This is to certify that the

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ASSESSMENT OF ROOT MORPHOLOGY AS AN INDICATOR OF DROUGHT RESISTANCE IN COMMON BEAN (*Phaseolus vulgaris* L.)

presented by

Maurice D. Yabba

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ASSESSMENT OF

RESIST

ASSESSMENT OF ROOT MORPHOLOGY AS AN INDICATOR OF DROUGHT RESISTANCE IN COMMON BEAN (*Phaseolus vulgaris* L.)

By

Maurice D. Yabba

A THESIS

Submitted to
Michigan State University
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MASTER OF SCIENCE

Crop Physiology - Crop and Soil Science

1997

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ABSTRACT

ASSESSMENT OF ROOT MORPHOLOGY AS AN INDICATOR OF DROUGHT RESISTANCE IN COMMON BEAN (*Phaseolus vulgaris* L.)

By

Maurice D. Yabba

Drought limits yield in most common bean (*Phaseolus vulgaris* L.) growing areas and evidence suggests that roots may regulate shoot growth during moisture stress. This study was conducted to assess yield of eight bean genotypes under moisture stress and non-stress conditions and to compare root morphological response in 10^{-6} M abscisic acid (ABA), -0.52 and -1.07 MPa polyethylene glycol (PEG), and 0.76 m x 30 mm polyvinyl chloride (PVC) tubes under limiting and non-limiting moisture conditions. The research was conducted in Michigan using a rainshelter for field trials, a growth chamber for ABA and PEG experiments, and a greenhouse for the PVC experiments. Moisture stress reduced yield up to 46%. The geometric mean and stress tolerance index were better predictors than the drought susceptibility index of yield under limiting moisture. ABA increased total root length. ABA, PEG, and moisture stress increased the percentage of smaller diameter roots. Significant correlations occurred between total root length in PVC tubes and total root length in ABA and PEG. Seed weight affected total root length.

Dedicated to my children

Micheal, Bonakala, and Elangeni

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I wish to express my gratitude to Dr. Eunice F. Foster for her guidance and encouragement during my stay at Michigan State University. Her helpful suggestions through the different phases of this research and my life along with her patience were instrumental for the completion of my studies. I appreciate your patience deeply.

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The assistance of Greg Parker and all those who helped with the irrigation and maintaining the rainshelter at the Kellogg Biological Research Station is greatly appreciated.

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ensuring that I was able to conduct the experiments smoothly.

I would like to thank Charles Heimiller, Eric Baka, Ester Nobles, Mike Carroll, and Tawainga Katsvairo for all their assistance throughout this research. Their assistance were invaluable.

Special thanks goes to wife Sundra Philletta Yabba for keeping my head above water.

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Introduction

Common bean (*Phaseolus vulgaris L.*) is an important legume that is grown and consumed on all continents (Adams et al., 1985). The crop has the potential to be well adapted to subsistence agricultural systems (Graham, 1981; Bliss, 1985) but drought is a persistent problem in most bean growing areas. Thus, it is important to develop drought resistant cultivars.

Plants are constantly exposed to stress under both natural and agricultural conditions. Some environmental stresses such as air temperature occurred within a few minutes, whereas others took days, (e.g. soil water) or even weeks or months (e.g. mineral nutrients) to develop (Taiz and Zeiger, 1991). It has been estimated that physiochemical stresses have reduced the yield of field grown crops in the United States to only 22% of the crop's genetic potential (Boyer, 1982).

The physiological mechanisms that help impart drought tolerance are still poorly understood. Carbon and nitrogen partitioning and remobilization, stomatal closure, osmotic adjustment, and root development may be involved (Hale and Orcutt, 1987; Foster et al., 1995). Plants are usually classified as drought resistant or drought susceptible based upon the level of yield reduction during water stress (Hale and Orcutt, 1987). Rapid, inexpensive, and reliable methods for screening large numbers of germplasm would greatly aid efforts to

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Drought is a meteorological and environmental event that can be classified as permanent or seasonal based on the duration of the water stress (Kramer, 1980), and drought resistance is not a simple response. It is conditioned by a number of component responses which interact and which differ for different crops and in response to the intensity and duration of water deficit. The degree of plant water deficit depends on the extent to which water potential and cell turgor are reduced below their optimum values (Kramer, 1980).

In most crops, advances in crop yields have been obtained through breeding for increased yield potential and crop management (Hale and Orcutt, 1987). However, in developing countries, bridging the gap between actual and potential yields in adverse environmental conditions can be more valuable than efforts to increase the yield potential of the crop (Acosta-Gallegos, 1988). Yield stability can be achieved through breeding for adaptation to adverse environmental stresses, and this is a more realistic approach to increasing yields in unpredictable environments (Acosta-Gallegos, 1988).

Water stress causes many changes in metabolism and development that can affect yield performance. Stomatal closure is one of the changes that occurs and the role of abscisic acid (ABA) in stomatal closure has been documented in many plants (Taiz and Zeiger, 1991), including cowpea (*Vigna unguiculata*) and cassava (*Manihot esculenta*). ABA is also thought to affect root growth in water stressed environments (Taiz and Zeiger, 1991). Drought stress inhibited root growth (Robertson et al., 1990), however, plants often increased

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their root to shoot ratio under water limiting conditions. Robertson et al., (1990) concluded that ABA mediates drought-induced changes in the primary development of sunflower (*Helianthus annus*) roots.

Root size, morphology, depth, length, density, and function are important in maintaining high leaf water potential against evapotranspiration demands. Considering all root attributes, root length density is probably the major operative factor (Newman, 1974). Past research on bean adaptation to water deficits has indicated that genotypic differences in biomass and yield are correlated with differences in root growth (Sponchiado et al., 1989). Furthermore, studies using grafted plants to compare the relative contribution of the root and shoot genotype to adaptation to water deficits demonstrated that differences in yield under water stress were due primarily to variation in root genotype (White and Castillo, 1989). Thus, root development appears to be an important characteristic to consider when breeding for drought resistance.

Numerous methods have been reported for investigating root growth (Brar et al., 1990). In order to be useful to plant breeders, methods must be reliable, relatively inexpensive, and must permit rapid evaluation of large numbers of germplasm (Brar et al., 1990). The growth pouch method outlined by McMichael et al. (1985) met this criteria with regard to screening for root growth. Polyethylene glycol (PEG) is an inert, nonionic, long chain polymer [$(HOCH_2-CH_2)x(CH_2OH)$] that has the advantage of providing a precise level of water deficit in plants. It has been used to simulate drought in plants.

The objectives of this study were (1) to investigate root morphological

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response to ABA or PEG in common bean (2) to assess the relationship between root growth of plants grown in 15.24 cm X 16.51 cm growth pouches and that of plants grown in 76.20 cm x 30.48 cm polyvinyl chloride (PVC) tubes, and (3) to assess the relationship of yield from field-grown plants under stress and non-stress conditions with root growth and development of plants grown in growth pouches and PVC tubes.

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Literature Review

Two centers of domestication for common bean or dry bean (*Phaseolus vulgaris* L.) are recognized: Mesoamerica, the center of evolution for small-seeded genotypes, and the Andes, the center of evolution for large-seeded genotypes (Gonzalez et al., 1995). Evidence for the existence of these two domestication centers comes from archeological, anatomical, and molecular studies (Evans, 1976; Kaplan, 1981; Kaplan and Kaplan, 1988; Gepts and Bliss, 1986; Debouck et al., 1993). The two gene pools differ in their yield potential. Generally, Andean accessions yield less than Mesoamerican accessions (Gonzalez et al., 1995).

Common bean supplies a large part of the daily protein requirement of the people of South America, the Caribbean, Africa, and Asia (Laing et al., 1983). It is rich in protein (20 to 25%) but, as with most legumes, the proteins are deficient in sulfur containing amino acids (Laing et al., 1984). Bean yield is low in most developing countries, averaging less than 1 t ha^{-1} and increasing to less than 1.4 t ha^{-1} in most developed countries (Laing et al., 1984).

When grown in tropical and subtropical environments, bean is affected by an array of diseases, pests, water stress, and soil fertility problems (Schwartz and Pastor-Corrales, 1989). Although diseases and low soil fertility are the most widespread problems, more than 60% of beans grown in the developing countries of Latin America, Africa, and Asia suffer from water stress at some

stage of crop growth (White and Singh, 1991). A recent study on bean distribution by environment in Latin America showed that the physiological water requirement of the plant was not fulfilled in 93% of the areas where beans are grown (Fairbairn, 1993).

Because of scarce and irregular rainfall patterns, beans grown in rainfed areas in Latin America commonly suffer moisture deficits during their reproductive phase (Laing et al., 1983). In semi-arid areas, the soils have a low organic matter content and water holding capacity, so yields are often reduced by drought (Fairbairn, 1993).

Kadam and Salunkhe (1989) observed that 91% of the mean annual world production of dry bean in 1982 was produced in developing countries. Land area devoted to bean production in developing countries has increased steadily in the last several decades (CIAT, 1992). However, production has not kept pace with population growth and must increase 42% and 72% in Latin America and Africa, respectively, by the year 2000 in order to satisfy expected demand (Janssen, 1989). Bean production in developing countries often occurs on marginal land, and few developing countries have significant reserves of arable land that can be opened to bean cultivation. Thus, increased bean production will largely have to come through increased yield per hectare rather than expansion of land under cultivation (Yan et al., 1995). Given the importance of bean as a human food source in developing countries, more research should be devoted to improving productivity of the crop (Laing et al., 1984).

Root Growth

The type of root system is determined genetically and is responsive to environmental factors such as soil moisture. Soil strength, aeration, temperature, salinity and toxic concentration of aluminum or other substances were additional environmental factors that affected root growth (Taylor, 1983; Gregory, 1989).

The lack of moisture and available nutrients in arid and semi-arid regions (Al-Karaki et al., 1995) confined root growth to the upper soil horizons. Low mineral availability and moisture shortages in soil inhibited root growth and reduced access to subsoil moisture (Pothuluri et al., 1986; Welbank et al., 1973). Reduced root growth hastened the onset and increased the severity of plant water deficit during drought conditions (Al-Karaki et al., 1995). Deep and extensive root systems contributed to drought resistance and mineral uptake, for example phosphorus efficiency in plants (CIAT, 1990; Markhart, 1985).

