from minimal values of 1.2 and 2.1% for water content, relative water content and leaf temperature, respectively, up to maximum values of 30.1 and 34.7% observed in pods without seed and seed size. The average value of the GCV was 13.6%. The lowest GCV were found for yield, days to flower, water relation traits (water content, relative water content, water potential and moisture retention capacity) and in six out of seven of the water use traits under study.

High heritability and high GCV values (Table 3.2) were observed for pods w/o seed, seed per pod, stem weight, harvest index, economic growth rate, seed growth rate, relative sink strength, days to maturity and days of seed fill. Within the physiological traits, water potential, moisture retention capacity, stomatal conductances (abaxial, adaxial and total) and transpiration rate exhibited high level of heritability and the largest GCV of this set of traits.

The product of the square root of heritability and the genetic coefficient of variation was calculated as a response to selection factor (RSF). The product of this factor and the standard selection index, which is arbitrarily determined by the breeder, is the gain from selection expressed as percent of the population mean. In this study the factor rather than the gain for selection as percent of the population mean was used because the value of the last index will depend on the chosen level of selection while the factor remains constant regardless of selection intensity. The response to selection factor value (Table 3.2) was lower than 5% for transpiration rate, yield, percentage of adaxial stomatal conductance, relative water content, leaf temperature and water content. RSF values were between 6 and 10% for moisture retention capacity, water potential, total biomass, abaxial stomatal conductance, days to flower, total stomatal conductance, percentage of adaxial stomatal conductance, and biomass growth rate. RSF values between 10 to 20% were obtained for adaxial stomatal conductance, harvest index, days to

Table 3.2. Estimates of heritability, genetic coefficient of variation and factor of response to selection for morphological, phenological and physiological characteristics of dry bean genotypes grown under drought and non-limiting conditions. East Lansing, MI, 1988.

TRAIT	HERITABILITY ENTRY MEAN	HERITABILITY SINGLE PLOT	MEAN	GCV %	RED %	RSF %
YIELD	16	5	25.48	9.3	78	4
YIELD COMPONENTS						
Pods with Seed			28.15		57	
Pods w/o Seed	76	21	4.43	30.1	-20	26
Pods Total Number			32.53		49	
Seed Number			99.32		74	
Seeds per Pod	91	66	3.23	19.0	35	18
Seed Size	98	86	25.27	34.7	24	34
BIOMASS						
Stem Weight	67	43	11.54	27.9	52	23
Pod Weight			8.01		66	
Total Biomass	25	10	44.53	12.4	70	6
PARTITIONING						
Harvest Index	92	49	0.51	12.2	30	12
Economic Growth Rate	68	27	0.26	18.6	73	15
Seed Growth Rate	77	33	0.49	24.8	68	22
Relative Sink Strength	92	50	1.00	18.1	17	17
Biomass Growth Rate	55	21	0.45	13.5	63	10

Table 3.2. (cont'd)...

TRAIT	HERITABILITY ENTRY MEAN	HERITABILITY SINGLE PLOT	MEAN	GCV %	RED %	RSF %
PHENOLOGY						
Days to Flower	97	71	44.48	7.4	-3	7
Days to Maturity	86	54	95.38	14.6	16	14
Days of Seed Fill	83	44	50.90	21.9	30	20
WATER RELATIONS						
Water Content	84	49	81.17	1.2	1	1
Relative Water Content	73	39	76.25	2.1	4	2
Water Potential	94	64	-0.68	-6.3	33	-6
Moisture Retention Capacity	42	15	21.15	8.9	-82	6
WATER USE						
Abaxial Stomatal Conductance	55	15	0.98	8.8	46	7
Adaxial Stomatal Conductance	57	24	0.38	14.5	58	11
Total Stomatal Conductance	64	21	1.37	10.3	49	8
Abaxial Stomatal Conductance%	76	40	73.78	3.6	-9	3
Adaxial Stomatal Conductance%	76	40	26.23	10.2	21	9
Transpiration Rate	61	16	10.61	6.8	30	5
Leaf temperature	60	23	29.88	2.1	-5	2

GCV = Genetic Coefficient of Variation (%)
RED = Percentage of reduction in phenotypic expression due to drought
RSF = Response to Selection Product = ($H^{1/2}$ x GVC)

maturity, economic growth rate, relative sink strength, seeds per pod and days of seed fill. The largest RSF were obtained for seed growth rate, stem weight, pods without seed and seed size, traits showing values larger than 20%. In general, the lowest response to selection at the drought intensity reached in 1988 are expected to be found for physiological traits, yield, total biomass and days to flower.

The results for 1990 are summarized in Tables 3.3 and 3.4. In 1990, the drought intensity was 63%. Genetic variances were smaller than the error variance in 27 out of 31 traits under evaluation (Table 3.3). Only days to flower, days to maturity, stem weight and water content had larger genotypic variances. In 1990, under a mild drought intensity, the genetic variance for yield was three times smaller than the error variance. In 22 out of 31 traits the genetic variance was larger than the GE variance. The frequency of traits displaying GE variances larger than the genetic variance was greater for physiological traits such as water relations and water use characteristics. Only water potential displayed negative genetic variance. The phenotypic variances on an entry mean basis were smaller than those estimated on a plot basis for all the traits. Heritabilities on an entry mean basis were larger than the estimates based on a single plot. Table 3.4 shows low heritability for pods without seed and water potential. In the latter trait the value of the genetic variance was zero because the mean square of both genotypes and GE interaction were the same. Yield shows a medium heritability at the level of drought intensity of this study. The heritability value was larger at the more severe level of drought intensity in 1988. In addition to yield, other traits with medium levels of heritability were pods without seed, total number of pods, total number of seeds, pod weight, leaf retention, harvest index, economic growth rate, water content, moisture retention capacity, stomatal conductance, transpiration rate, leaf temperature, leaf size and leaf area index. High heritability

Table 3.3. Estimates of variance components and phenotypic variances for morphological, phenological and physiological characteristics of dry bean genotypes grown under drought and non-limiting conditions. East Lansing, MI, 1990.

TRAIT	VARIANCES[1] GENETIC	 GXE	 ERROR	PHENOTYPIC VARIANCES ENTRY MEAN	 SINGLE PLOT
YIELD	5.3375	4.9200	15.1500	11.5850	25.4075
YIELD COMPONENTS					
Pods with Seed	4.7725	3.2800	10.9400	9.1475	18.9925
Pods w/o Seed	0.5625	0.0000	9.1400	2.8475	9.7025
Pods Total Number	2.2650	5.8650	15.7800	9.1425	23.9100
Seed Number	119.9000	108.5800	307.2500	251.0025	535.7300
Seeds/pod	0.1935	0.0075	0.3890	0.2945	0.5900
Seed Size	10.0325	1.3300	10.4900	13.3200	21.8525
BIOMASS					
Stem Weight	4.1450	1.4150	2.5700	5.4950	8.1300
Pod Weight	0.3375	0.8150	0.6400	0.9050	1.7925
Leaf Retention	0.5300	1.4000	1.4500	1.5925	3.3800
Total Biomass	18.6725	14.0950	28.3200	32.8000	61.0875
PARTITIONING					
Harvest Index	0.0025	0.0000	0.0100	0.0050	0.0125
Economic Growth Rate	0.0008	0.0005	0.0020	0.0015	0.0033
Seed Growth Rate	0.0040	0.0025	0.0080	0.0073	0.0145
Relative Sink Strength	0.0285	0.0015	0.0670	0.0460	0.0970
Biomass Growth Rate	0.0018	0.0015	0.0030	0.0033	0.0063

Table 3.3. (cont'd)...

TRAIT	VARIANCES[1] GENETIC	 GXE	 ERROR	PHENOTYPIC VARIANCES ENTRY MEAN	 SINGLE PLOT
Days to Flower	5.0275	0.3200	1.8700	5.6550	7.2175
Days to Maturity	42.2725	4.1700	27.4600	51.2225	73.9025
Days of Seed Fill	19.5175	5.8950	26.3900	29.0625	51.8025
WATER RELATIONS					
Water Content	0.4550	1.2600	1.3700	1.4275	3.0850
Relative Water Content	3.5425	3.3050	4.0400	6.2050	10.8875
Water Potential	0.0000	0.0000	0.0037	0.0009	0.0037
Moisture Retention Capacity	3.8225	0.0000	16.2000	7.8725	20.0225
WATER USE					
Stomatal Conductance	0.0450	0.0300	0.1400	0.0950	0.2150
Transpiration Rate	0.5400	0.8800	3.2000	1.7800	4.6200
Leaf Temperature	0.0650	0.0900	0.2400	0.1700	0.3950
OTHERS					
Leaf Orientation	0.2325	0.0050	0.3500	0.3225	0.5875
Specific Leaf Weight	0.0550	0.0150	0.1800	0.1075	0.2500
Leaf Size	9.6300	10.9250	16.1100	19.1200	36.6650
Leaf Area Index	0.2625	0.4700	2.1900	1.0450	2.9225
Stem Diameter	0.2575	0.0000	0.1600	0.2975	0.4175

G x E = Genotype x Environmental Condition Interaction.

[1] The best estimator of negative variances is zero

values were found in pods with seed, seeds per pod, seed size, stem weight, total biomass, seed growth rate, relative sink strength, biomass growth rate, days to flower, days to maturity, days of seed fill, relative water content, leaf orientation, specific leaf weight and stem diameter.

Genetic coefficients of variation (Table 3.4) ranged from the minimum values of 0.8 and 1.0% found in water content and leaf temperature, respectively, to maximum values of 33.2 to 42.5% observed in stem weight and leaf retention, respectively. The average of the GCV was 14.4%. Days to flower, relative water content, leaf temperature and water content, in that order, showed the lowest GCV.

High heritability and medium to high GCV values were observed in pods with seed, seeds per pod, seed size, stem weight, total biomass, economic growth rate, seed growth rate, relative sink strength, biomass growth rate, days of seed fill, moisture retention capacity, leaf orientation and stem diameter.

RSF values (Table 3.4) ranging between 0 and 5% were exhibited by total number of pods, days to flower, transpiration rate, relative water content, leaf temperature and water content. RSF values between 6 and 10% were observed for harvest index, leaf area index, specific leaf weight, leaf size, days to maturity, seed per pod, days of seed fill, stomatal conductance, pod weight, and stem diameter. RSF values between 11 and 20% were detected for seed size, relative sink strength, leaf orientation, yield, biomass growth rate, pods without seed, total seed number, seed growth rate and moisture retention capacity. RSF larger than 20% were obtained by leaf retention and stem weight.

Table 1B shows the differences between variances obtained at mild (0.63) and severe (0.78) levels of drought intensity for 25 characteristics. Fifteen out of twenty five traits showed larger error variances at the highest drought intensity. The other ten traits had environmental variances larger than the genetic variances

Table 3.4. Estimates of heritabilites, genetic coefficient of variation and factor of response to selection for morphological, phenological, and physiological characteristics of dry bean genotypes grown under drought and non-limiting conditions. East Lansing, MI, 1990.

TRAIT	HERITABILITY ENTRY MEAN	HERITABILITY SINGLE PLOT	MEAN	GCV %	RED %	RSF %
YIELD	46	21	13.49	17.1	63	12
YIELD COMPONENTS						
Pods with Seed	52	25	12.14	18.0	62	13
Pods w/o Seed	20	6	2.38	31.6	-33	14
Pods Total Number	25	9	14.15	10.6	51	5
Seed Number	48	22	52.71	20.8	62	14
Seeds/pod	66	33	4.31	10.2	0	8
Seed Size	75	46	25.83	12.3	2	11
BIOMASS						
Stem Weight	75	51	6.13	33.2	45	29
Pod Weight	37	19	3.58	16.2	60	10
Leaf Retention	33	16	1.71	42.5	11	25
Total Biomass	57	31	23.20	18.6	58	14
PARTITIONING						
Harvest Index	50	20	0.55	9.0	10	6
Economic Growth Rate	50	23	0.15	18.8	57	13
Seed Growth Rate	55	28	0.30	20.8	48	15
Relative Sink Strength	62	29	1.19	14.2	-9	11
Biomass Growth Rate	54	28	0.25	16.8	53	12

Table 3.4. (cont'd)...

TRAIT	HERITABILITY ENTRY MEAN	HERITABILITY SINGLE PLOT	MEAN	GCV %	RED %	RSF %
PHENOLOGY						
Days to Flower	89	70	47.71	4.7	-3	4
Days to Maturity	83	57	91.69	7.1	11	6
Days of Seed Fill	67	38	43.98	10.0	24	8
WATER RELATIONS						
Water Content	32	15	83.94	0.8	1	0
Relative Water Content	57	33	80.12	2.3	1	2
Water Potential					3	0
Moisture Retention Capacity	49	19	7.78	25.1	-24	18
WATER USE						
Stomatal Conductance	47	21	1.76	12.1	23	8
Transpiration Rate	30	12	13.66	5.4	33	3
Leaf Temperature	38	16	25.66	1.0	-4	1
OTHERS						
Leaf Orientation	72	40	3.56	13.5	-10	11
Specific Leaf Weight	51	22	2.74	8.6	15	6
Leaf Size	50	26	33.92	9.1	25	6
Leaf Area Index	25	9	4.49	11.4	30	6
Stem Diameter	87	62	4.66	10.9	19	10

GCV = Genetic Coefficient of Variation (%)
RED = Percentage of reduction in phenotypic expression due to drought.
RSF = Response to Selection Product = (H^2 x GVC)

at the less severe drought intensity. Traits showing the latter response were pods w/o seed, seeds per pod, harvest index, relative sink strength, water content, relative water content, water potential, moisture retention capacity, stomatal conductance and transpiration rate. Eight out of ten traits displaying the response were physiological characteristics.

The differences between GE variances (Table 1B) showed that in 17 out of 25 traits the GE variance was larger at the highest level of drought intensity. Harvest index did not change from one drought intensity level to the other. The other 8 traits showed larger GE variances at the lowest level of drought intensity. Traits showing the latter response were seed size, relative sink strength, days to flower, water content, relative water content, water potential, stomatal conductance and transpiration rate. Six out of the eight traits showing the response were physiological traits. Thus, for the physiological traits relative sink strength, water content, relative water content, water potential, stomatal conductance and transpiration rate the non-genetic components of variation were larger at the lowest than at the highest level of drought intensity.

Four yield-related characteristics and four physiological traits (Table 1B) exhibited smaller genetic variances at the highest drought intensity than at the lowest drought intensity. The genetic component of variation was negative in the yield-related traits like pods with seed, total number of pods, seed number and pod weight. The genetic component of variation for yield was not significantly different at either level of drought intensity.

Heritability values on an entry mean basis (Table 2B) were higher for yield and traits related with pod setting but not for other yield components at the lowest drought intensity. The same results were observed for biomass related traits, such as stem weight, pod weight and total biomass, and also for moisture retention capacity. In this way, these traits showed their highest heritability at the lowest drought intensity. Seventeen other traits, mostly phenological and physiological, showed their highest heritability at the most severe drought intensity. Thus, the heritability of these traits was enhanced by water stress.

Genetic coefficients of variation (Table 2B) were higher at the lowest drought intensity for yield and pod-setting related traits but not for other yield components. Similar results were obtained for the following characteristics: the biomass related traits, stem weight, pod weight and total biomass; the partitioning traits, economic growth rate and biomass growth rate; and the physiological traits, relative water content, water potential, moisture retention capacity and stomatal conductance. The other eleven traits showed high GCV at the more severe drought intensity. Those traits included harvest index, relative sink strength, seed growth rate, days to flower, days to maturity, days of seed fill, water content, transpiration rate, leaf temperature, and seed per pod and seed size. In these traits water stress seemed to enhance both heritability and GCV.

The combined analysis of variation of the performance of the genotypes LEF-2RB, Sierra, AC-1028 and AC-1022 grown over two years and two contrasting drought conditions are shown in Table 3B. Estimates of components of variation are presented in Table 3.5. Estimates of phenotypic variances, heritabilities and genetic coefficients of variation derived from the mean squares of the combined analysis are shown in Table 3.6. The combined analysis removed the Genotype x Year (GY), Genotype x Environment (GL) and Genotype x Year x Environment (GYL) interactions from the genetic component of variation.

The estimates of the genetic variances (Table 3.5) for yield, pods w/o seed, total number of pods, pod weight, transpiration rate and stomatal conductance were negative. The negative values resulted from the large mean square values of the interactions and the error. The results indicate the strong influence of non-genetic components of variation on the expression of these traits

Table 3.5. Estimates of variance components for morphological, phenological and physiological characteristics of four dry bean genotypes grown under drought and non-limiting conditions in 1988 and 1990. East Lansing, MI.

	VARIANCES[1]				
TRAIT	GENETIC	GL	GY	GYL	ERROR
YIELD	0.0000	1.9420	0.0000	71.2235	39.4400
YIELD COMPONENTS					
Pods with Seed	0.0000	22.4583	0.0000	22.1045	25.6560
Pods w/o Seed	0.1250	0.3125	0.0000	6.3125	1.9060
Pods Total Number	0.0000	33.9585	0.0000	15.9790	32.7500
Seeds per Pod	0.3658	0.0095	0.0693	0.0880	0.0770
Seed Number	44.1875	596.875	0.0000	626.0105	888.3440
Seed Size	57.9168	2.6250	13.7915	1.1355	1.3440
BIOMASS					
Stem Weight	13.2520	0.0000	0.0000	9.484	6.3180
Pod Weight	0.0000	4.6243	0.0000	5.9835	4.0780
Total Biomass	27.9976	20.0910	0.0000	167.3965	96.1780
PARTITIONING					
Harvest Index	0.0034	0.0000	0.0000	0.0035	0.0030
Economic Growth Rate	0.0011	0.0000	0.0000	0.0100	0.0030
Seed Growth Rate	0.0134	0.0000	0.0000	0.0575	0.0080
Relative Sink Strength	0.0579	0.0000	0.0000	0.0690	0.0190
Biomass Growth Rate	0.0019	0.0000	0.0000	0.0190	0.0050

Table 3.5. (cont'd)...

TRAIT	VARIANCES[1] GENETIC	GL	GY	GYL	ERROR
PHENOLOGY					
Days to Flower	7.7500	0.0000	0.0000	1.5000	3.0000
Days to Maturity	172.7083	0.0000	0.0000	133.635	21.4380
Days of Seed Fill	122.6875	0.0000	0.0000	114.729	23.2500
WATER RELATIONS					
Water Content	0.7464	0.0000	0.0000	2.0575	1.1720
Relative Water Content	5.6749	0.0000	0.0000	8.3675	1.9900
Water Potential	0.0000	0.0000	0.0000	0.0000	0.0006
Moisture Retention Capacity	1.8043	6.8138	0.1603	0.1670	11.4150
POROMETRY					
Transpiration Rate	0.0000	1.5100	0.0000	3.1215	3.8270
Stomatal Conductance	0.0000	0.0478	0.0000	0.0735	0.1070
Leaf Temperature	0.1370	0.0098	0.0510	0.0000	0.1600

G = Genotypes = 4; Y = Years = 2; L = Drought Environments = 2; r = Replications = 2
GL = Genotype x Environment Interaction
GY = Genotype x Year Interaction
GYL = Genotype x Year x Environment Interaction
1. The best estimator of negative variances is zero

under conditions of water stress. The genetic component of variation was larger than the error and interaction variances for seeds per pod, seed size, stem weight, harvest index, relative sink strength, days to flower, days to maturity, days of seed fill, relative water content and leaf temperature. In most of the twenty five traits under study, the GYL interaction was larger than both the GL and GY interactions. GYL and GL were the most important interactions for most of the traits in this study.

Table 3.6 shows the phenotypic variances, heritability estimates and the genetic coefficients of variation of 18 plant characteristics. Heritability estimates were not calculated when the genetic variance was negative as in yield, pods with seed, total number of pods, pod weight, water potential, transpiration rate and stomatal conductance. Low heritability estimates (between 0 and 20%) were obtained for pods without seed and seed number. Medium heritability estimates (between 20 and 50 %) were observed for total biomass, economic growth rate, seed growth rate, biomass growth rate and moisture retention capacity. High heritability estimates (> 50%) were obtained for seeds per pod, seed size, stem weight, harvest index, relative sink strength, days to flower, days to maturity, days of seed fill, water content, relative water content and leaf temperature.

GCV ranged from the minimal values of 1.1 and 1.3% observed for water content and leaf temperature, to the maximum values of 29.7 and 26.9% observed for seed size and seed growth rate. The average for GCV was 14.2%. The smallest GCV were observed for water content, leaf temperature, relative water content, days to flower and seed number, in that order.

Heritability estimates larger than 50% and GCV larger than 10% were observed for seeds per pod, seed size, stem weight, harvest index, relative sink strength, days to maturity, and days of seed fill. Seed growth rate showed high GCV and a medium heritability. Among the physiological traits, water content,

Table 3.6. Estimates of phenotypic variances, heritabilities, mean, genetic coefficient of variation and response to selection within dry bean genotypes grown under drought and non-limiting conditions in 1988 and 1990. East Lansing, MI.

TRAIT[1]	PHENOTYPIC VARIANCES ENTRY MEAN	PHENOTYPIC VARIANCES SINGLE PLOT	HERITABILITY ENTRY MEAN	HERITABILITY SINGLE PLOT	MEAN	GCV %	RSF %
YIELD COMPONENTS							
Pods w/o Seed	2.0976	8.6560	6	1	3.44	10.3	3
Seed Number	610.1706	2155.4170	7	2	85.22	7.8	2
Seeds per Pod	0.4368	0.6095	84	60	4.02	15.0	14
Seed Size	66.5769	76.8127	87	75	25.66	29.7	28
BIOMASS							
Stem Weight	16.4128	29.0540	81	46	10.25	35.5	32
Total Biomass	91.9145	311.6631	30	9	38.31	13.8	8
PARTITIONING							
Harvest Index	0.0046	0.0099	73	34	0.54	10.8	9
Economic Growth Rate	0.0040	0.0141	28	8	0.22	15.1	8
Seed Growth Rate	0.0288	0.0789	47	17	0.43	26.9	18
Relative Sink Strength	0.0775	0.1459	75	40	1.11	21.8	19
Biomass Growth Rate	0.0073	0.0259	26	7	0.39	11.2	6

Table 3.6. (cont'd)...

TRAIT[1]	PHENOTYPIC VARIANCES ENTRY MEAN	SINGLE PLOT	HERITABILITY ENTRY MEAN	SINGLE PLOT	MEAN	GCV %	RSF %
PHENOLOGY							
Days to Flower	8.5000	12.2500	91	63	46.81	5.9	6
Days to Maturity	208.7968	327.7813	83	53	95.44	13.8	13
Days of Seed Fill	154.2760	260.6665	80	47	48.63	22.8	20
WATER RELATIONS							
Water Content	1.4073	3.9759	53	19	82.10	1.1	1
Relative Water Content	8.0155	16.0324	71	35	77.39	3.1	3
Moisture Retention Capacity	6.7599	20.3603	27	9	14.40	9.3	5
POROMETRY							
Leaf Temperature	0.1874	0.3578	73	38	27.63	1.3	1

1. Pods with seed, total number of pods, pod weight, water potential, transpiration rate, and stomatal conductance showed negative genetic variance.

GCV = Genetic Coefficient of Variation

RCF = Factor of Response to Selection (H^b x GVC) relative water content and leaf temperature showed high heritability values but very low GCV.

RSF values (Table 3.6) between 0 and 5% were obtained by leaf temperature, total seed number, pods without seed, relative water content and moisture retention capacity. RSF values between 6 and 10% were obtained for days to flowering, biomass growth rate, total biomass, economic growth rate and harvest index. RSF values between 11 and 20% were observed in days to maturity, seeds per pod, seed growth rate, relative sink strength and days of seed fill. RSF values larger than 20% were obtained for seed size and stem weight.

DISCUSSION

The effects of water stress on components of variation, heritabilities, genetic coefficients of variation and on response to selection are discussed in this chapter as a means to assess the genetic value of drought resistance related traits in dry bean.

Differences in components of variation due to changes in drought intensity and changes in the relative proportion of each component within each level of drought intensity were the two major effects of water stress on components of variation detected in this study. Differences between components of variation of 25 traits estimated at mild (0.63) and severe (0.78) levels of drought intensity are displayed in Table 1B. It is noticeable that the response to drought caused variable effects on the variance of the error and the variance of the GxE interaction for each trait. Thus, some traits showed greater error and interaction variances at lower drought intensity while other traits had larger values for both variances at higher drought intensity. Although the influence of water stress on components of variation was not consistent, yield and its components associated with pod setting, biomass traits, and partitioning and phenological characteristics showed larger error and interaction variances at the severe level of drought intensity. Thus, in these traits, the non-genetic components of variation were increased at higher levels of drought intensity, in this way these components became more important for the phenotypic expression at the severe level of drought intensity. In contrast, physiological traits, including harvest index and relative sink strength, and yield components such as seeds per pod and seed size showed smaller error and interaction variances under severe water stress. Thus, drought intensity had a differential effect on components of variation.