Roots played an important role in the growth and survival of plants during periods of drought stress. Under drought, the root was characterized by a low root density in the dry surface layer and a higher root proliferation in the deeper , wetter soil layers (Smucker et al., 1991). However, under non-stress conditions, roots proliferated in the soil zone with the lowest soil water retention (Garay and Wilhelm, 1983). Garay and Wilhelm (1983) observed in peanuts (*Arachis hypogaea* L.) drought stress significantly reduced root growth in the upper 40 cm of the soil profile from 20 to 50 days after planting. In contrast, Hudak and Patterson (1996) examined two varieties of soybean [*Glycine max* (L.) Merr.] and

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concluded that the ability of a plant to survive under drought stress may reside in it's ability to exploit the upper soil horizons (above 60 cm) with a network of fibrous roots.

A 37% reduction in wheat (*Triticum aestivum* L.) roots occurred in the top 20 cm of soil during an 18 day drought period and a 50% increase in root number occurred at the 60 to 150 cm depth (Box et al.,1989). This response to short term drought suggested that large quantities of photo-assimilated carbon may have been lost to the rhizosphere in the shallow root zone, while new allocations of plant carbon were required for the growth of new roots at the greater soil depths. Several authors have reported increased root growth at greater depths under drought stress (De Vries et al., 1989; Smucker et al., 1991; Stofella et al., 1979a), and an increase in total root growth occurred in cowpea (*Vigna unguiculata*) under mild drought stress (Nagarajah and Schulze 1983).

Although total growth has been reported in some studies during water stress, root growth is generally favored relative to shoot growth. It is frequently assumed that root dry matter is 10% of total crop dry matter after flowering under non-stress conditions, producing root/shoot (R/S) ratios of 0.1 in temperate regions (Smucker et al., 1991). However in drier regions R/S ratios of 20% were found in barley (*Hordeum vulgare*) and 45% in wheat (*Triticum aestivum* L.) (Gregory, 1989). The R/S ratio under drought conditions have increased up to 0.3 (Passioura, 1983).

Root development and capacity of plants to absorb water are closely related. As root width, depth, and branching increased, plant water stress

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decreased (Hurd, 1976). When ground water was available, deep rooted plants showed greater drought avoidance than shallow rooted ones but they showed lower avoidance, when deeper soil moisture was not present (Levitt, 1972). Rooting depth and the resistance to water flow within the root were important attributes of root systems when plants were grown in drought prone environments (Taylor, 1980). Passioura (1982) concluded that axial flow did not limit the uptake of water in legumes because their facility for secondary growth normally ensured abundant vessels. Only a vascular disease or a large resistance at the nodes or at the junctions between roots caused a problem. Similar results have been reported by others (Hurd, 1976; Sheriff and Muchow, 1984; Blum, 1988; Gregory, 1989). According to their work, soil-to-leaf water flux and the associated water potential were affected by root length, density, root axial resistance, and root adaxial resistance when the root system was limited to a drying soil with no additional moisture reserves at deeper soil layers. Small root resistance and a large root-length density contributed to the maintenance of a higher leaf-water potential (Blum, 1988).

White et al. (1990) reported that drought resistance in bean was related to rooting depth. Soil exploration by roots was associated with nutrient acquisition, especially in the case of immobile nutrients such as phosphorus (Lynch and Van Beem, 1993). Genetic differences in bean were reported for root biomass, R/S ratio (Fawole et al., 1982; Stoffela et al., 1979a), and for root biomass distribution among distinct root types (Stofella et al., 1979b).

Root architecture may also be important for soil resource acquisition

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(Lynch and Van Beem, 1993). Fitter (1991) developed topological indices to quantify root architecture in two-dimensions, ranging from a herringbone structure at one extreme to a highly branched, dichotomous structure at the other extreme. Based on comparisons of ecologically distinct species and simple modeling exercises, Fitter (1991) proposed that root architecture may influence the efficiency of plant nutrient uptake.

Drought Resistance

Drought resistance in ecological terms is described as the ability of a plant to survive periods of low water supply (Turner, 1979). In addition, plant species selected for crop production must have the ability to produce an adequate yield (Blum, 1988). Agriculturally, drought resistance is the ability of a crop species or variety to grow and yield well in areas subjected to periodic water deficit (Turner, 1979).

Drought resistance is conferred by a number of morphological and physiological characteristics of the plant (Begg and Turner, 1976; Morgan, 1984; Turner, 1986; Acevedo,1987; Singh, 1989). Drought resistance and its related characteristics have been classified by different researchers (Levitt, 1980; Kramer, 1983; Blum, 1985, 1988; Ludlow and Muchow, 1990), but no consensus has been reached about the most useful aspects or categories of drought resistance (Levitt, 1980; Kramer, 1980; Turner and Burch, 1983; Turner, 1986).

The mechanisms of drought resistance in crop plants has been divided into three categories: drought escape, dehydration avoidance and dehydration

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tolerance (Kramer, 1980, 1983; Levitt, 1980; Turner, 1986; Blum, 1988; Ludlow and Muchow, 1990). Drought escape is the ability of a plant to escape drought by completing its life cycle during the favorable moisture conditions prior to the drought. Dehydration avoidance is the ability of a plant to prevent water loss by stomatal closure resulting in the maintenance of turgor during periods favoring high rates of transpiration. Dehydration tolerance is the ability of a plant to withstand injury when plants are under drought stress. Drought escape or evasion has sometimes been incorrectly equated to drought avoidance (Levitt, 1980; Blum, 1988).

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 potentials at various stages of the plant's life cycle (Simpson, 1981; Ibarra, 1985; Elizondo, 1987; Acosta-Gallegos, 1988). The different mechanisms of adaptation are not mutually exclusive because plants may possess more than one type of adaptation (Turner, 1979; Kramer, 1980). 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, and symbiotic associations in addition to the structure and genetics of the population (Kramer, 1980).

Acosta-Gallegos and Adams (1991) concluded that the most practical method to improve performance of common bean is through the direct

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measurement of yield-related characteristics because seed yield is the most important economic yield of the crop. The drought susceptibility index (DSI), stress tolerance index (STI), and geometric mean (GM) have been used as a means to identify genotypes exhibiting consistent yield performance across water treatments. DSI is based on a reduction in yield adjusted for the drought intensity of a particular experiment. A value of one indicates average performance. The greater the value above one the more susceptible the genotype and the lower the value below one, the more resistant the genotype (Fischer and Maurer, 1978). However, White and Singh (1991) and Schneider et al. (1997) concluded that DSI rankings resulted in the mis-classification of some genotypes. GM is believed to assess genotypic yield potential (Acosta-Gallegos, 1988). Acosta-Gallegos and Adams (1991) observed that genotypic rankings for drought resistance were ordered differently when based on GM than when based on percentage reduction in yield or DSI. Schneider et al. (1997) concluded that GM was the single strongest predictor of yield performance under stress and non-stress conditions. STI reportedly identifies genotypic yield potential and resistance to drought (Fernandez, 1993). The larger the STI value for a genotype, the higher its drought resistance and yield potential.

Effects of Drought on Growth, Development, and Yield

Maintenance of a high water status throughout the life of the crop (Laing et al., 1984) is essential for maximum yield. While the ultimate effect of drought was limitation of growth and yield, specific physiological effects of water stress

varied depending on the history of the crop and the timing and intensity of stress (White and Castillo, 1989).

In bean, the most sensitive phase of development to water stress was from flowering to early pod set (Dubetz and Mahalle, 1969; Laing et al., 1983 and 1984; Halterlein, 1983; Sheriff and Muchow, 1984). Prolonged stress before flowering restricted canopy development, which in turn limited yield (Laing et al., 1984). The relative sensitivity of different stages of development to water stress varied with the degree of stress (Begg and Turner, 1976).

The most common effect of water deficit during bean growth was reduction in plant size and yield (Kramer, 1983). Drought stress affected many physiological and morphological characteristics associated ultimately with seed yield. The phenological stage of the crop at the time of the stress as well as the intensity and duration of the water stress determined the amount of damage done to the crop and therefore yield (Acosta-Gallegos and Adams, 1991). Acosta-Gallegos and Shibata (1989) reported that the induction of drought stress at the beginning of the reproductive phase in common bean reduced seed yield twice as much as when the stress was induced at the vegetative phase. Stem length, number of branches, pods per plant, seeds per pod and yield were all reduced.

The number of pods per plant was the yield component that was most affected by water stress. Pod number varied greatly while seeds per pod and particularly seed size showed comparatively small changes across environments and treatments (Acosta-Gallegos and Shibata, 1989). It was hypothesized that

bean plants adjusted potential sink size (pod number) to the available source and then proceeded to fill that sink as rapidly as possible (Acosta-Gallegos and Shibata, 1989).

Final yield was affected by morphological traits such as biomass (Laing et al., 1983; Scully and Wallace, 1990; Scully et al., 1991), leaf area duration, leaf area index (Laing et al., 1983, 1984), growth habit (Laing et al., 1983, 1984), basal internode diameter, basal internode length (Davis and Evans, 1977), hypocotyl diameter (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).

Part of the genetic improvement in crop yield has also derived from a higher percentage of the biological yield (total plant dry weight) being partitioned into plant parts comprising economic yield (grain or seed weight). This ratio of economic yield to biological yield is termed as harvest index (HI) (Rasmusson and Gengenbach, 1988). Economic yields can be increased by increasing biological yield without changing the HI or by partitioning more of the dry matter production into economic yield. Wallace et al., (1982) reported that the HI in wheat had increased from 32% in the early 1900's to 49% for current high yielding semidwarf varieties.

Effect of drought on photosynthesis and stomatal conductance

Dry matter accumulation in plants is largely a function of net photosynthesis and light interception by the canopy. At least 90% of the dry

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matter of higher plants is derived from CO_2 assimilated by photosynthesis (Zelith, 1982). Zelith suggested that the method of selection for yield may not have yet explored the potential photosynthetic capacity and that it may be predicted that only modest rate increases in photosynthesis could have been obtained during selection for higher yield.

CO_2 assimilation and stomata responded fairly independently, in spite of a certain degree of coupling, to short term variations of environmental factors (Kuppers et al., 1988). Also, net photosynthesis and leaf conductance were not equally sensitive to soil drying. Initially, leaf conductance declined by 40% while CO_2 assimilation rate remained constant. Kuppers et al. (1988) concluded that the response of CO_2 assimilation and stomatal conductance during soil drying was fairly independent of the water status of the leaf. Similar observations were reported by Bates and Hall (1981), indicating that stomatal closure due to soil water depletion was not associated with changes in leaf water status.

In cotton (*Gossypium hirsutum* L.), an increase in stomatal resistance was associated with a substantial reduction in the photosynthetic rate as a result of moisture stress (Epthrath et al., 1990). In their work, stomata limited the photosynthetic process in well-watered and mildly stressed plants, while mesophyll resistance was the main factor reducing photosynthesis under more severe moisture stress. Epthrath et al., (1990) concluded that when moisture stress was initiated at 21 days after planting, plants had lower stomatal resistance and a higher photosynthetic rate than plants in which stress was initiated at 40 days after planting.