A similar pattern of variation was observed for the genetic component, because four yield-related traits and four physiological traits showed smaller genetic variances at higher drought intensity while all the other traits had greater genetic variances at the severe level of drought intensity.

The dependency of the phenotypic expression of yield on non-genetic components of variation is supported by the following observations: 1) The genetic variance for yield was almost the same at the two levels of drought intensity despite the differences between sets of genotypes evaluated in both years; 2) the genetic component of variation was negative for pods without seed, total number of pods, total seed number and pod weight at the severe level of water stress: and 3) a larger non-genetic component of variation for yield occurred at the severe level of drought intensity. The relationship between genetic and non-genetic components of variation may help to explain the strong reduction of the phenotypic expression of these traits due to water stress (Table 2B). The general observation that lower genotypic variances are frequent under stress conditions is supported by many authors (Frey, 1964: Johnson and Frey, 1967; Rosielle and Hamblin, 1981; Blum, 1988; Atlin and Frey, 1989). A similar observation for pod set related traits, and the physiological traits, relative water content, moisture retention capacity, stomatal conductance and transpiration rate was made in this study. These traits showed lower genetic variances when the drought intensity was higher. However, the same argument does not apply to traits such as yield components not related with pod setting, phenological traits, partitioning and efficiency traits and the two physiological traits water potential and stomatal conductance, since they showed larger genetic components of variation at the highest water stress.

Another way in which the increase in water stress affected the variance components was by changing the relative proportion of the non-genetic components (Tables 3.1 and 3.3). Thus, the relationships between genetic and non-genetic components differed from one level of drought intensity to the other. The changes were either in magnitude, e.g. stem weight, or in both magnitude and direction, e.g. seed size. Changes in magnitude were slightly more frequent than changes in magnitude and direction. In both years of evaluation the genetic variances were smaller than the environmental variances and larger than the GxE interaction variances for most of the traits, although the number of traits displaying this relation was larger at the lowest drought intensity. The observation (Johnson and Frey, 1967; Rumbaugh *et al*., 1984) that the genetic variance for yield under stress is lower than the non-genetic environmental component of variation was detected in this study on dry bean and may be extended for most of the traits under study at the range of drought intensity evaluated. However, the genetic variances for some traits may be larger than the environmental variance as in stem weight, days to flower, days to maturity, water content, seeds per pod and seed size. From these results, it is possible to conclude that in dry bean the relationships between genetic and non-genetic components of variation are dynamics, trait dependent and sensitive to fluctuations in drought intensity.

Since heritability estimates are dependent on the magnitude of all the components of variation and the relationships between genetic and non-genetic components of variation, it is expected that changes in any variance component will affect the index (Falconer, 1960). Thus, changes in the relationships between variance components due to increases in water stress observed in this research lead to changes in heritability values. The differences between heritability estimates obtained at two different levels of drought intensity may be seen in Tables 3.2, 3.4 and 2B. However, changes in heritability induced by increases of plant water stress at higher drought intensity were not consistent for all traits. The changes in heritability in 25 traits evaluated at two different levels of drought intensity are a good example of this observation. The results showed that seven characteristics associated with yield and biomass accumulation and moisture retention capacity had lower heritability values at higher levels of water stress. These traits were yield, pods without seed, total number of pods, seed number, stem weight, pod weight and total biomass. The results agree with previous reports on yield (Frey, 1964; Johnson and Frey,1967; Blum, 1988; Atlin and Frey, 1989). The changes in heritability for these traits were caused mainly by larger environmental variances or GxE interaction variance or both at the higher drought intensity. Another seventeen traits showed larger heritability estimates at the higher level of water stress than at the lower level. Interestingly, most of those traits are directly or indirectly related with plant efficiency. These traits are partitioning and efficiency indices (harvest index, economic growth rate, seed growth rate, relative sink strength and biomass growth rate), phenological characteristics (days to flower, days to maturity and days of seed filling), physiological traits (water content, relative water content, water potential, stomatal conductance, transpiration rate and leaf temperature) and three yield components (pods without seed, seed number and seed size). In these traits the larger heritabilities resulted from the reduction in the GxE interaction variance or increase in genetic variances. Thus, for some traits the proportion of the GxE interaction component of variation was lower making the phenotypic expression dependent only on environmental and genetic effects at severe levels of water stress. In this way selection for these traits will be more efficient when the genotypes are subjected to severe water stress because under these conditions the differences between genotypes will be due to the additive effect of the environment on genotypes.

The most important implication of these finding is concerned with the choice of the selection environment. Thus, for a set of traits involving yield and yield components such as yield, pods with seed, total number of pods, seed number, and pod weight; biomass accumulation, such as stem weight and total biomass; and moisture retention capacity, the best environment for selection would be from low to medium drought intensity. For other traits involving phenological, partitioning and efficiency indices, and physiological characteristics and responses, such as pods without seed, seed per pod, seed size, harvest index, economic growth rate, seed growth rate, relative sink strength, biomass growth rate, days to flower, days to maturity, days of seed filling, water content, relative water content, water potential, the most appropriate selection environment would be more severe levels of drought intensity. The experimental evidence allows one to conclude that since the magnitude and direction of change in heritability vary accordingly with the trait, the best level of drought intensity to select for specific characteristics and responses will depend on the trait under selection, and that a particular level of drought intensity is not equally favorable for selecting all traits.

The importance of the interactions for the estimation of heritability can be seen in Tables 3.5 and 3.6 when the analysis combined over years and levels of drought intensity was used to derive the components of variation. Traits such as yield, pods with seed, total number of pods, pod weight, water potential, stomatal conductance and transpiration rate exhibited high values of the non-genetic components of variation (variance of the error and interactions) which did not allow a positive estimation of the genetic variance, resulting in negative values. The three-way GYL interaction was the most important interaction and to lesser degree the GL interaction. Therefore, at severe levels of water stress the individual genotypic capabilities for environmental adjustment are minimized in these traits.

The low to medium heritability estimates in this study for yield and yield components are in agreement with previous studies conducted under nonstressed conditions (Coyne, 1969; Chung and Goulden, 1971; Davis and Evans, 1977; Scully *et al*., 1991). The results also showed that yield and number of pods have low heritability while the other two yield components, seeds per pod and seed size, have high heritability in environmental conditions involving mild and severe levels of drought intensity. Similar results have been reported under non-limiting conditions (Davis and Evans, 1977; Nienhuis and Singh, 1988). The high levels of heritability found for phenological traits are in agreement with other reports on dry bean (Conti, 1985; Scully *et al*, 1991) and soybean (Brim, 1973) in non-limiting water conditions.

For morphological traits such as stem diameter, a broad-sense heritability estimate of 84% found under mild water stress was higher than estimates reported under non-stress conditions (Paniagua and Pinchinat, 1976; Davis and Evans, 1977; Acquaah *et al*., 1991). Heritabilities for total biomass (from 25 to 57%) were lower than estimates reported for studies conducted under non-limiting conditions (Mahon, 1983; Scully *et al*., 1991), while in this study a similar trend was detected because the heritability of the trait was lower at more severe levels of water stress. A similar pattern was detected for specific leaf weight because heritability in this study (51%) was lower than values reported for peas (Mahon, 1983) and soybean (Nelson and Schweitzer, 1988) at non-limiting conditions.

Heritabilities for physiological traits such as harvest index, economic growth rate, seed growth rate and biomass growth rate were high in this study, however, their values were lower than those reported under non-stress conditions in dry bean by Scully *et al*. (1991). Thus smaller heritabilities were observed when the stress is increased, since the highest values of heritability in this study occurred at the severe level of water stress.

Heritability values for relative water content ranged from 57 to 73% and were within the range of values reported by Schonfeld *et al*. (1988) for wheat. The authors observed that heritability was increased when drought stress was intensified. A similar trend was observed in this study, because the highest heritability was observed at the most severe water stress. Heritability estimates for moisture retention capacity were similar to the values reported by Clarke and Townley-Smith (1986) for wheat. Roark and Quisenberry (1977) reported a similar broad sense heritability of 37% for stomatal resistance in cotton and that heritability estimates were higher at highest levels of water stress in agreement with the results of this study.

The highest heritability values based on data from 1988 and 1990 (Tables 3.2 and 3.4) were displayed by phenological traits (days to flower, days to maturity and days of seed fill), yield components others than number of pods with seed (seed size and seeds per pod), partitioning traits (harvest index and relative sink strength) and stem weight. The lowest heritability values were observed for yield and its components related with pod setting (pods with seed, seed number, pod weight and total number of pods). The other traits showed intermediate values of heritability. However, within set of traits there was variation in heritability. The most constant sets over drought treatments were partitioning and phenological traits, while the sets with more variability among traits were yield components and biomass characteristics. The twenty five traits were classified in three levels: low, medium and high, based on the average of the heritability estimates of 1988 and 1990, as described in Table 3.7.

Table 3.7. Heritability[1] of morphological, phenological, and physiological traits of dry bean.

Level	Range	Trait
High	> 50%	Seeds per pod, seed size, stem weight, harvest index, economic growth rate, seed growth rate, relative sink strength, biomass growth rate, days to flower, days to maturity, days of seed fill, water content, relative water content, and stomatal conductance.
Medium	20 - 50%	Yield, pod with seed, pod w/o seed, total seed number, total biomass, water potential, moisture retention capacity, transpiration rate and leaf temperature.
Low	< 20%	Total number of pods and pod weight.

1. **Average of estimations at two drought intensities.**

Of the additional morphological traits evaluated in 1990, leaf orientation, specific leaf weight, leaf size and stem diameter showed high heritabilities while leaf area index showed medium heritability. The classification of traits based on the average of the estimates of heritability of 1988 and 1990 (Table 3.7) agrees for many of the traits with the ranking based on heritability estimates derived from the combined analysis over years for four genotypes (Table 3.6).

The usefulness of a secondary trait for indirect selection is determined by its heritability because the index indicates the effectiveness with which selection of genotypes can be based on phenotypic performance (Johnson *et al.*, 1955). However, the heritability value by itself does not provide indication about the amount of genetic progress that would result from selecting the best individuals.

The usefulness of heritability can be increased if heritability estimates are used in combination with the genetic coefficient of variation (GCV). This product of both variables gives the best information on the amount of advance to be expected from selection. Furthermore, the GCV is useful to compare genetic variability in various populations and characters and to estimate the maximum effect of selection. In the expression of the genetic advance as percent of the mean the product of the GCV and the standard index of selection (k) provides information about the maximum effect of selection, while heritability in the same expression indicates how closely the maximum can be approached (Johnson *et al.*, 1955). The genetic advance expressed in this way shows the relationship between GCV and heritability (Hanson *et al.*, 1956). In the study discussed herein, differences for GCV between traits at the same and different levels of drought intensity (Tables 3.2, 3.4 and 3.6) and for the same trait at different levels of drought intensity (Table 2B) were observed. There was no consistent pattern of variation between levels of drought intensity for all the traits (Table 2B). However, several tendencies were observed concerning the relative value of GCV for different traits within levels of drought intensity. The lowest GCV values were observed for water content, water potential and leaf temperature for both levels of drought intensity (Tables 3.2 and 3.4) and for drought treatments over years (Table 3.6). In these traits heritability but not genetic variation was larger at the highest level of drought intensity. Medium to high values were obtained for phenological traits and partitioning indices in both levels of drought intensity (Tables 3.2 and 3.4). The highest values were observed for traits such as pods without seed, stem weight and seed growth rate for both levels of drought intensity (Tables 3.2 and 3.4) and for drought conditions over years (Table 3.6).

The response to selection factor (RSF) seems to be a more suitable characteristic by which to assess the value of a trait from a breeding perspective.

RSF may be particularly useful because many different combinations of heritability and GCV are possible and because heritability values alone may lead to incorrect choices in the selection of traits. For example, there are traits showing high heritability values, but their GCV's are extremely low, which is the case for the physiological traits such as water content, relative water content and leaf temperature. These traits appear to be appropriate to assist in the selection for drought resistance because their heritability is high and their value is enhanced at severe levels of stress, however, they consistently show an inherently low genetic variability. Thus, a trait may be chosen for its high heritability but its usefulness in selection will be limited by its low variability, resulting in a minimal response to selection for the trait. Although, it seems that the best combination for a desirable trait may be high heritability and high GCV, in some cases a high GCV value may compensate for a moderate heritability. The contrary will not be useful because high heritability and low GCV results in low response to selection.