Peng et al. (1991) observed that photosynthesis measured at the single leaf level prior to flowering in sorghum (*Sorghum bicolor* L.) was a trait which could be used to select genotypes for higher productivity. They found that leaf photosynthesis, total biomass and grain production were significantly reduced by limited water supply and that leaf photosynthesis was positively correlated with total biomass and grain production. Hamdani et al. (1991) concluded that genotypic reduction in water potential, stomatal conductance and photosynthesis had the potential to be used as screening tools for drought resistance of sorghum genotypes at the vegetative stage of growth. Manthe (1994) concluded that water stress decreased photosynthesis of common bean and cowpea (*Vigna unguiculata* L. (Walp)) late in the growing season when the stress was severe, while stomatal conductance was affected earlier in the season.

ABA and Drought

ABA is sometimes referred to as the "stress hormone" because of its possible role in maintaining winter dormancy of buds and because it accumulates when plants are deprived of water (Purves et al., 1992). Apart from its widely recognized role as an agent of stomatal closure, ABA may have additional regulatory roles in the adaptation of plants to drought stress (Jones, 1978). The observation that ABA levels increase in the roots of water-stressed plants (Hubick et al., 1985; Lachno, 1984; Walton et al., 1976) and that this increase does not depend on transport from the shoot (Walton et al., 1976) is particularly provocative.

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Several studies (Hubick, 1983; King and Evans, 1977) reported similarities between the effects of exogenously applied ABA on plant development and the behavior of water stressed plants. Barlow and Pilet (1984) showed that exogenously applied ABA reduced cell division and DNA synthesis in the root apical meristem in corn. Similarly, Creelman et al., (1990) using soybean seedlings, observed that exogenously applied ABA had the same effect on growth and dry weight as seedlings suffering from low water potential. Earlier studies with sunflower (*Helianthus annus* L.) seedlings found that drought stress inhibited root growth (Hubick, 1983) and increased ABA levels in the root tissue (Hubick, 1983; Hubick et al., 1985).

Creelman et al. (1990) found that exogenously applied ABA increased root growth of soybean seedling. Leskovar and Cantliffe (1992) working with pepper (*Capsicum annuum* L.) seedlings noted that exogenously applied ABA reduced root fresh and dry weights while increasing stem fresh weight and dry weight thereby, decreasing the R/S ratio. In contrast, Robertson et al., (1990), reported an increase in R/S ratio of sunflower (*Helianthus annus* L. Cv. Russian Grant) due to exogenously applied ABA.

ABA accumulated in roots, particularly at the tips, of water-stressed plants (Saab et al., 1990; Ribaut and Pilet, 1991). It may have stimulated ion and sugar accumulation in the root (Karmoker and Van Steveninck, 1979; Van Steveninck, 1984; 1983), thereby affecting root turgor, or it may have acted as a signal for the initiation of regulatory processes involved in adaptation during growth at low water potential (Davies et al., 1986; Bradford and Hsiao, 1982).

Two types of evidence support the hypothesis that messengers from the root system may affect stomatal response to water stress. First, stomatal conductance is often much more closely related to soil water status than to leaf water status, and the root system is the only plant part that can be directly affected by soil water status. Second, roots produce ABA and export it through the xylem sap (Taiz and Zeiger, 1991).

Polyethylene (PEG) and drought

Polyethylene glycol (PEG) induces a primary water stress by provoking a reduction in water availability (Izzo et al., 1989). The most serious limitation of PEG as an osmoticum has been its toxicity (Izzo et al., 1989). PEG is an inert, nonionic, long chain polymer [$(HOCH_2\text{-}CH_2)x(CH_2OH)$] and has the advantage of providing a precise level of water deficit in plants.

Graves and Wilkins (1991) observed that PEG caused a reduction in the root and shoot dry weights among seedlings of honey locust (*Gleditsia triacanthos* var. *inermis* Willd.). Perez-Molphe-Balch et al., (1996) concluded that water deficit imposed by PEG inhibited germination and shoot and root growth and also altered the pattern of protein synthesis in the roots of three rice (*Oryza sativa*) cultivars.

Kaufman and Eckard (1971) concluded that PEG produced changes in plant water relations similar to those caused by drying soil at the same water potential. Studies utilizing PEG have been conducted with many species,

including maize

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including maize (*Zea mays*) (Izzo et al., 1989), coleus (Krizek, D.T. and Semeniuk, P., 1979), white clover (Robin et al., 1989), and *Capsicum annum* (Schaefer et al., 1979).

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Literature cited

Acevedo, E. 1987. Assessing crop and plant attributes for cereal improvement in water limited Mediterranean environments. Proceedings of an international workshop, 27-31 October, 1985, Capri, Italy.

Acosta-Gallegos, J.A. 1988. Selection of common bean (*Phaseolus vulgaris* L.) genotypes with enhanced drought tolerance and biological nitrogen fixation. Ph.D. diss. Michigan State University, East Lansing, MI. U.S.A.

Acosta-Gallegos, J.A., and J.K. Shibata. 1989. Effect of water stress on growth and yield of indeterminate dry bean (*Phaseolus vulgaris*) cultivars. Field Crops Res. 20:81-93.

Acosta-Gallegos, J.A., and M.W. Adams. 1991. Plant traits and yield stability of dry bean (*Phaseolis vulgaris* L.) cultivars under drought stress. J. Agric. Sci. (Cambridge) 117:213-219.

Acquaah, G., M.W. Adams, and J.D. Kelly. 1991. Identification of effective indicators of erect plant architecture in dry bean. Crop Science 31(2):261-264.

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

Al-Karaki, G.N., R.B. Clark, and C.Y. Young. 1995. Effects of phosphorus and water stress levels on growth and phosphorus uptake of bean and sorghum cultivars. Journal of Plant Nutrition, 18(3):563-578.

Barlow, P.W., and P.E. Pilet. 1984. The effect of abscisic acid on cell growth, cell division, and DNA synthesis in the maize root meristem. Plant Physiol. 62:125-137.

Bates, L.M. and A.E. Hall. 1981. Stomatal closure with soil water depletion not associated with changes in bulk leaf water status. Oecologia 50(1):62-65.

Begg, J.E. and N.C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

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

Blum, A

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Box, J.

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Brar, G

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Davies,

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Debouc

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Blum, A. 1985. Breeding crop varieties for stress environments. Critical reviews in plant sciences 2(3):199-238.

Blum, A. 1988. Plant breeding for stress environments. CRC Press, Boca Raton, Fla.

Box, J.E. Jr., A.J.M. Smucker, and J.T. Ritchie. 1989. Minirhizotron installation techniques for investigating root responses to drought and oxygen stresses. Soil Science Society of America Journal 53(1):115-118.

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

Bradford, K.C. and T.C. Hsiao. 1982. Physiological responses to moderate water stress. In: O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler, Eds., Encyclopedia of Plant Physiology (New Series), Vol 12B. Physiological Plant Ecology II. Springer-Verlag, Berlin, pp 263-324.

Brar, G.S., A.G. Matches, H.M. Taylor, B.L. McMichael, and J.F. Gomez. 1990. Two methods for characterizing rooting depth of forage-legume seedlings in the field. Crop Science 30:413-417.

CIAT (Centro Internacional de Agricultura Tropical). 1990. Tolerance to poor soils, pp. 145-150. *In* Bean Program, Annual Report, 1989. Working Document No.68. CIAT, Cali, Columbia.

CIAT (Centro Internacional de Agricultura Tropical). 1992. Trends in CIAT commodities, 1992. Working Document 111. CIAT, Cali, Columbia.

Creelman, R.A., H.S. Mason, R.J. Bensen, J.S. Boyer, and J.E. Mullet. 1990. Water deficit and abscisic acid cause differential inhibition of shoot *versus* root growth in soybean seedlings. Plant Physiol. 92:205-214.

Davies, W.J., J. Metcalfe, T.A. Lodge, and A.R. da Costa. 1986. Plant growth substances and the regulation of growth under drought. Australia Journal of Plant Physiology 13:105-125.

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

Debouck, D.G., O. Toro, O.M. Paredes, W.C. Johnson, and P. Gepts. 1993. Genetic diversity and ecological distribution of *Phaseolus vulgaris* (Fabaceae) in Northwestern South America. Econ. Bot. 47:408-423.

DeVries, H.E. II, L.A. Rupp, and K.W. Mudge. 1989. Effect of

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Garay,

aminocyclopropane carboxylic acid and aminoethoxyvinylglycine on ethylene production by ectomycorrhizal fungi. Canadian Journal of Botany 67(2):483-485.

Dubetz, S. and P.S. Mahalle. 1969. Effect of soil water stress on bush beans (*Phaseolus vulgaris* L.) At three stages of growth. J. Amer. Hortic. Sci. 94:479-481.

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

Ephrath, J.E., A. Mavani, and B.E. Bravdo. 1990. Effects of moisture stress on stomatal resistance and photosynthetic rate in cotton (*Gossypium hirsutum*) I. Controlled levels of stress. Field Crops Res. 23:113-117.

Evans, A.M. 1976. Beans, pp.168-172. *In* N.W. Simmonds (ed.). Evolution of crop plants. Longman, New York.

Fairbairn, J.N. 1993. Evaluation of soils, climate and land use information at three scales:The case of low income bean farming in Latin America. Ph.D. diss. University of Reading, Reading, U.K.

Fawole, I., W.H. Gabelman, and G.C. Gerloff. 1982. Genetic control of root development in beans (*Phaseolus vulgaris* L.) grown under phosphorus stress. J. Am. Soc. Hort.Sci. 107:98-100.

Fernandez, C.J. G. 1993. Effective selection criteria for assessing plant stress tolerance. *In* Adaptation of food crops to temperature and water stress:Proceedings of an international symposium, Taiwan, 13-18 August, 1992. AVRDC. pp257-270.

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

Fitter,A.H. 1991. Characteristics and functions of root systems. P. 3-24. *In* Y. Waisel, A. Eshel, and U. Kafkafi (ed.) Plant Roots, the hidden half. Marcel Dekker, Inc., New York.

Foster, E.F., A. Parjarito, and J.A. Acosta-Gallegos. 1995. Moisture stress impact on N partitioning, N remobilization and N-use efficiency in beans (*Phaseolus vulgaris* L.). J. Agric. Sci. (Cambridge) 124:27-37.

Garay, A.F., and W.W. Wilhelm. 1983. Root system characteristics of two soybean isolines undergoing water stress conditions. Agro. J. 75:973-

975.

Gepts, P.L., and F.A. Bliss. 1986. Phaseolin variability among wild and cultivated common beans (*Phaseolus vulgaris*) from Columbia. Econ. Bot. 40(4):469-478.

Gonzalez, A., J.P. Lynch, J.M. Tohme, S.E. Beebe, and R.E. Macchiavelli. 1995. Characters related to leaf photosynthesis in wild populations and land races of common bean. Crop Sci. 35:1468-1476.

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

Graves, W., and L. Wilkins. 1991. Growth of honey locust seedlings during high root-zone temperature and osmotic stress. HortScience 26(10):1312-1315.

Gregory, P.J. 1989. The role of root characteristics in moderating the effects of drought. P. 141-150. *In*: F.W.G. Baker (ed.) Drought resistance in cereals. C.A.B. Int., Wallingford, England.

Hale, M.G. and D.M. Orcutt. 1987. The physiology of plants under stress. John Wiley and Sons, New York.

Halterlein, A.J. 1983. Bean water requirements, root system, irrigation, drought behavior in kidney beans. *In*: Crop-water relations. I.D. Tesar and M.M. Peet (eds). John Wiley Press, New York.

Hamdani, S.H.A., J.M. Murphy, and G.W. Todd. 1991. Stomatal conductance and CO_2 assimilation as screening tools for drought resistance in sorghum. Can. J. Plant Sci. 71:689-694.

Hubick, K.T. 1983. Some studies on the effect of drought stress on plant growth regulators in *Helianthus annuus* L. Ph.D. Thesis. University of Calgary, Calgary, Alberta.

Hubick, K.T., J.S. Taylor, and D.M. Reid. 1985. The effect of drought on levels of abscisic acid, cytokinins, gibberellins, and ethylene in aeroponically grown sunflower plants. Plant Growth Regul. 16(2):234-241.

Hudak, C.M., and R.P. Patterson. 1996. Root distribution and soil moieture depletion pattern of a drought resistant soybean plant introduction. Agron. J. 88:478-485.

Hurd, E.A. 1976. Plant breeding for drought resistance. *In*: T.T. Kozlowski (ed.),

Ibarr

Izzo,

Janss

Jones

Kadar

Kapla

Kaplar

Karmo

Kaufma

King, R

Kramer,

Kramer,

Krizek,

Soil Water Measurements, Plant Responses and Breeding for Drought Resistance. Academic Press pp.317-353.

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

Izzo, R., F. Navari-Izzo, and M.F. Quartacci. 1989. Growth and mineral contents of roots and shoots of maize seedlings in response to increasing water deficits induced by PEG solutions. Journal of Plant Nutrition, 12:1175-1193.

Janssen, W. 1989. A socio-economic perspective on earliness in beans. P. 135-155. *In* S. Beebe (ed.) Current topics in breeding of common bean. Working Document 47. Bean Program, CIAT, Cali, Columbia.

Jones, H.G. 1978. How plants responds to stress. Nature 271:610.

Kadam, S.S. and D.K. Salunkhe. 1989. CRC handbook of world food legumes: Nutritional chemistry, processing technology, and utilization. CRC Press, Boca Raton, Fla.

Kaplan, L. 1981. What is the origin of the common bean? Econ. Bot. 35(2):240-254.

Kaplan, P. and L.N. Kaplan. 1988. Phaseolus in archeology. P. 125-142. *In* P. Gepts (ed.) Genetic resources of *Phaseolus* beans. Kluwer Academic Publishers, Dordrecht, Holland.

Karmoker, J.L. and R.F.M. Steveninck. 1979. The effect of abscisic acid on sugar levels of *Phaseolus vulgaris* L. cv Redland Pioneer. Planta 146:25-30.

Kaufman, M.R. and A.N. Eckard. 1971. Evaluation of water stress control with polyethylene glycols by analysis of guttation. Plant Physiol. 47:453-456.

King, R.W. and L.T. Evans. 1977. Inhibition of flowering in *Lolium temulentum* L. by water stress: A role for abscisic acid. Aust. J. Plant Physiol. 9:481-488.

Kramer, P.J. 1980. Adaptation of plants to water and high temperature stress. John Wiley, New York.

Kramer, P.J. 1983. Water relations of Plants. Academic Press, New York.

Krizek, D.T. and P. Semeniuk. 1979. Differential sensitivity of eleven cultivars of

Kuppe

Lachm

Laing,

Laing, I

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Levitt, J

Levitt, J

Ludlow,

Lynch,

Manthe,

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McMicha

coleus to water stress following application of polyethylene glycol 600. HortScience 14(3): 404 (Abstract).

Kuppers, B.I.L., M. Kuppers, and E.D. Schulze. 1988. Soil drying and its effect on leaf conductance and CO_2 assimilation of *Vigna unguiculata* (L.) Walp. I. The response to climatic factors and to the rate of soil drying in young plants. Oecologia 75(1):99-104.

Lachno, D.R. 1984. Abscisic acid and indole-3-acetic acid in maize roots subjected to water, salt, and mechanical stress. News bulletin: Br Pl Gr Reg Gr Mono 6:16.

Laing, D.R., P.J. Kretchmer, S. Zuluaga, and P.G. Jones. 1983. Field bean, pp.227-248. *In* IRRI (ed.). Potential productivity of field crops under different environments. IRRI, Los Banos, Philippines.

Laing, D.R., P.J. Jones, and J.H.C. Davis. 1984. Common bean (*Phaseolus vulgaris* L.), pp.305-351. *In* P.R. Goldsworthy and N.M. Fisher (eds.) The physiology of tropical field crops. Wiley, New York.

Leskovar, D., and D. Cantliffe. 1992. Pepper seedling growth response to drought stress and exogenous abscisic acid. Journal American Society Horticultural Science 117:389-393.

Levitt, J. 1972. Responses of plant to environmental stresses pp 697. New York and London: Academic.

Levitt, J. 1980. Responses of plant to environmental stresses. Academic Press, New York.

Ludlow, M.M. and R.C. Muchow. 1990. A critical evaluation of traits for improving crop yields in water limited environments. Advances in agronomy 43:107-153.

Lynch, J. and J.J. van Beem. 1993. Growth and architecture of seedling roots of common bean genotypes. Crop Sci. 33:1253-1257.

Manthe, M. 1994. The effect of soil moisture stress on dry beans (*Phaseolus vulgaris* L.) and cowpeas (*Vigna unguiculata* L. (Walp)). Ph.D. Thesis. Michigan State University, East Lansing, Michigan.

Markhart, A.H. 1985. Comparative water relations of *Phaseolus vulgaris* L. and *P. Acutifolius* A. Gray. Plant Physiol. 77:113-117.

McMichael, B.L., J.J. Burke, J.D. Berlin, J.L. Hatfield, and J.E. Quisenberry.

1985. Root vascular bundle arrangement among cotton strains and cultivars. Environ. and Exp. Bot. 25:23-30.

Morgan, J.M. 1984. Osmoregulation and water stress in higher plants. Annual review of plant physiology 35:299-319.

Nagarajah, S. and E.D. Schulze. 1983. Responses of *Vigna unguiculata* (L.) Walp. to atmospheric and soil drought (Cowpeas, growth, and gas exchange). Australia Journal of Plant Physiology 10(4):385-394.

Newman, E.K. 1974. In plant root and its environment. (E.W. Carson ed.) pp:363-440: Charlottesville. Univ. Press of Virginia.

Passioura, J.B. 1982. The role of root system characteristics in the drought resistance of crop plants transport of soil water. IRRI 414:71-82.

Passioura, J.B. 1983. Roots and drought resistance (Water stress in plants). Agricultural water management, Amsterdam. Elsevier Scientific 7(1):264-280.

Peng, S., F.S. Girma, and D.R. Krieg. 1991. Leaf photosynthetic rate is correlated with biomass and grain production in grain sorghum lines. Photosynthesis Res. 28:1-7.

Pothuluri, J.V., D.E. Kissel, D.A. Whitney, and S.J. Thein. 1986. Phosphorus uptake from soil layers having different soil test phosphorus levels. Agron. J. 78:991-994.

Purves, W.K., G.H. Orians, and H.C. Heller. 1992. Life: The science of biology. Sinauer Associates, Inc. W.H. Freeman and Co., Salt Lake City, Utah.

Perez-Molphe-Balch, E., M. Gidekel, M. Segura-Nieto, L. Herrera-Estrella, and N. Ochoa-Alejo. 1996. Effects of water stress on plant growth and root proteins in three cultivars of rice (*Oryza sativa*) with different levels of drought tolerance. Physiologia Plantarum 96:284-290.

Rasmusson, D.C., and B.G. Gengenbach. 1988. Genetics and use of physiological variability in crop breeding pp291-321. *In*: M.B. Tesar (ed) Physiological basis of crop growth and development. 1984. American Society of Agronomy, Madison, Wisconsin.

Ribaut, J.M. and P.E. Pilet. 1991. Effects of water stress on growth, osmotic potential and abscisic acid content of maize roots. Physiol. Plant 81:156-162.

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Singh,

Smucke

Robertson, J., K. Hubick, E. Yeung, and D.Reid. 1990. Developmental responses to drought and abscisic acid in sunflower roots 1. Root growth, apical anatomy, and osmotic adjustment. Journal of experimental Botany 41:325-337.

Robin, C., L. Shamsun-Noor, and A. Guckert. 1989. Effect of potassium on the tolerance to PEG-induced water stress of two white clover varieties (*Trifolium repens* L.). Plant and Soil 120:153-158.

Saab, I.N., R.E. Sharp, J. Prichard, and G.S. Voetberg. 1990. Increased endogenous abscisic acid maintains primary root growth and inhibits shoot growth of maize seedlings at low water potentials. Plant Physiology 93:1329-1336.

Schaefer, R.L., D.T. Krizek, and C.W. Reynolds. 1979. Relationship between leaf water potential and leaf conductance in *Capsicum annuum* 'Yolo Wonder'. HortScience 14:404 (Abstract).

Schneider, K.A., R. Rosales-Serna, F. Ibarra-Perez, B. Cazares-Enriquez, J.A. Acosta-Gallegos, P. Ramirez-Vallejo, N. Wassimi, and J.D. Kelly. 1997. Improving common bean performance under drought stress. Crop Science 37:43-50.

Schwartz, H.F. and M.A. Pastor-Corrales (ed.). 1989. Bean production problems in the tropics. 2nd ed. CIAT, Cali, Columbia.