The following traits exhibited high heritability and variability, expressed over a range from mild to severe water stress based on heritability values higher than yield and a RSF higher than 10%: 1) The yield related traits, pods without seed, seed size and seeds per pod; 2) The biomass related traits, stem weight and total biomass; 3) The partitioning traits, harvest index, economic growth rate, seed growth rate, relative sink strength and biomass growth rate; 4) The phenological traits, days to maturity and days of seed filling; 5) The physiological traits, moisture retention capacity and stomatal conductance; 6) The morphological traits stem diameter and leaf orientation. These traits are potential secondary traits that may be used to assist in the breeding of genotypes for yield under drought. The most useful of these traits for their practicability and relationships with yield seem to be the following: total biomass, harvest index, relative sink strength, days of seed filling, stomatal conductance, stem diameter and leaf orientation. Relative sink strength may be particularly important because this index integrates in a single relationship partitioning indices and phenological traits with high heritability, and it is highly associated with productivity under drought. Those traits are seed growth rate, biomass growth rate, harvest index, days to maturity and days of seed fill.

The results of the research reported herein have shown that the physiological traits studied were better expressed at higher levels of water stress and had levels of heritability from medium to high. However, they showed a consistent small genetic variability (small GCV). Good examples of this observation are leaf temperature, water potential, relative water content and water content which showed levels of heritability ranging from medium to high, but all of these traits showed very low GCV under any condition. The low GCV of these traits make them inefficient selection criteria even though they are highly heritable. In addition, these traits are labor and time consuming, and in some cases special equipment is required for their measurement. However, two traits which may be potentially useful are stomatal conductance and moisture retention capacity.

Stomatal conductance may be particularly useful given its strong direct relationship with biomass production and yield, because it is better expressed at high levels of drought intensity and because it is related with the basic strategy adopted by the crop to resist drought. Since the trait requires special equipment and is time and labor consuming its use may be restricted to selection of parental lines under rain-out shelters rather than in segregating populations. Given the practical limitations in measuring stomatal conductance, moisture retention capacity may be a good alternative for which to select because it is easy to measure. Although it is not directly related to yield and biomass, it is correlated with stomatal conductance and is better expressed under mild drought intensity. In this context, another potentially useful trait is specific leaf weight. The trait is directly related to stomatal conductance and transpiration rate, is easy to measure and is not destructive. In addition, the trait has been suggested as useful even for yield under non-water stress. Both traits may be particularly useful to assist in the selection for stomatal conductance in the evaluation of large number of progenies, mainly under limitations of labor and equipment in advanced generations.

The results have shown that partitioning, phenological, biomass and morphological traits may be more efficient and practical for use in the breeding for drought resistance, since they have high heritability and GCV, and are expressed at different levels of drought intensity. The traits are non-destructive, relatively easy to measure under field conditions which would allow the screening of large populations.

General Strategy for Breeding for Drought Resistance

An efficient program for drought resistance is difficult to develop by using yield under drought as the only selection criteria. It seems that the best strategy for the improvement of drought resistance should involve breeding for both yield potential and yield under drought, and seek the reduction of the gap between the expression of yield under both environmental conditions. In breeding for drought resistance it may be necessary to consider a trade-off between yield potential and yield stability. The improvement of yield under drought may be achieved through the incorporation and selection of drought related characteristics in high-yielding genotypes.

To achieve the objective, the contribution of susceptibility index together with the geometric mean should be used. Both indices have been shown to be particularly useful to characterize drought resistance in large segregating populations of different generations. In those breeding programs where the improvement for drought resistance is not the primary objective but some degree of tolerance is desired, the characterization of genotypes through these indices may be integrated in the breeding process as an additional selection criteria prior to the selection and release of varieties. In programs in which a larger degree of stability is required an additional evaluation of germplasm could be performed in F_4 or F_5 generations. This approach may be useful for regions where dry bean is grown under adequate rainfall conditions most of the years, but drought conditions may occur sporadically. Michigan is a good illustration of these environmental conditions. The method may also be appropriate for the characterization of drought resistance of introductions, either advanced lines or landraces, before their incorporation as parents into the breeding program. When available economical resources are limited, the use of these indices may be particularly useful in assisting breeding for drought resistance.

The testing of genotypes, however, should be done under both normal and drought conditions. The application of drought is an important methodological aspect to consider. Drought stress developed constantly and gradually throughout the stage of development under study may be the most appropriate to differentiate genotypes and drought resistance mechanisms of drought resistance but may not resemble actual drought stress. This condition may be attained for testing in locations where the likelihood of rainfall is low. Rainout-shelters may also create these conditions.

The best approach in breeding strictly for drought resistance will be the integration of multiple selection criteria. This approach will be appropriate for environments where critical water stress is a normal condition. This condition occurs in regions with unpredictable and limited rainfall, as in many regions of Mexico and Latin America. Based on their genetic attributes, practicability and relationship with plant productivity under drought, the most useful characteristics to consider in breeding dry bean for drought resistance and yield under drought would be days of seed filling, total biomass, harvest index, relative sink strength, stomatal conductance, stem diameter, leaf orientation, specific leaf weight and moisture retention capacity. Days of seed filling is a phenological adaptation. Total biomass, stem diameter, harvest index, and relative sink strength are characteristics associated with biomass accumulation and partitioning. Relative sink strength combines biomass growth rate, seed growth rate, days to maturity, days of seed filling and harvest index. All the characteristics are highly heritable even at severe levels of water stress and enhanced in its expression by water stress. Stomatal conductance is directly associated with transpiration capacity. Water use efficiency may be improved by breeding for leaf orientation, specific leaf weight and moisture retention capacity. The last two traits were not directly associated with yield, but they were related to stomatal conductance and transpiration rate. The two characteristics may be useful in screening a large number of families because they are relatively easy to measure under field conditions. Specific leaf weight has been found to be related with water use efficiency, osmotic adjustment and photosynthesis while moisture retention capacity has been found to be related with characteristics of the cuticle. Thus, the selection for stomatal conductance, specific leaf weight and moisture retention capacity may lead to the better integration of morphological and physiological characteristics leading to a more efficient plant under drought. Although leaf temperature and relative water content exhibited high heritability they showed limited genetic variability in populations studied. In addition, both plant responses are relatively easy to measure under field conditions, non destructive and correlated with plant productivity, so they could be important if they were selected in different parents. All these attributes make the traits potentially useful to be integrated into a breeding program but a larger genotypic variability should be explored and integrated. It is possible that using a larger number of parents selected for this characteristic and integrating them in a single population through a recurrent selection system may increase genetic variability and allow selection of different trait combinations. Leaf temperature could be particularly useful under conditions of severe water stress, where both phenotype and heritability are better expressed. Interestingly, all the traits, with the exception of stomatal conductance and moisture retention capacity, leaf temperature and relative water content, have been considered valuable by Adams (1982) for improving yield potential under normal conditions.

A generalized scheme for the integration of drought resistance related traits in a breeding program is shown in Figure 1, this scheme attempts to integrate the improvement of the components of drought resistance. The basic steps of the process are described as follows:

1. Screening high yielding genotypes for drought resistance. Testing of cultivars, advanced lines and/or landraces in replicated experiments under drought and normal conditions. The genotypes should be grouped by seed type, maturity or growth habit and further characterized by susceptibility index and geometric mean. This is the first step in the identification of parents.
2. Determination of mechanisms of drought resistance. This information is necessary to define the direction of selection for physiological traits.
3. Selection of parents for desired phenological, physiological and morphological characteristics. Selection criteria are: harvest index, stem diameter, relative sink strength, stomatal conductance, leaf orientation, specific leaf weight and moisture retention capacity.
4. Crossing of parents. At the early phases of the breeding process, single crosses between high-yielding adapted genotypes and genotypes showing desired characteristics may be the most important. In later phases

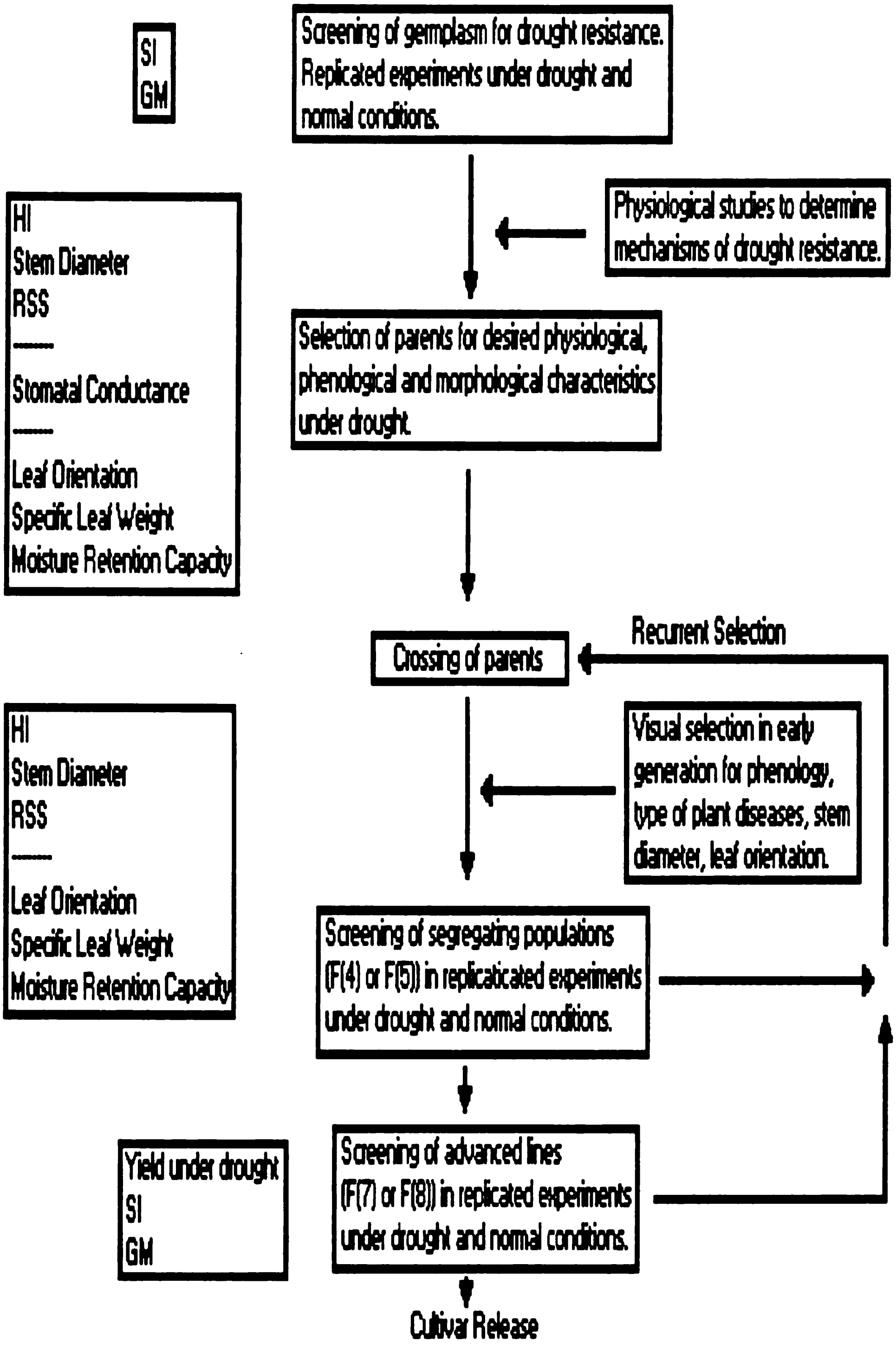

Figure 1. Scheme of a generalized plant breeding program for drought resistance in dry bean involving morphological, physiological and phenological characteristics.

intercrossing following a recurrent selection scheme to combine expression of quantitative traits influencing drought tolerance will be critical.