Scully, B.T., D.R. Viands, and D.H. Wallace. 1991. Heritability and correlation of biomass, growth rates, harvest index, and phenology to the yield of common bean. J. Am. Soc. Hortic. Sci. 116:127-130.

Scully, B.T. and D.H. Wallace. 1990. Variation in and relationship of biomass, growth rate, harvest index, and phenology to yield of common bean. J. Am. Soc. Hortic. Sci. 115(2):218-225.

Sheriff, D.W. and R.C. Muchow. 1984. The water relations of crops. *In:* The physiology of tropical field crops. P.R. Goldsworthy and N.M. Fisher (Eds.). Wiley Press, Chichester, England.

Simpson, G.M. 1981. Water stress on plants. Praeger, New York.

Singh, S.P. 1989. Common bean improvement in the tropics. Plant Breed. Rev. 10:199-269.

Smucker, A.J.M., A.K. Srivastava, M.W. Adams, and B.D. Knezek. 1991. Secondary tillage and traffic compaction modifications of the growth and

production of dry edible beans and soybeans. Applied engineering in agriculture 7(2):149-157.

Sponchiado, B.N., J.W. White, J.A. Castillo, and P.G. Jones. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Exp. Agric.25:249-257.

Stofella, P.J., R.F. Sandsted, R.W. Zobel, and W.L. Hymes. 1979a. Root characteristics of black beans. I. Relationship of root size to lodging and seed yield. Crop Sci. 19:823-826.

Stofella, P.J., R.F. Sandsted, R.W. Zobel, and W.L. Hymes. 1979b. Root characteristics of black beans. II. Morphological differences among genotypes. Crop Sci. 19:826-830.

Taiz, L. and E. Zeiger. 1991. Plant Physiology. The Benjamin/Cummings Publishing Company, Inc. Redwood City, California.

Taylor, H.M. 1980. Postponement of severe stress in soybeans by rooting modifications: A progress report. *In*: Proceedings of the world soybean research conference II, Raleigh, N.C. 26-29 March, 1979, p.161-178 (ed. F.T. Corbin). Boulder, Colorado: Westview Press.

Taylor, H.M. 1983. A program to improve increase plant available water through rooting modifications. *In*: Root ecology and it's practical implications, p.463-472. Int. Symp. Gumpenstein, 1982, Bundesantalt Gumpenstein A-8952 Irdning, 1983.

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

Turner, N.C. 1986. Crop water deficits: A decade of progress. Advances in agronomy 39:1-51.

Turner, N.C. 1986. Adaptation to water deficits: a changing perspective. Australian journal of plant physiology 13(1):175-190.

Turner, N.C. and G.J. Burch. 1983. The role of water in plants: Root growth, water absorption. *In*: Crop-water relations. I.D. Tesar and M.M. Peet (Eds). John Wiley, New York.

Van Steveninck, R.F.M. 1984. Regulatory role of abscisic acid in nutrient transport and osmoregulation. In. W.J. Cram, K. Janacek, R. Rybova, K. Sigler, Eds, Membrane Transport in Plants. John Wiley and Sons, New

Van S

Walla

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Welba

White,

White,

White,

Yan, X.

Zelith, I.

York, pp:453-458.

Van Steveninck, R.F.M. and M.E. Van Steveninck. 1983. Abscisic acid and membrane transport. In. F.T. Addicott, ed, Abscisic Acid. Praeger Publishers, New York, pp:171-235.

Wallace, M., H.J. Dufner, and G.W. Erlandson. 1982. Dry edible beans: production and marketing, Red River Valley. North Dakota agricultural experiment station, North Dakota State University.

Walton, D.C., M.A. Harrison, and P. Cote. 1976. The effects of water stress on abscisic acid levels and metabolism in roots of *Phaseolus vulgaris* L. And other plants. Planta 147:43-49.

Welbank, I.J., M.J. Gibb, P.J. Taylor, and E.D. Williams. 1973. Root grow th of cereal crops. Rothamsted Experiment Station, Report Part 2. Rothamsted, England.

White, J.W. and J.A. Castillo. 1989. Relative effect of root and shoot genotypes on yield of common bean under drought stress. Crop Sci. 29:360-362.

White, J.W., G. Hoogenboom, J.W. Jones, and K.J. Boote. 1990. Beangro version 1.0 a phaseolus computer simulation model. Annual report of the Bean Improvement Cooperative 33:39-40.

White, J.W. and S.P. Singh. 1991. Breeding for adaptation to drought. p.501-560. *In* A. van Schoonhoven and O.Voysest (ed.) Common beans: Research for crop improvement. CAB International, Wallingford, U.K., and CIAT, Cali, Columbia.

Yan, X., J. P. Lynch, and S. E. Beebe. 1995. Genetic variation for phosphorus efficiency of common bean in contrasting soil types: I. Vegetative Response. Crop Sci. 35:1086-1093.

Zelith, I. 1982. The close relationship between net photosynthesis and crop yield. Bioscience 32(10):796-802.

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Chapter 1

Field selection for drought tolerance.

Introduction

Bean is the principal food legume for over 500 million people in Latin America and Africa, and it is the leading source of dietary protein for more than 100 million people (FAO, 1984). Soil fertility and drought are the primary constraints to bean production in many developing countries, affecting at least 80% of the area planted to beans in Latin America (CIAT, 1988; Fairbairn, 1993). Consequently, improving the genetic adaptation of beans to edaphic constraints is important in international agriculture (Lynch and van Beem, 1993).

Breeding for drought resistance has been elusive and frustrating. Arnon (1980) pointed out that breeding for drought resistance was probably the least productive breeding effort in the entire field of plant breeding. Drought is multifaceted, varying greatly over different production regions and often interacting with other detrimental factors such as high temperatures, pathogenic soil fungi and the use of marginal soils (White and Singh, 1988; Schwartz and Pastor-Corrales, 1989). Similarly, the difference in timing and intensity of drought stress can influence crop yield in various ways.

Acosta-Gallegos and Adams (1991) concluded that seed yield is the most important economic trait of common bean, therefore, the most practical method

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to improve performance is through the direct measurement of yield-related characteristics. The Drought susceptibility index (DSI) (Fischer and Maurer, 1978), stress tolerance index (STI) (Fernandez, 1993), and geometric mean (GM) have been used in an attempt to identify genotypes exhibiting consistent performance across stress treatments. The DSI is based on a reduction in yield adjusted for performance of all genotypes in a stress and nonstress environment. DSI values below one indicate tolerance and a value of zero indicates maximum tolerance (Fischer and Maurer, 1978). A DSI value of one indicates average performance and the greater the value above one, the more susceptible the genotype. The drought intensity index (DII) is a very useful index for the characterization of the severity of drought stress among experiments used in the evaluation of genotypes (Fischer and Maurer, 1978). White and Singh (1991) and Schneider et al. (1997) found that DSI rankings resulted in the mis-classification of some genotypes. GM assesses the yield potential of a genotype, its performance under optimal conditions (Acosta-Gallegos, 1988). Acosta-Gallegos and Adams (1991) observed that genotypic rankings based on GM were ordered differently than when based on percentage reduction in yield or DSI. STI reportedly identifies genotypes with regard to yield potential and stress resistance. The larger the value of STI for a genotype in a stress environment, the higher its stress resistance and yield potential (Fernandez, 1993).

Drought adaptive mechanisms may be morphological, phenological, physiological and/or biochemical, but the current most reliable approach to

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selection for drought tolerance is the assessment of total biomass or economic yield produced under stress in the field (White and Singh, 1988).

The objectives of this study were (1) to determine yield response to drought stress in eight field-grown bean genotypes, and (2) to determine if the geometric mean, DSI, or STI are reliable predictors of bean yield under limiting and/or non-limiting soil moisture conditions.

Materials and Methods

A field study was conducted on a Kalamazoo sandy loam (Fine-Loamy, mixed mesic, typic Hapludolf, FAO classification) at the Kellogg Biological Station [(KBS) 42^0 25' N, and 85^0 30' W. 2500 masl] in Hickory Corners, MI. during the summers of 1995 and 1996. The experimental design was a split plot with soil moisture as the main plot, genotype as the subplot, and four replications.

Eight common bean genotypes varying in their response to moisture stress were included in the study. They were Sierra, a commercially grown bean in Michigan; Bat 477, documented by CIAT (1984) to be drought resistance; 8-42-M-2, developed at Michigan State University and documented as drought susceptible when grown in Michigan conditions; Lef-2-RB which exhibits some degree of drought resistance in Michigan conditions; and four "T" lines (T3008-1, T3016-1, T3110-2, and T3147-2) that were developed at the Michigan State University bean breeding program and which vary in their yield potential under stress (Table 1). Seeds were planted on June 13 and 14, 1995 and on June 4

Table 1. Chara

at Kellog

Genotypes	
Sierra	
T3110-2	
T3147-2	
Lef-2-RB	
Bat 477	
8-42-M-2	
T3016-1	
T3008-1	

£ MSU = Michi

CIAT = Centr

INIFAP = Nat

Liv

¥ M=Medium.

‡ Type II = Inde

Type III = Ind

§ Derived from

(Kelly et al., 1

Table 1. Characteristics of common bean genotypes grown in field experiments at Kellogg Biological Station, Hickory Corners, MI. in 1995 and 1996.

Genotypes	Pedigree	Origin£	Seed¥ Size	Seed Color	Plant‡ Type
Sierra	Not identified§	MSU	M	Pinto	II
T3110-2	Sierra X Lef-2-RB	MSU	M	Striped	III
T3147-2	Sierra X Lef-2-RB	MSU	M	Striped	III
Lef-2-RB	(Ver 10/Chis 143)/pue 144	INIFAP	M	Black (striped)	III
Bat 477	(51051 X ICA Bunsi) X (51012 X Cornell 49-242)	CIAT	M	Brown	II
8-42-M-2	N81017 X Lef-2-RB	MSU	M	Tan or Brown	III
T3016-1	Sierra X AC 1028	MSU	M	Tan or Brown	III
T3008-1	Sierra x AC 1028	MSU	M	Tan or Brown	III

£ MSU = Michigan State University
CIAT = Centro Internacional de Agricultura Tropical
INIFAP = National Institute for Forestry, Agriculture, and Livestock Research, Mexico.

¥ M=Medium.