5. Visual selection in early generations on a single plant basis (F_2). Advance of generations under non-stress conditions. This step should be performed as in breeding for yield potential. Since yield potential and agronomic characteristics are also objective of the breeding process; this step is necessary to avoid the elimination of high-yielding genotypes or genotypes exhibiting desirable agronomic characteristic while maintaining variability. Traits for selection could be phenology, type of plant, disease resistance, stem diameter, leaf orientation and type size. In addition, selection for specific traits such as stomatal conductance, specific leaf weight, moisture retention capacity and leaf temperature is not practical nor desirable at this generations.
6. Screening of F_4 / F_5 lines in replicated trials. F_4 or F_5 families are grown under drought and normal conditions. Genotypes are selected for harvest index, stem diameter, relative sink strength, specific leaf weight, leaf orientation and moisture retention capacity under drought.
7. Screening of limited number of advanced lines (F_7 or F_8). Selection for yield under drought, susceptibility index and geometric mean. Genotype testing is performed under both drought and normal conditions.

The loops at the left hand side of the Figure 1 are intended to show that drought-resistance genotypes identified at different stages of the breeding process can reenter the crossing phase for recurrent selection and population improvement.

Since most of the physiological traits showed low genetic variability as compared with morphological and phenological characteristics, recurrent selection may be a useful breeding method to maintain or to increase such variability. Although the search for more variability through the identification of parents with a broader genetic basis is the first step of this process. The selection pressure for such traits should be low to avoid a drastic reduction of genetic variability. Recurrent selection may be the only method for the integration of populations with contrasting drought resistance and yield under drought, since it is possible that most of the genetic variance exhibited for these traits is additive and could be combined through recurrent selection. The additive nature of the genetic variance may result from the fact that these traits represent the integrated phenotypic expression of different physiological, morphological and anatomical individual characteristics.

Since genetic variability is necessary for an efficient selection program, the search of sources of variability is a critical step of the suggested plan. It is possible that genetic variability for drought resistance remains in populations that have been improved for yield under non-stress. In addition, some of the drought related traits have also been suggested as suitable traits for the improvement of yield under non-stress. Thus it is seems that the systematic evaluation of cultivars, advanced lines and even of genotypes which has been classified as drought susceptible in other breeding programs is an necessary step. The last point is important because a single mechanism to resist drought may not be suitable for all the agroecosystems. The evaluation should be done under both normal and drought conditions, since up to this point these evaluations have been done under either drought or non-drought conditions. Another important source of genetic variation may be found in bean landraces. An alternative to increase the genetic variability for drought resistance is the use of both wild and related species such as *Phaseolus acutifolius.* However the use of this germplasm may be limited to conditions of severe drought stress where the main mechanism of drought resistance is stomatal closure. The major limitation of this approach is that extreme drought resistance is linked to low productivity. In addition, basic physiological and genetic studies necessary for the adequate use of this approach and germplasm are lacking.

CONCLUSIONS

The experimental evidence obtained in this study on dry bean suggests the following conclusions.

1. Differential water stress affects the value of individual variance components and the relationships between components of variation.
2. The relationships between genetic and non genetic components of variation are dynamics, trait dependent and sensitive to fluctuations in drought intensity.
3. Changes in the level of water stress cause changes in heritability and trait expression but the magnitude and direction of such changes will vary accordingly with the nature of the trait. Thus the best environment for selection is not the same for all the plant traits, neither is a reduced level of stress ideal.
4. Since the best level of drought intensity for selection is trait dependent and an unique level of drought intensity is not equally favorable for all the traits, characteristics involving yield and its components related with pod set and biomass accumulation may be better selected at the lowest level of stress, while other traits involving phenological, partitioning and efficiency indices, and physiological characteristics and responses may be more efficiently selected at more severe levels of drought intensity.
5. A factor of response to selection seems to be a more suitable index to assess the value of a trait from a breeding perspective, since the factor estimates the maximum expected gain from selection and integrates in a single value heritability and genetic variability. The index may be particularly useful in assisting the selection of drought resistance related traits in dry bean.
6. Based on their genetic attributes, practicability, and relationship with plant productivity under drought, total biomass, harvest index, relative sink strength,

days of seed filling, stomatal conductance, stem diameter and leaf orientation may be the most useful characteristics to consider in breeding dry bean for drought resistance and yield under drought. Specific leaf weight and moisture retention capacity may also be alternative characteristics to consider, mostly to assist in selection for stomatal conductance.

7. Although most of the physiological traits under study were better expressed at high levels of water stress and had from medium to high heritability, they showed a consistent low variability. The lack of variability of traits like leaf temperature and relative water content limits their use as selection criterion in a breeding program. Thus, the genetic attributes of these traits limit their usefulness even though they may be importantly related with plant productivity and practical to measure under field conditions.
8. Among the physiological traits, only stomatal conductance seems to be particularly useful because it is strongly related with biomass production and yield, is better expressed than yield at high levels of drought intensity and is related to the basic strategy adopted by the crop to resist drought.
9. Partitioning, phenological, biomass and morphological traits may be more efficient and practical in a breeding program for drought resistance rather than physiological traits others than stomatal conductance, because a number of these traits are highly heritable, exhibited adequate genetic variability and are expressed at different levels of drought intensity. In addition, they are relatively easy to measure under field conditions, non destructive and highly responsive to selection.
10. The results of this study have demonstrated that the physiological characterization of traits in terms of their relationships with yield or productivity-related processes is insufficient to choice useful traits in breeding dry bean for drought resistance; that the genetic characterization of such traits is necessary

to assess their value from a breeding perspective; that heritability by itself is not sufficient argument in the selection of traits to assist in the breeding for drought resistance; and that the identification of traits with higher heritability than yield and genetic variability, in addition to their physiological and practical attributes, is possible.

APPENDIX A

Table 1A. Observed and normal precipitation and temperature for the growing season of experiments conducted at East Lansing, MI, 1991.

YEAR	JUNE		JULY		AUGUST		SEPTEMBER		TOTAL	
	P*	T**	P*	T**	P*	T**	P*	T**	(1)	(2)
1987	3.30	70.60	3.35	74.60	5.69	65.40	4.88	62.30	12.30	17.17
1988	0.20	68.10	2.56	74.60	5.08	69.40	5.97	61.20	7.84	13.81
1989	3.61	65.80	0.93	71.30	4.90	72.60	3.49	59.80	9.44	12.93
1990	2.50	66.50	3.61	69.30	2.40	68.40	4.00	62.10	8.51	12.51
NORMAL (3)	3.50	66.20	2.78	70.80	3.04	68.40	2.54	61.60	9.32	11.86

SOURCE: Local climatological data for Lansing, Michigan.
Annual summary with comparative data. 1990. NOAA.

* Precipitation in inches

** Temperature in degres Fahrenheit

1. Total of the period from June to August.
2. Total of the period from June to September.
3. Normal based on the 1951-1980 period.

Table 2A. Soil moisture content in percentage of weight at four depths (0 - 15; 16 - 30; 31 - 45; 45 - 60 cm) for stressed and non-stressed environments of experiments conducted in 1988. East Lansing, MI.

SAMPLE DATE		DAP[1]	DEPTH (cm)							
			0 - 15		16 - 30		31 - 45		46 - 60	
			N[2]	S[3]	N	S	N	S	N	S
July	19	32	8.86	8.37	8.84	7.55	7.61	7.87	8.14	10.20
	26	39	6.78	6.01	7.89	7.59	8.46	8.30	8.48	8.94
August	1	45	7.77	4.15	7.01	6.11	7.77	6.90	7.98	7.94
	9	53	5.20	3.36	6.00	3.93	6.78	5.12	6.50	8.34
	16	60	6.56	4.00	5.63	4.42	5.45	4.90	6.12	6.85
	25	69	8.72	2.50	7.86	3.96	7.00	4.24	6.25	6.36
	31	75	7.55	2.59	8.05	3.97	7.30	5.52	6.41	6.35
September	6	81	7.73	3.23	7.63	3.53	7.83	4.76	6.94	5.40
	14	99	7.32	3.18	7.19	3.81	7.67	4.20	6.95	6.50
Mean			7.39	4.15	7.34	4.99	7.32	5.76	7.09	7.43

[1] Days after planting
[2] Non-stressed environment
[3] Stressed environment
Average flowering date: 45 DAP

Table 3A. Soil water content in percentage of volume[a] at three depths (30, 60, 90 cm) for stressed and non-stressed environments of experiments conducted in 1990. East Lansing, MI.

SAMPLE DATE		DAP[1]	DEPTH (cm)					
			30		60		90	
			N[2]	S[3]	N	S	N	S
August	8	44	11.93	10.86	23.94	20.80	28.32	28.57
	21	57	15.82	9.86	24.45	17.92	25.85	27.65
	29	65	10.88	8.84	21.70	19.31	24.97	26.91
September	5	72	8.45	7.82	17.57	16.46	21.94	25.88
	12	79	16.46	7.31	18.30	15.64	20.47	25.50
	18	85	21.20	7.25	21.94	15.61	20.71	26.78
	25	92	20.16	7.15	23.25	15.66	21.17	26.49
Mean			14.99	8.60	21.59	18.41	23.34	26.83

[1] Days after planting
[2] Non-stressed enviroment
[3] Stressed environment
[a] Values estimated by the Neutron-probe method
Average flowering date: 49 DAP

Table 4A. Seed yield, pod number, weight of pod, leaf moisture retention capacity, growth habit and seed type of genotypes evaluated under drought. East Lansing, MI, 1987.

GENOTYPE	YIELD[1] (g/pl)	POD NUMBER PER PLANT	POD WEIGHT (g/pl)	MRC[a] %	GROWTH HABIT	SEED TYPE	ORIGEN
Sierra	23.53**	22.50**	6.23**	20.70	II	Pinto	MSU
LEF2RB	17.01**	19.50**	5.14**	23.60	III[2]	Stripped	INIFAP
B83302	13.63	21.60**	4.28**	25.10	II	Black	MSU
AC-1028	11.97	13.60	3.40	8.30	III	Bayo	MSU[5]
AC-1022	11.65	28.60**	3.77	31.80**	III	Navy	MSU[5]
N-84004	8.38	15.50	2.71	45.10**	II	Navy	MSU
T-291	7.96	8.33	3.19	27.00	II	Pinto	MSU
Seafarer	5.77	28.60**	3.13	15.70	I	Navy	MSU
N80068	5.19	13.93	1.48	21.60	II	Navy	MSU
A-195	1.19	4.20	0.80	7.30	I[3]	R. B.[4]	CIAT
Mean	10.63	16.36	3.41	20.14			
CV (%)	35.9	33.0	29.3	23.4			
Significance	***	**	**	***			
LSD 0.05	7.49	12.18	2.26	10.62			

Levels of significance: 0.10(*); 0.05(**); 0.01(***)

[a] Leaf moisture retention capacity

[1] Grams of seed/plant. Average of five plants

[2] Type II in Mexico

[3] Photoperiod sensitive in Michigan

[4] Reddish brown

Table 5A. Analysis of variance of seven yield related traits measured on five dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

SOURCE	df	YIELD	PODS W/ SEED	PODS W/O SEED	TOTAL PODS	SEED NUMBER	SEED SIZE	SEEDS PER POD
Environment	1	15713.05***	7848.82***	15.00 NS	6784.07**	199462.01***	721.07***	28.30***
Genotype	4	416.29 NS	76.98NS	28.89*	163.03NS	7041.06NS	941.06***	4.97**
G x E	4	348.82***	285.39***	6.88 NS	335.86***	7981.98***	18.03NS	0.46**
Error	50	51.37	29.83	6.61	34.22	811.38	11.29	0.14

Level of significance: 0.10(*); 0.05(**); 0.01(***).

Table 6A. Analysis of variance of biomass traits and partitioning indexes of five dry bean genotypes grown under drought and non-stress conditions. Lansing, MI, 1988.

SOURCE	df	STEM WEIGHT	PODS WEIGHT	TOTAL BIOMASS	HARVEST INDEX	ECONOMIC GROWTH RATE	SEED GROWTH RATE	RELATIVE SINK STRENGHT
Environment	1	968.98**	953.05**	33692.87***	0.497***	1.320***	3.827***	0.539***
Genotype	4	185.37NS	51.40NS	1456.92NS	0.050***	0.040 NS	0.231*	0.408***
G x E	4	60.71***	68.63***	1093.41***	0.003NS	0.013**	0.054*	0.014NS
Error	50	4.44	4.11	109.84	0.004	0.005	0.025	0.033
CV (%)		18.25	25.31	23.54	12.760	26.830	32.520	18.060

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 7A. Analysis of variance of phenological traits of five dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

SOURCE	df	DAYS TO FLOWER	DAYS TO MATURITY	DAYS OF SEED FILLING
Environment	1	25.35*	4420.41**	5112.26**
Genotype	4	135.93***	2714.36**	1804.06*
G x E	4	4.68NS	383.29**	308.56*
Error	50	4.30	122.46	129.23
CV (%)		4.66	11.60	26.83

Significance: 0.10(*); 0.05(**); 0.01(***).