‡ Type II = Indeterminate-bush, erect stem and branches
Type III = Indeterminate-bush, prostrate main stem and branches

§ Derived from crosses of Durango Race Pinto with Mesoamerican Race Black (Kelly et al., 1990).

and 5, 1996. Uniformly sized seeds were inoculated with one strain of *Rhizobium phaseoli*. Forty Kg of N per hectare were applied as 20-20-20 prior to planting in both years. Seeding rate was 8 seeds per 30 cm. After emergence, seedlings were thinned to 4 seeds per 30 cm. Experimental plots consisted of four rows, 3.10 m long with an inter-row spacing of 50 cm. Moisture stress was initiated 45 days after planting (DAP).

Three applications of fungicide (Benlate for anthracnose and Sevin for Japanese beetles at 1.12 Kg ha^{-1}) were made in 1995 at two week intervals starting on July 14. In 1996 only two applications of Benlate were made. Both years, soil moisture was recorded using a neutron probe to determine moisture at three depths: 0-38 cm, 39-76 cm, and 77-114 cm. Porometer (LI-Cor, LI-1600 Steady State Porometer) and ceptometer (Decagon Sunfleck Ceptometer, Pullman, WA.) data were recorded weekly for 8 weeks in both years beginning at 34 DAP. The Porometer measured leaf transpiration, diffusive resistance, and leaf temperature. The ceptometer measured the difference between the amount of photosynthetically active radiation (PAR) above and below the canopy. In 1996, leaf temperature was taken at the V2 and V5 stage of development (Singh, 1982) using an infrared thermometer (Horiba, Non-contact Infrared Thermometer IT-330, Kyoto, Japan). The MSTAT micro-computer statistical package for agricultural sciences was used for data analysis.

Calculations

Y_s = The potential yield of a given genotype in a nonstress environment.

Y_s = The yield of a given genotype in a stress environment.

Y_a = Mean yield in nonstress environment.

Y_s = Mean yield in stress environment.

Y_d = Stress yield from a single genotype.

Y_p = Nonstress yield from a single genotype.

Stress tolerance index (STI) = $(Y_a \times Y_s)/Y_a^2$

Geometric mean (GM) = $\sqrt{(Y_a)(Y_s)}$

Drought intensity index (DII) = $1 - (Y_s/Y_a)$

Drought susceptible index (DSI) = $(1 - Y_d/Y_p)/DII$

Results and Discussion

1995 field experiment

A significantly greater quantity of PAR was intercepted by the canopy of the nonstress than stress treatment in 1995 on 41, 48, and 71 DAP ($P \leq 0.10$, 0.10, and 0.05, respectively) (Figure 1), indicating a more fully developed canopy in the nonstress treatment. There was a tendency for greater PAR interception in the nonstress treatments at all other sampling dates except day 1. The difference in PAR intercepted by the canopy ranged from 375 to 1300 µmol m^{-2} s^{-1} over the length of the growing season. Leaf temperature was significantly higher at 51, 72, and 86 DAP, ($P \leq 0.01$, 0.05, and 0.05, respectively), in stress plants, (Figure 2) suggesting stomatal closure in the stress treatment. Yet, transpiration did not differ between stress and nonstress treatments (Figure 3). At soil depth 1 to 33 cm, soil moisture content was

160

140

120

100

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60

40

20

Ceptometer counts (µmol m^{-2} s^{-1})

Figure

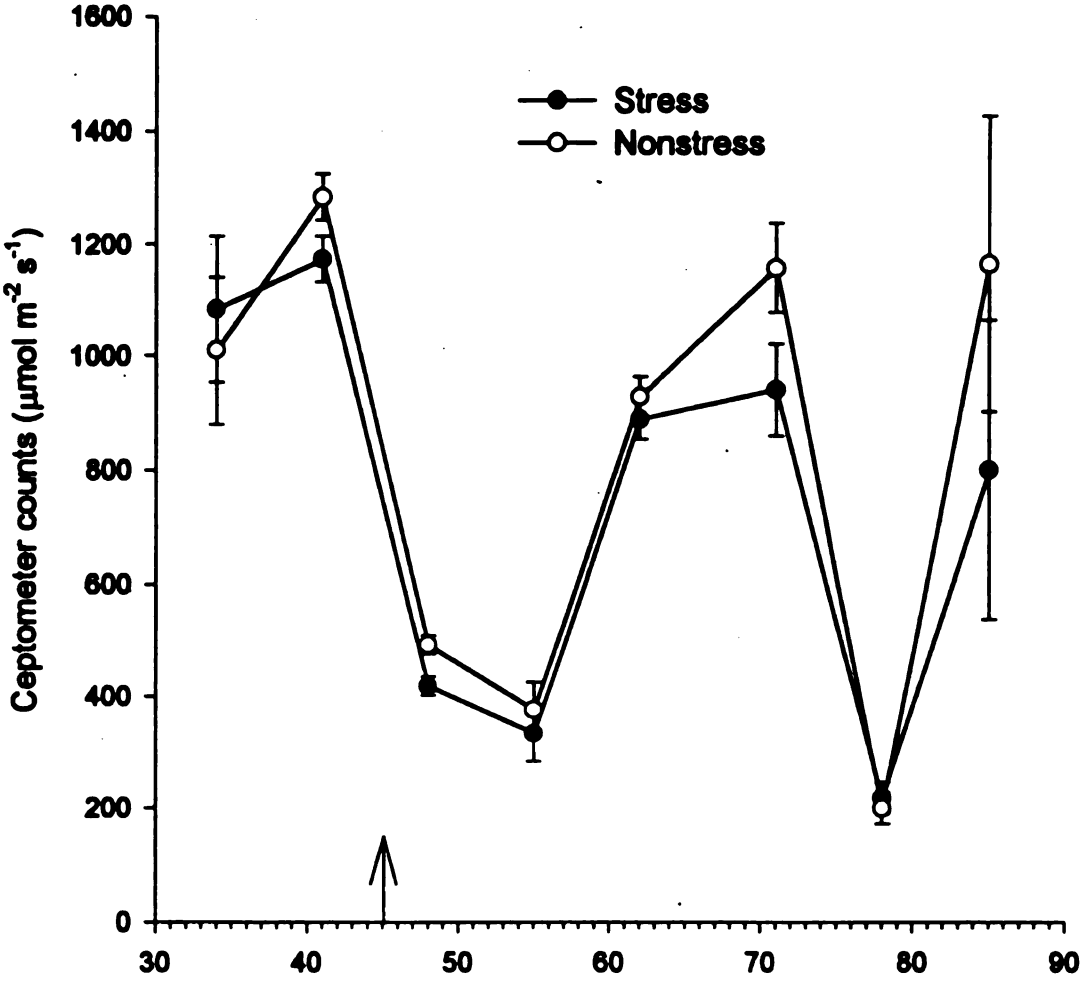

Figure 1. PAR intercepted by the canopy of eight genotypes of common bean grown under stress and nonstress moisture conditions at the Kellogg Biological Station, Hickory Corners, MI. in 1995.
Bars indicate standard error of the mean at $P \leq 0.05$.
Vertical arrow indicates when stress was induced.

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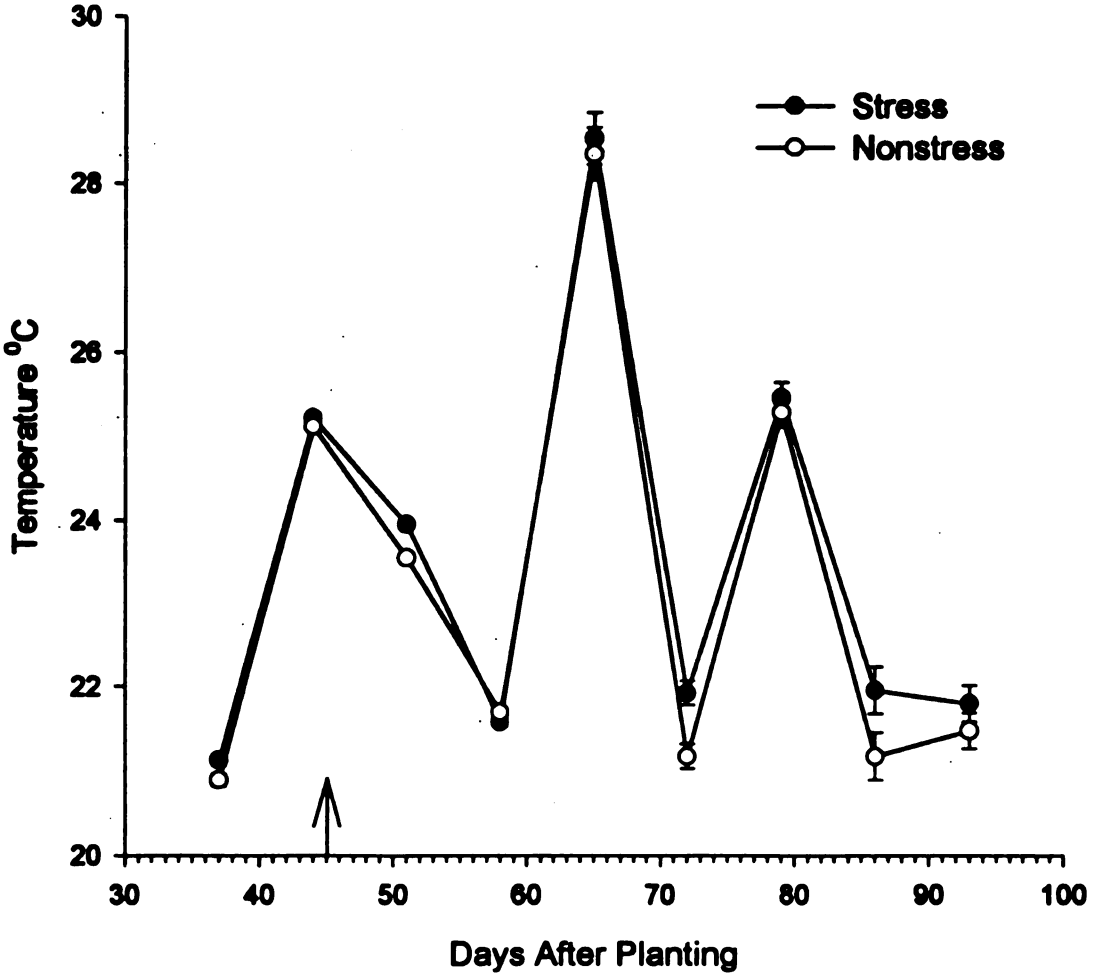

Figure 2. Leaf temperature of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1995. Bars indicate standard error of the mean at $P \leq 0.05$. Vertival arrow indicates when stress was induced.