Table 8A. Analysis of variance of water status traits of five dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

SOURCE	df	WATER CONTENT (%)	RELATIVE WATER CONTENT (%)	WATER POTENTIAL (MPa)	MOISTURE RETENTION CAPACITY (%)
Environment	1	2.73 NS	96.15**	0.3500***	1506.02**
Genotype	4	8.97*	29.48NS	0.0150***	67.37NS
G x E	4	1.48 NS	8.02**	0.0005 NS	38.84**
Error	30	0.80	2.96	0.0010	14.19
CV (%)		1.12	2.26	5.6	17.81

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 9A. Analysis of variance of water use traits of five dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1988.

SOURCE	df	BELOW CONDUCTANCE	ABOVE CONDUCTANCE	TOTAL CONDUCTANCE	% ABAXIAL CONDUCTANCE
Environment	1	3.44***	0.97***	8.07***	378.22***
Genotype	4	0.11 NS	0.04 NS	0.25 NS	76.27*
G x E	4	0.05 NS	0.02**	0.09 NS	18.48*
Error	30	0.04	0.01	0.07	8.19
CV (%)		19.10	21.64	18.98	3.88

SOURCE	df	% ADAXIAL CONDUCTANCE	TRANSPIRATION RATE	LEAF TEMPERATURE
Environment	1	378.22**	142.66**	22.41**
Genotype	4	76.27*	6.35 NS	5.27 NS
G x E	4	18.48*	2.19 NS	2.11 NS
Error	30	8.19	2.67	1.09
CV (%)		3.88	15.40	3.49

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 10A. Significance of mean squares of yield components, biomass, partitioning, and phenology related traits of twenty dry bean genotypes grown under drought and non-stressed conditions. East Lansing, MI, 1990.

TRAIT	ENVIRONMENT (E)	BLOCKS/ ENVIRONMENT	GENOTYPE (G)	GXE	ERROR
YIELD COMPONENTS					
Yield	3012.410 ***	0.480	46.340 *	24.990 *	15.150
Pods w/ Seed	2365.310 ***	0.460	36.590 *	17.500 NS	10.940
Pods w/o Seed	18.050 NS	7.400	9.930 NS	7.680 NS	9.140
Pods Total Number	1970.110 **	4.360	36.570 NS	27.510 *	15.780
Seed Number	44604.010 **	23.460	1004.010 *	524.410 *	307.250
Seed/Pod	0.205 NS	0.050	0.184 ***	0.070 NS	0.070
Seed Size	5.580 NS	1.190	53.280 ***	13.150 NS	10.490
BIOMASS					
Stem Weight	255.040 **	5.570	21.980 ***	5.400 **	2.570
Pod Weight	188.960 **	0.170	3.620 NS	2.270 ***	0.640
Leaf Retention	0.730 NS	0.840	6.370 NS	4.250 ***	1.450
Total Biomass	7156.870 ***	10.850	131.200 **	56.510 **	28.320
PARTITIONING					
Harvest Index	0.070 NS	0.010	0.020 **	0.010 NS	0.010
Biomass Growth Rate	0.636 **	0.001	0.013 **	0.006	0.003
Economic Growth Rate	0.272 ***	0.0001	0.006 **	0.003 NS	0.002
Seed Growth Rate	0.724 **	0.001	0.029 **	0.013 *	0.008
Relative Sink Strength	0.215 NS	0.051	0.184 **	0.070 NS	0.067
PHENOLOGY					
Days to Flower	51.520 *	1.490	22.620 ***	2.510 NS	1.870
Days to Maturity	2215.510 **	37.560	204.890 ***	35.800 NS	27.460
Days of Pod Filling	2942.740 **	25.560	116.250 ***	38.180 NS	26.390

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 11A. Significance of mean squares of water use, water relations and other traits of twenty dry bean genotypes grown under drought and non-stress conditions. East Lansing, MI, 1990.

TRAIT	ENVIRONMENT (E)	BLOCKS/ ENVIRONMENT	GENOTYPE (G)	GXE	ERROR
WATER USE					
Stomatal Conductance	4.750 NS	0.790	0.380 *	0.200 NS	0.140
Transpiration Rate	573.460 *	31.380	7.120 NS	4.960 NS	3.200
Leaf Temperature	17.790 **	0.460	0.680 NS	0.420 *	0.240
WATER RELATIONS					
Water Content	4.550 NS	1.490	5.710 NS	3.890 ***	1.370
Relative Water Content	161.430 *	3.210	24.820 **	10.650 ***	4.040
Water Potential	0.007 NS	0.002	0.001 NS	0.001 **	0.004
Leaf Moisture Retention Capacity	93.210 NS	9.760	22.130 ***	6.840 NS	16.200
OTHERS					
Leaf Orientation	2.450 NS	0.270	1.290 ***	0.360 NS	0.350
Specific Leaf Weight	4.190 NS	0.830	0.430 *	0.210 NS	0.180
Leaf Size	1161.210 *	48.800	76.480 *	37.960 **	16.110
Leaf Area Index	50.480 NS	3.300	4.180 NS	3.130 NS	2.190
Stem Diameter	18.620 **	0.120	1.180 ***	0.150 NS	0.160

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 12A. Significance of correlation coefficients (n=5) of drought resistance estimates with yield components, biomass traits, phenological and morphological characteristics, and efficiency and partitioning indexes in five genotypes grown under drought conditions. East Lansing, MI, 1988.

TRAIT	SI (1)	YR (2)	GM (3)	AM (4)
YIELD COMPONENTS				
YIELD (D)	-0.852 **	-0.857 **	0.854 **	0.449
Pods with Seed	-0.872 **	-0.877 **	0.828 *	0.412
Pods w/o Seed	0.924 ***	0.920 ***	-0.426	0.030
Pods Total Number	-0.847 *	-0.853 **	0.348	-0.131
Seeds/Pod	0.801 *	0.803 *	-0.072	0.351
Seed Number	-0.279	-0.289	0.576	0.373
Seed Size	-0.844 *	-0.849 **	0.830 *	0.454
BIOMASS				
Stem Weight	0.249	0.246	0.468	0.756
Pod Weight	-0.880 **	-0.884 **	0.819 *	0.401
Total Biomass	-0.693	-0.699	0.921 **	0.648
PHENOLOGY				
Days to Flower	0.294	0.288	0.552	0.857 **
Days to Maturity	0.374	0.378	0.171	0.500
Days of Seed Fill	0.375	0.383	0.010	0.321
PARTITIONING				
Harvest Index	-0.845 *	-0.852 **	0.561	0.073
Economic Growth Rate	-0.875 **	-0.881 **	0.785 *	0.334
Seed Growth Rate	-0.836	-0.843 *	0.764	0.319
Biomass Growth	-0.834 *	-0.841 *	0.861 **	0.458
Relative Sink Strength	-0.710	-0.718	0.519	0.086

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

1. SI = Susceptibility Index.
2. YR = Yield Reduction.
3. GM = Geometric Mean.
4. AM = Arithmetic Mean.

Table 13A. Significance of correlation coefficients (n=5) of drought resistance estimates with physiological traits of five genotypes grown under drought. East Lansing, MI, 1988.

TRAIT	SI (1)	YR (2)	GM (3)	AM (4)
Water Potential	0.344	0.340	0.582	0.867 **
Moisture Retention Capacity	-0.040	-0.045	-0.309	-0.469
Relative Water Content	0.290	0.277	-0.046	0.048
Water Content	0.179	0.172	0.649	0.893 **
Transpiration Rate	0.238	0.236	-0.256	-0.270
SC (5)	-0.429	-0.424	-0.022	-0.382
SC%(6)	0.886 **	0.889 **	-0.192	0.308
Leaf Temperature	0.509	0.504	-0.647	-0.401

Level of Significance: 0.10(*); 0.05(**); 0.01(***)
1. SI =Susceptibility Index
2. YR = Yield Reduction
3. GM = Geometric Mean
4. AM = Arithmetic Mean
5. Stomatal Conductance (Below leaf)
6. Ratio of stomatal conductance below leaf relative to the total stomatal conductance

Table 14A. Significances of correlations coefficients of yield components under drought on a plot basis (n=30). East Lansing, MI, 1988.

TRAITS	YIELD (D)	Pods with Seed	Pods w/o Seed	Total Number of Pods	Seed Number
Pods with Seed	0.778 ***				
Pods w/o Seed	-0.639 ***	-0.441 ***			
Total Number of Pods	0.418 **	0.788 ***	0.199		
Seed Number	0.682 ***	0.591 ***	-0.478 ***	0.291	
Seed Size	0.888 ***	0.696 ***	-0.591 ***	0.364	0.309 *

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 15A. Significances of correlation coefficients of biomass components with phenological and partitioning traits under drought on a plot basis (n=30). East Lansing, MI, 1988.

TRAITS	Stem Weight	Pod Weight	Total Biomass
Days to Flower	0.527 ***	0.112	0.257
Days to Maturity	0.616 ***	-0.112	0.062
Days of Seed Fill	0.570 ***	-0.185	-0.023
Harvest Index	-0.441 **	0.664 ***	0.580 ***
Economic Growth Rate	-0.087	0.878 ***	0.856 ***
Seed Growth Rate	-0.163	0.830 ***	0.793 ***
Stem Weight	----	0.214	
Total Biomass	0.417 **	0.938 ***	

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 16A. Significances of correlation coefficients (n=30) of yield components with biomass components, phenological traits and partitioning variables under drought. East Lansing, MI, 1988.

TRAITS	YIELD (D)	Pods with Seed	Pods w/o Seed	Total Number of Pods	Seed Number	Seed Size
Stem Weight	0.052	-0.094	0.287	0.108	-0.108	0.114
Pod Weight	0.917***	0.847***	-0.454**	0.620***	0.566***	0.866**
Total Biomass	0.926***	0.711***	-0.455**	0.466***	0.572***	0.856***
Days to Flower	0.078	-0.245	0.073	-0.190	-0.188	0.180
Days to Maturity	0.168	-0.443**	0.159	-0.358*	-0.341*	-0.042
Days of Seed Fill	-0.243	-0.463**	0.171	-0.377**	-0.357*	-0.124
Harvest Index	0.821***	0.736***	-0.739***	0.278	0.748***	0.672
Economic Growth Rate	0.979***	0.806***	-0.641***	0.434**	0.712***	0.848***
Seed Growth Rate	0.939***	0.773***	-0.626***	0.409**	0.704***	0.798***

Level of Significance: 0.10(*); 0.05(**); 0.10(***).

Table 17A. Significance of correlation coefficients (n=40) among yield components of twenty genotypes grown under non-stress conditions. East Lansing, MI, 1990.

TRAIT	YIELD (P)	Pods with Seed	Pods w/o Seed	Total Number of Pods	Seed Number	Seed Size
Pods with Seed	0.848***					
Pods w/o Seed	-0.304*	-0.232				
Total Number of Pods	0.819***	0.983***	-0.072			
Seed Number	0.875***	0.868***	-0.239	0.855***		
Seed Size	0.026	-0.228	0.067	-0.227	-0.381**	
Seeds/Pod	0.498***	0.220	-0.219	0.205	0.626***	-0.391**

Levels of Significance: 0.10(*); 0.05(**); 0.01(***).

Table 18A. Significance of correlation coefficients (n=40) among yield components with morphological and phenological traits and partitioning indices of twenty genotypes grown under non-stress. East Lansing, MI, 1990.