Figure

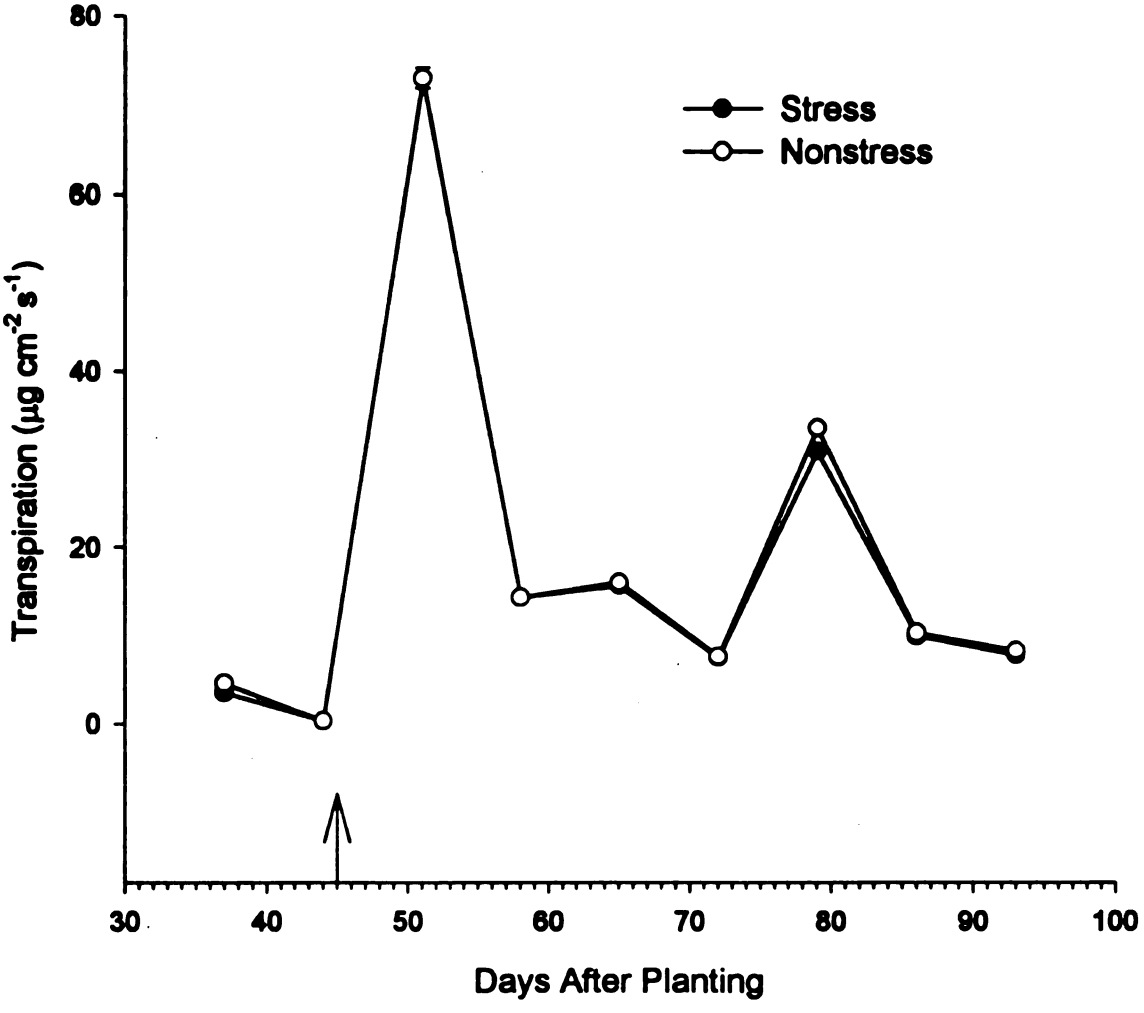

Figure 3. Transpiration rate of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1995.
Bars indicate standard error of the mean.
Arrow indicates when stress was induced.

significantly higher in the nonstress treatment throughout the growing season (Figure 4), except for 48 and 55 DAP. However at soil depth 33 to 63.4 and 63.5 to 91.4 cm there was no significant difference between stress and nonstress soil moisture content (Figure 5 and 6, respectively), although there was a tendency for the nonstress treatment to contain more soil moisture at all sampling dates of the two depths except 48 and 55 DAP at soil depth 33 to 63.4 cm (Figure 5). Monthly mean air temperature ranged from a minimum of 60.1 to a maximum of 83.7 ^{0}F (Figure 7).

Yield of the eight genotypes in 1995 ranged from 1057 to 1863 Kg ha^{-1} under adequate moisture stress with a drought intensity index (DII) of 0.35 (Table 2), suggesting a moderate moisture stress. Sierra, Lef-2-RB, and their progeny (T3110-2 and T3147-2) were among the top four performers (Table 2). When stress and non-stress treatments were combined, Lef-2-RB had the highest yield and was significantly higher than all other genotypes except T3110-2 (Table 2). The genotype Bat 477 was used as the drought resistant check since numerous studies have documented its resistance (CIAT, 1984; Sponchiado et al., 1989). Its yield ranged from 987 Kg ha^{-1} under stress to 1431 Kg ha^{-1} under sufficient moisture. Based upon previous nonpublished work at MSU, 8-42-M-2 was used as a drought susceptible check. Its yield ranged from 894 Kg ha^{-1} under moisture stress conditions to 1393 Kg/ha^{-1} under adequate soil moisture conditions (Table 2). Yield reduction for the eight genotypes ranged from 30 to 46%. The genotype, Lef-2-RB had the lowest yield reduction, and T3008-1 had the greatest (Table 2). The geometric mean for the eight

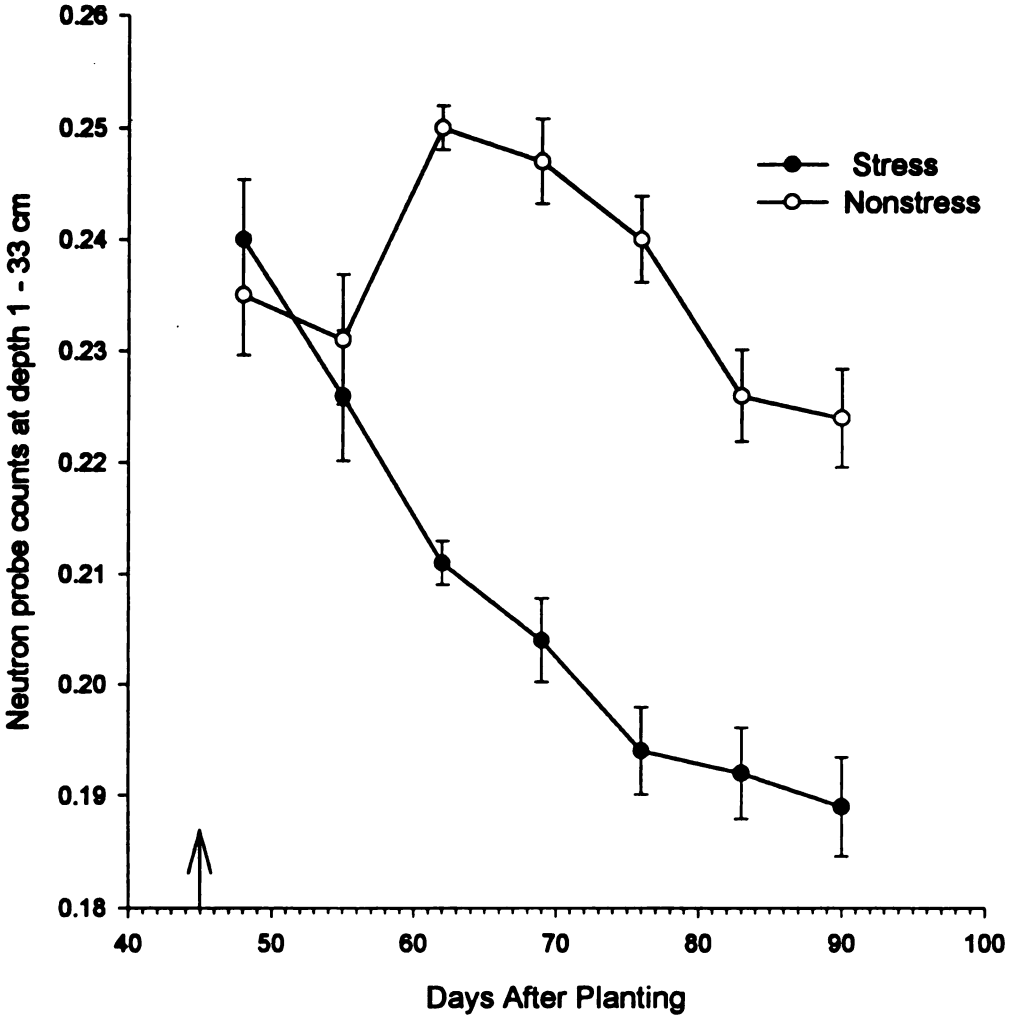

Figure 4. Neutron probe counts of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1995. Bars indicate standard error of the mean at $P \leq 0.05$. Vertical arrow indicates when stress was induced.