TRAIT	YIELD (P)	PWS	PWOS	PTN	SN	SS	S/P
STW	0.518 ***	0.672 ***	-0.184	0.651 ***	0.560 ***	-0.300	0.123
PW	0.795 ***	0.887 ***	-0.286 *	0.862 ***	0.759 ***	-0.191	0.176
TB	0.934 ***	0.904 ***	-0.300 *	0.874 ***	0.862 ***	-0.113	0.383 **
DF	0.063	0.154	-0.374 **	0.127	0.090	-0.080	-0.039
MAT	0.015	0.122	-0.342 **	0.082	0.069	-0.042	-0.034
DSF	-0.009	0.083	-0.258 *	0.045	0.046	-0.016	-0.024
HI	0.493 ***	0.228	-0.103	0.226	0.323 **	0.358 **	0.458 ***
EGR	0.964 ***	0.792 ***	-0.206	0.773 ***	0.821 ***	0.066	0.477 ***
SGR	0.920 ***	0.748 ***	-0.168	0.736 ***	0.769 ***	0.085	0.445 ***
RSS	0.459 ***	0.202	-0.061	0.208	0.280 *	0.349 **	0.401 ***
BGR	0.940 ***	0.878 ***	-0.203	0.860 ***	0.846 ***	-0.080	0.392 **

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
Yield (P) = Yield Potential.
PWS = Pods with Seed.
PWOS = Pods w/o Seed.
PTN = Total Number of Pods.
SN = Seed Number.
SS = Seed Size.
S/P = Seeds/ Pod.
STW = Stem Weight.
PW = Pod Weight.

TB = Total Biomass.
DF = Days to Flower.
MAT = Days to Maturity.
DSF = Days of Seed Fill.
HI = Harvest Index.
EGR = Economic Growth Rate.
SGR = Seed Growth Rate.
RSS = Relative Sink Strength.
BGR = Biomass Growth Rate.

Table 19A. Significance of correlation coefficients (n=40) among yield components with morphological traits of stem and leaf of twenty genotypes grown under non-stress conditions. East Lansing, MI, 1990.

TRAIT	YIELD (P)	PWS	PWOS	PTN	SN	SS	S/P
LR	0.047	0.280 *	0.029	0.271 *	0.170	-0.374 **	-0.003
SD	0.655 ***	0.668 ***	-0.213	0.639 ***	0.623 ***	-0.186	0.283 *
LO	-0.128	-0.361 **	0.029	-0.376 **	-0.174	0.227	0.161
LS	0.096	0.103	-0.307 *	0.047	0.110	-0.195	0.046
LAI	0.022	-0.015	-0.249	-0.057	-0.001	-0.095	0.158
SLW	0.154	0.266 *	-0.201	0.224	0.216	-0.223	0.171

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

Yield (P) = Yield potential.
PWS = Pods with Seed.
PWOS = Pods w/o Seed.
PTN = Total Number of Pods.
SN = Seed Number.
SS = Seed Size.
S/P = Seeds/Pod

LR = Leaf Retention.
SD = Stem Diameter.
LO = Leaf Orientation.
LS = Leaf Size.
LAI = Leaf Area Index.
SLW = Specific Leaf Weight.

Table 20A. Significance of correlation coefficients (n=40) among biomass traits with phenological and morphological traits of stem and leaf of twenty genotypes grown under non-stress conditions. East Lansing, MI, 1990.

TRAIT	STW	PW	TB	LR
DF	0.426***	0.342**	0.236	0.134
MAT	0.377**	0.206	0.167	0.146
DSF	0.278*	0.104	0.102	0.121
SD	0.849***	0.790***	0.829***	0.442***
LO	-0.444***	-0.421***	-0.297	-0.234
SLW	0.278*	0.175	0.217	0.330**
LS	0.207	0.166	0.156	0.060
LAI	0.051	0.045	0.038	-0.090
PW	0.784***			
TB	0.784***	0.926***		
LR	0.675***	0.212	0.283*	

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

STW = Stem Weight.
PW = Pod Weight.
TB = Total Biomass.
LR = Leaf Retention.
DF = Days to Flower.
MAT = Days to Maturity.
DSF = Days of Seed Fill.
SD = Stem Daimeter.
LO = Leaf Orientation.
SLW = Specific Leaf Weight.
LS = Leaf Size.
LAI = Leaf Area Index.

Table 21A. Significance of correlation coefficients (n=40) among partitioning indices with biomass and morphological traits of twenty genotypes grown under non-stress conditions. East Lansing, MI, 1990.

TRAIT	HI	EGR	SGR	RSS	BGR
STW	-0.321 **	0.398 **	0.352 **	-0.329 **	0.674 ***
PW	0.000	0.707 ***	0.672 ***	0.008	0.870 ***
TB	0.206	0.857 ***	0.808 ***	0.184	0.959 ***
LR	-0.341 **	0.015	-0.006	-0.330 **	0.240
DF	-0.294 *	-0.120	-0.118	-0.253	0.040
MAT	-0.260 *	-0.244	-0.350 **	-0.466 ***	-0.112
DSF	-0.191	-0.248	-0.379 **	-0.463 ***	-0.156
SD	-0.101	0.587 ***	0.538 ***	-0.129	0.779 ***
LO	0.284 *	-0.008	0.024	0.314 **	-0.178
SLW	0.021	0.141	0.139	0.017	0.206
LS	-0.202	0.018	-0.017	-0.225	0.081
LAI	0.015	-0.005	0.001	0.026	0.013
HI		0.569 ***	0.572 ***	0.947 ***	0.303 ***
EGR			0.987 ***	0.586 ***	0.939 ***
SGR				0.637 ***	0.920 ***
RSS					0.333 **

Level of Significance: 0.10(*); 0.05(**); 0.01(***).

HI = Harvest Index.
EGR = Economic Growth Rate.
SGR = Seed Growth Rate.
RSS = Relative Sink Strenght.
BGR = Biomass Growth Rate.
STW = Stem Weigth.
PW = Pod Weight.
TB = Total Biomass.
LR = Leaf Retention.

DF = Days to Flower.
MAT = Days to Maturity.
DSF = Days of Seed Fill.
SD = Stem Diameter.
LO = Leaf Orientation.
SLW = Specific Leaf Weight.
LS = Leaf Size.
LAI = Leaf Area Index.

Table 22A. Significance of correlation coefficients (n=40) among water use and water relation traits with yield components, biomass, phenology, morphology and partitioning related traits of twenty genotypes grown under non-stress conditions. East Lansing, MI, 1990.

TRAIT	WP	MRC	RWC	WC	TR	SC	LT
YIELD COMPONENTS							
Yield	0.177	0.030	-0.447 ***	-0.538 ***	-0.105	-0.065	-0.111
Pods with Seed	0.060	0.006	-0.559 ***	-0.531 ***	-0.111	-0.102	0.018
Pods w/o Seed	-0.125	-0.128	0.393 *	0.218	0.258 *	0.261 *	-0.161
Total Number of Pods	0.050	-0.002	-0.506 ***	-0.516 ***	-0.050	-0.038	-0.015
Seeds/Pod	0.344***	0.064	-0.331 **	-0.258 *	0.183	0.192	-0.127
Seed Number	0.248	0.009	-0.511 ***	-0.436 ***	-0.020	-0.006	-0.020
BIOMASS							
Stem Weight	-0.103	-0.351 **	-0.485 ***	-0.205	-0.255	-0.350 **	0.361 **
Pod Weight	-0.094	-0.141	-0.563 ***	-0.437 ***	-0.202	-0.216	0.102
Leaf Retention	-0.038	-0.219	-0.228	0.008	-0.213	-0.281*	0.271 *
Total Biomass	0.067	-0.124	-0.561 ***	-0.505 ***	-0.192	-0.200	0.067
PHENOLOGY							
Days to Flower	-0.357**	-0.285 *	-0.248	0.190	-0.254	-0.378 **	0.477 ***
Days to Maturity	-0.136	-0.452***	-0.320 **	0.055	-0.272 *	-0.337 **	0.404 ***
Days of Seed Fill	-0.009	-0.432***	-0.285 *	-0.017	-0.222	-0.248	0.287 *

Table 22A. (cont'd)...

TRAIT	WP	MRC	RWC	WC	TR	SC	LT
MORPHOLOGY							
Specific Leaf Weight	-0.048	-0.074	-0.328 **	-0.088	-0.220	-0.173	-0.190
Leaf Size	0.291*	-0.110	-0.407 ***	0.203	-0.224	-0.268 *	0.173
Leaf Area Index	0.318**	-0.063	-0.169	0.013	0.060	-0.012	0.014
Stem Diameter	0.206	-0.297 *	-0.419 ***	-0.406 ***	-0.195	-0.196	0.084
PARTITIONING							
Harvest Index	0.221	0.338 **	-0.070	-0.350 **	0.095	0.172	-0.285 *
Economic Growth Rate	0.192	0.187	-0.349 **	-0.574 ***	0.025	0.093	-0.271*
Seed Growth Rate	0.153	0.235	-0.298 *	-0.540 ***	0.052	0.112	-0.277 *
Biomass Growth Rate	0.103	0.051	-0.433 *	-0.544 ***	-0.033	-0.005	-0.123
Relative Sink Strength	0.152	0.463 ***	-0.035	-0.334 **	0.161	0.238	-0.392 **

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
WP = Water Potential.
MRC = Moisture Retention Capacity.
RWC = Relative Water Content.
WC = Water Content.
TR = Transpiration Rate.
SC = Stomatal Conductance.
LT = Leaf Temperature.

Table 23A. Significance of correlation coefficients (n=40) among water use traits with water relation traits of twenty genotypes grown under non-stress conditions. East Lansing, MI, 1990.

TRAIT	WP	MRC	RWC	WC	TR	SC
MRC	-0.101					
RWC	-0.035	-0.001				
WC	0.124	-0.330 **	0.361 **			
TR	-0.358 **	0.111	0.154	0.100		
SC	-0.441 ***	0.141	0.189	-0.022	0.946 ***	
LT	0.381 **	-0.081	-0.192	0.076	-0.214	-0.469***

Level of Significance: 0.10(*); 0.05(**); 0.01(***).
WP = Water Potential.
MRC = Moisture Retention Capacity.
RWC = Relative Water Content.
WC = Water Content.
TR = Transpiration Rate.
SC = Stomatal Conductance.
LT = Leaf Temperature.

APPENDIX B

Table 1B. Differences between estimates of variance components and phenotypic variances of morphological, phenological, and physiological characteristics evaluated in 1988 and 1990 on dry bean genotypes grown under drought and non-limiting conditions. East Lansing, MI.

		VARIANCES			PHENOTYPIC VARIANCES	
TRAIT	DI	GENETIC (1)	GXE	ERROR	ENTRY MEAN	SINGLE PLOT
YIELD	78	5.6225	49.5750	51.3700	34.6908	106.5675
	63	5.3375	4.9200	15.1500	11.5850	25.4075
DIFFERENCE	15	0.2850	44.6550	36.2200	23.1058	81.1600
YIELD COMPONENTS						
Pods with Seed	78	0.0	42.5933	29.8300	23.7825	72.4233
	63	4.7725	3.2800	10.9400	9.1475	18.9925
DIFFERENCE	15	-4.7725	39.3133	18.8900	14.6350	53.4308
Pods w/o Seed	78	1.8333	0.0467	6.6100	2.3575	8.4900
	63	0.5625	0.0	9.1400	2.8475	9.7025
DIFFERENCE	15	1.2708	0.0467	-2.5300	-0.4900	-1.2125
Pods Total Number	78	0.0	50.2733	34.2200	27.9884	84.4933
	63	2.2650	5.8650	15.7800	9.1425	23.9100
DIFFERENCE	15	-2.2650	44.4083	18.4400	18.8459	60.5833
Seed Number	78	0.0	1195.1000	811.3800	665.1600	2006.4800
	63	119.9000	108.5800	307.2500	251.0025	535.7300
DIFFERENCE	15	-119.9000	1086.5200	504.1300	414.1575	1470.7500
Seeds/pod	78	0.3758	0.0533	0.1400	0.4141	0.5692
	63	0.1935	0.0075	0.3890	0.2945	0.5900
DIFFERENCE	15	0.1823	0.0458	-0.2490	0.1196	-0.0208
Seed Size	78	76.9192	1.1233	11.2900	78.4217	89.3325
	63	10.0325	1.3300	10.9400	13.3200	21.8525
DIFFERENCE	15	66.8867	-0.2067	0.3500	65.1017	67.4800

Table 1B. (cont'd)...

		VARIANCES			PHENOTYPIC VARIANCES	
TRAIT	DI	GENETIC (1)	GXE	ERROR	ENTRY MEAN	SINGLE PLOT
BIOMASS						
Stem Weight	78	10.3883	9.3783	4.4400	15.4475	24.2067
	63	4.1450	1.4150	2.5700	5.4950	8.1300
DIFFERENCE	15	6.2433	7.9633	1.8700	9.9525	16.0767
Pod Weight	78	0.0	10.7867	4.1100	5.7358	14.8967
	63	0.3375	0.8150	0.6400	0.9050	1.7925
DIFFERENCE	15	-0.3375	9.9717	3.4700	4.8308	13.1002
Total Biomass	78	30.2925	163.9283	109.8400	121.4100	304.0608
	63	18.6725	14.0950	28.3200	32.8000	61.0875
DIFFERENCE	15	11.6200	149.8333	81.5200	88.6100	242.9733
PARTITIONING						
Harvest Index	78	0.0039	0.0	0.0040	0.0042	0.0079
	63	0.0025	0.0000	0.0100	0.0050	0.0125
DIFFERENCE	15	0.0014	0.0	-0.0060	-0.0008	-0.0046
Economic Growth Rate	78	0.0023	0.0013	0.0050	0.0034	0.0086
	63	0.0008	0.0005	0.0020	0.0015	0.0033
DIFFERENCE	15	0.0015	0.0008	0.0030	0.0019	0.0053
Seed Growth Rate	78	0.0148	0.0048	0.0250	0.0193	0.0446
	63	0.0040	0.0025	0.0080	0.0073	0.0145
DIFFERENCE	15	0.0108	0.0023	0.0170	0.0120	0.0301
Relative Sink Strenght	78	0.0328	0.0	0.0330	0.0356	0.0658
	63	0.0285	0.0015	0.0670	0.0460	0.0970
DIFFERENCE	15	0.0043	-0.0015	-0.0340	-0.0104	-0.0312
Biomass Growth Rate	78	0.0037	0.0047	0.0090	0.0068	0.0173
	63	0.0018	0.0015	0.0030	0.0033	0.0063
DIFFERENCE	15	0.0019	0.0032	0.0060	0.0035	0.0110

Table 1B. (cont'd)...

TRAIT	DI	VARIANCES GENETIC (1)	GXE	ERROR	PHENOTYPIC VARIANCE ENTRY MEAN	SINGLE PLOT
PHENOLOGY						
Days to Flower	78	10.9375	0.0633	4.3000	11.3275	15.3008
	63	5.0275	0.3200	1.8700	5.6550	7.2175
DIFFERENCE	15	5.9100	-0.2567	2.4300	5.6725	8.0833
Days to Maturity	78	194.2558	43.4717	122.4600	226.1966	360.1875
	63	42.2725	4.1700	27.4600	51.2225	73.9025
DIFFERENCE	15	151.9833	39.3017	95.0000	174.9741	286.2850
Days of Seed Fill	78	124.6250	29.8883	129.2300	150.3383	283.7433
	63	19.5175	5.8950	26.3900	29.0625	51.8025
DIFFERENCE	15	105.1075	23.9933	102.8400	121.2758	231.9408
WATER RELATIONS						
Water Content	78	0.9363	0.1700	0.8000	1.1213	1.9063
	63	0.4550	1.2600	1.3700	1.4275	3.0850
DIFFERENCE	15	0.4813	-1.0900	-0.5700	-0.3062	-1.1787
Relative Water Content	78	2.6830	1.2650	2.9600	3.6855	6.9080
	63	3.5425	3.3050	4.0400	6.2050	10.8875
DIFFERENCE	15	-0.8595	-2.0400	-1.0800	-2.5195	-3.9795
Water Potential	78	0.0018	0.0	0.0010	0.0019	0.0028
	63	0.0000	0.0	0.0037	0.0009	0.0037
DIFFERENCE	15	0.0018	0.0	-0.0027	0.0010	-0.0009
Moisture Retention Capacity	78	3.5663	6.1625	14.1900	8.4213	23.9188
	63	3.8225	0.0	16.2000	7.8725	20.0225
DIFFERENCE	15	-0.2562	6.1625	-2.0100	0.5488	3.8963

Table 1B. (cont'd)...

TRAIT	DI	VARIANCES GENETIC (1)	 GXE	 ERROR	PHENOTYPIC VARIANCES ENTRY MEAN	 SINGLE PLOT
WATER USE						
Abaxial Stomatal Conductance	78	0.0075	0.0025	0.0400	0.0138	0.0500
	63	0.0450	0.0300	0.1400	0.0950	0.2150
DIFFERENCE	15	-0.0375	-0.0275	-0.1000	-0.0813	-0.1650
Transpiration Rate	78	0.5200	0.0	2.6700	0.8538	3.1900
	63	0.5400	0.8800	3.2000	1.7800	4.6200
DIFFERENCE	15	-0.0200	-0.8800	-0.5300	-0.9263	-1.4300
Leaf Temperature	78	0.3950	0.2550	1.0900	0.6587	1.7400
	63	0.0650	0.0900	0.2400	0.1700	0.3950
DIFFERENCE	15	0.3300	0.1650	0.8500	0.4887	1.3450

DI = Drought Intensity

G x E = Genotype x Drought Environmental Condition Interaction

1. The best estimator of negative variances in zero

Table 2B. Differences between estimates of heritabilities and genetic coefficients of variation of morphological, phenological and physiological characteristics evaluated in 1988 and 1990 in dry bean genotypes grown under drought and non-limiting conditions. East Lansing, MI.

		HERITABILITY				
TRAIT	DI	ENTRY MEAN	SINGLE PLOT	MEAN	GCV %	RED %
YIELD	78	16	5	25.48	9.3	78
	63	46	21	13.49	17.1	63
DIFFERENCE	15	-30	-16	11.99	-7.8	15
YIELD COMPONENTS						
Pods with Seed	78	—	—	28.15	—	57
	63	52	25	12.14	18.0	62
DIFFERENCE	15	-52	-25	16.01	-18.0	-5
Pods w/o Seed	78	76	21	4.43	30.1	-20
	63	20	6	2.38	31.6	-33
DIFFERENCE	15	56	15	2.05	-1.5	13
Pods Total Number	78	—	—	32.53	—	49
	63	25	9	14.15	10.6	51
DIFFERENCE	15	-25	-9	18.38	-10.6	-2
Seed Number	78	—	—	99.32	—	74
	63	48	22	52.71	20.8	62
DIFFERENCE	15	-48	-22	46.61	-20.8	12
Seeds/pod	78.	91	66	3.23	19.0	35
	63	66	33	4.31	10.2	0
DIFFERENCE	15	25	33	-1.08	8.8	35
Seed Size	78	98	86	25.27	34.7	24
	63	75	46	25.83	12.3	2
DIFFERENCE	15	23	40	-0.56	22.4	22
BIOMASS						
Stem Weight	78	67	43	11.54	27.9	52
	63	75	51	6.13	33.2	45
DIFFERENCE	15	-8	-8	5.41	-5.3	7
Pod Weight	78	—	—	8.01	—	66
	63	37	19	3.58	16.2	60
DIFFERENCE	15	-37	-19	4.43	-16.2	6
Total Biomass	78	25	10	44.53	12.4	70
	63	57	31	23.20	18.6	58
DIFFERENCE	15	-32	-21	21.33	-6.2	12

Table 2B. (cont'd)...

TRAIT	DI	HERITABILITY ENTRY MEAN	HERITABILITY SINGLE PLOT	MEAN	GCV %	RED %
PARTITIONING						
Harvest Index	78	92	49	0.51	12.2	30
	63	50	20	0.55	9.0	10
DIFFERENCE	15	42	29	-0.04	3.2	20
Economic Growth Rate	78	68	27	0.26	18.6	73
	63	50	23	0.15	18.8	57
DIFFERENCE	15	18	4	0.11	-0.2	16
Seed Growth Rate	78	77	33	0.49	24.8	68
	63	55	28	0.30	20.8	48
DIFFERENCE	15	22	5	0.19	4.0	20
Relative Sink Strenght	78	92	50	1.00	18.1	17
	63	62	29	1.19	14.2	-9
DIFFERENCE	15	30	21	-0.19	3.9	26
Biomass Growth Rate	78.	55	21	0.45	13.5	63
	63	54	28	0.25	16.8	53
DIFFERENCE	15	1	-7	0.20	-3.3	10
PHENOLOGY						
Days to Flower	78	97	71	44.48	7.4	-3
	63	89	70	47.71	4.7	-3
DIFFERENCE	15	8	1	-3.23	2.7	0
Days to Maturity	78	86	54	95.38	14.6	16
	63	83	57	91.69	7.1	11
DIFFERENCE	15	3	-3	3.69	7.5	5
Days of Seed Fill	78	83	44	50.90	21.9	30
	63	67	38	43.98	10.0	24
DIFFERENCE	15	16	6	6.92	11.9	6
WATER RELATIONS						
Water Content	78	84	49	81.17	1.2	1
	63	32	15	83.94	0.1	1
DIFFERENCE	15	52	34	-2.77	1.1	0
Relative Water Content	78	73	39	76.25	2.1	4
	63	57	33	80.12	2.3	1
DIFFERENCE	15	16	6	-3.87	-0.2	3
Water Potential	78	94	64	-0.68	-6.3	33
	63	—	—	—	—	3
DIFFERENCE	15	94	64	-0.68	-6.3	30
Moisture Retention Capacity	78	42	15	21.15	8.9	-82
	63	49	19	7.78	25.1	-24
DIFFERENCE	15	-7	-4	13.37	-16.2	-58

Table 2B. (cont'd)...

TRAIT	DI	HERITABILITY ENTRY MEAN	 SINGLE PLOT	MEAN	GCV %	RED %
WATER USE						
Abaxial Stomatal Conductance	78	55	15	0.98	8.8	46
	63	47	21	1.76	12.1	23
DIFFERENCE	15	8	-6	-0.78	-3.3	23
Transpiration Rate	78	61	16	10.61	6.8	30
	63	30	12	13.66	5.4	33
DIFFERENCE	15	31	4	-3.05	1.4	-3
Leaf temperature	78	60	23	29.88	2.1	-5
	63	38	16	25.66	1.	-4
DIFFERENCE	15	22	7	4.22	1.1	-1

GCV = Genetic Coefficient of Variation (%)

RED = Percentage of reduction in phenotypic expression due to drought.

Table 3B. Mean squares for the combined analysis of variation of four dry bean genotypes grown under drought and non-limiting conditions in 1988 and 1990. East Lansing, MI.

	MEAN SQUARES				
TRAIT	G	GY	GL	GLY	ERROR
YIELD	84.319	110.637	189.655	181.887**	39.440
YIELD COMPONENTS					
Pods with Seed	45.365	42.698	159.698	69.865	25.656
Pods w/o Seed	14.531	12.281	15.781	14.531***	1.906
Pods Total Number	85.208	59.375	200.542	64.708**	32.750
Seeds per Pod	3.494*	0.530	0.291	0.253	0.077
Seed Number	4790.948	2049.948	4527.865	2140.365	888.344
Seed Size	532.615**	58.781**	14.115	3.615	1.344
BIOMASS					
Stem Weight	99.873	2.980	16.163	25.286**	6.318
Pod Weight	22.454	7.481	34.542	16.045**	4.078
Total Biomass	518.493	214.148	511.335	430.971**	96.178
PARTITIONING					
Harvest Index	0.032	0.010	0.005	0.010**	0.003
Economic Growth Rate	0.011	0.012	0.013	0.023	0.003
Seed Growth Rate	0.093	0.051	0.058	0.123***	0.008
Relative Sink Strength	0.397**	0.041	0.050	0.157***	0.019
Biomass Growth Rate	0.023	0.024	0.027	0.043***	0.005

Table 3B. (cont'd)...

	MEAN SQUARES				
TRAIT	G	GY	GL	GLY	ERROR
PHENOLOGY					
Days to Flower	65.125***	4.125	5.000	6.000	3.000
Days to Maturity	1241.208**	39.208	109.042	288.708***	21.438
Days of Pod Fill	873.250***	68.083	76.375	252.708***	23.250
WATER RELATIONS					
Water Content	1.325	1.775	2.285	1.687	1.513
Relative Water Content	39.740**	7.801	5.265	18.725***	1.990
Water Content	4.871	1.901	2.286	5.287**	1.172
Water Potential	0.00033	0.00033	0.00066	0.00066	0.00063
Moisture Retention Capacity	54.079	12.390	39.004	11.749	11.415
POROMETRY					
Transpiration Rate	3.481	3.786	16.110	10.070*	3.827
Stomatal Conductance	0.226	0.129	0.445	0.254*	0.107
Leaf Temperature	1.436	0.301	0.136	0.097	0.160

Level of significance: 0.10(*); 0.05(**); 0.01(***).
G = Genotype
GY = Genotype x Year Interaction
GL = Genotype x Drought Environment Interaction
GLY = Genotype x Year x Drought Environment Interaction

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