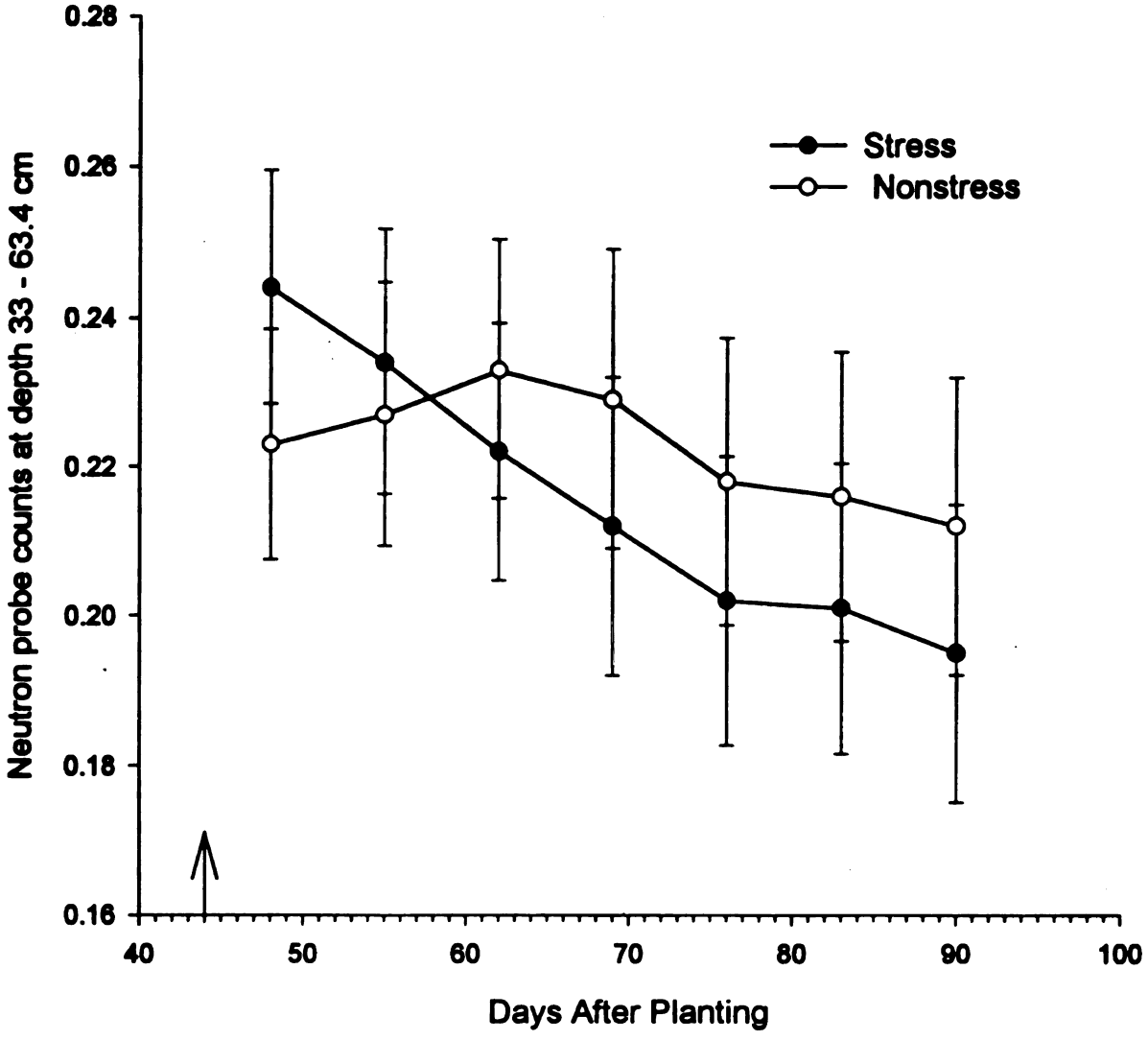

Figure 5. Neutron probe counts of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1995.
Bars represent standard error of the mean.
Vertival arrow indicates when stress was induced.

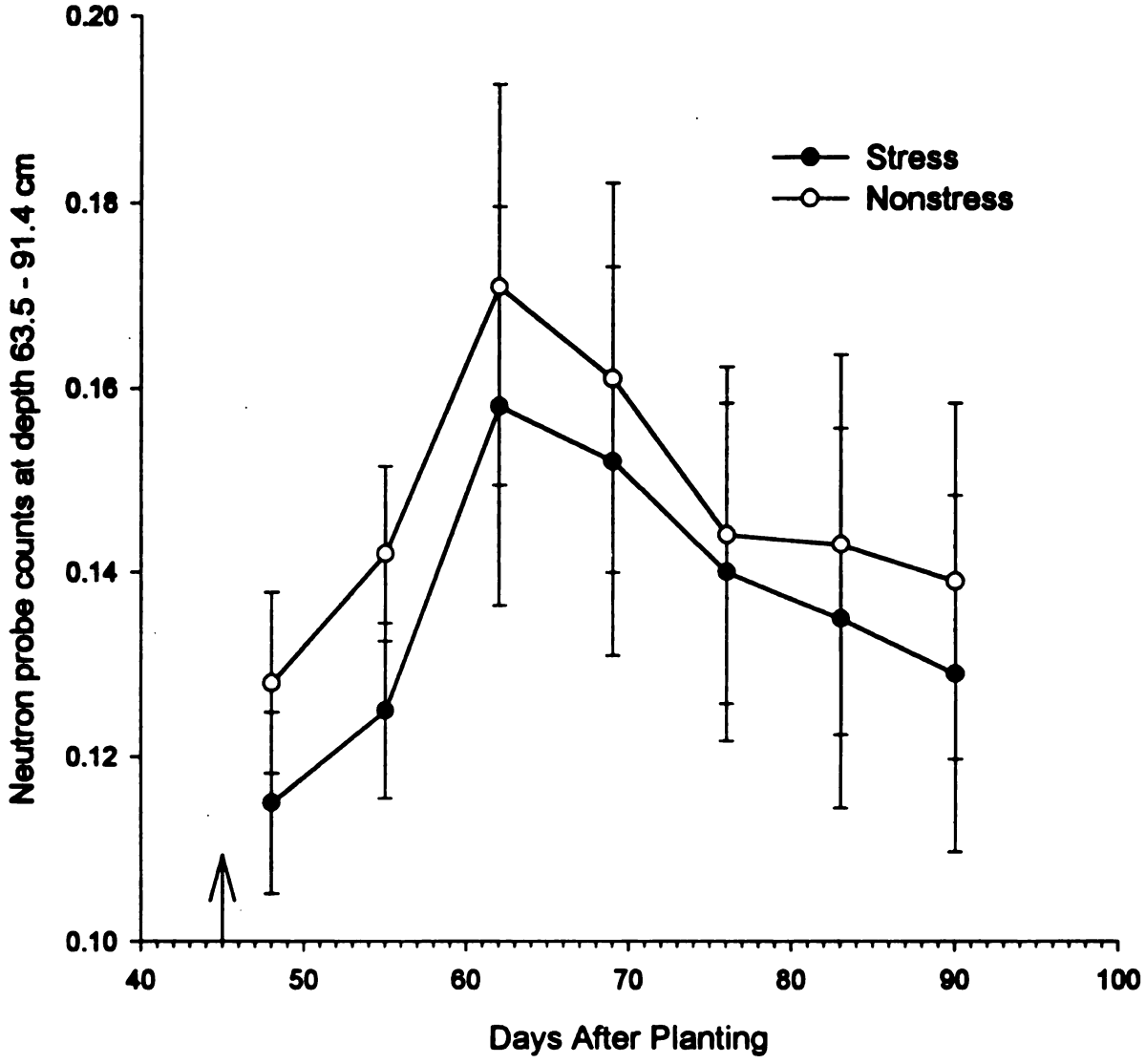

Figure 6. Neutron poobe counts of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1995.
Bars represent standard error of the mean.
Vertical arrow indicates when stress was induced.

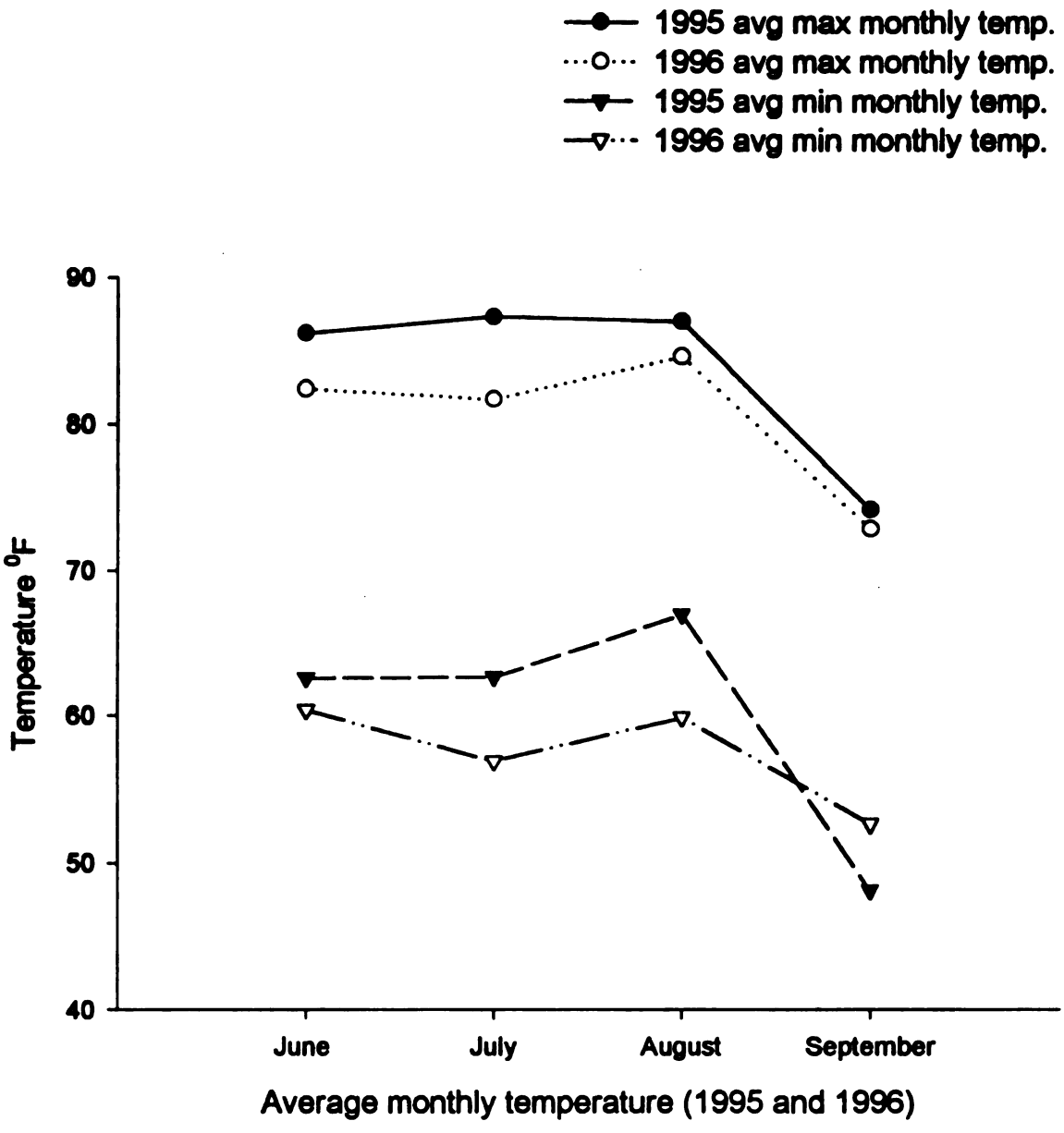

Figure 7. Mean monthly maximum and minimum temperature (^{0}F) recorded at the Kellogg Biological Station, Hickory Corners, MI. in 1995 and 1996.

Table 2. Yield of non-stress treatment, percent yield reduction, combined yield for stress and non-stress treatments, drought susceptible index (DSI), Geometric mean, and stress tolerance index (STI) of eight bean (*Phaseolus vulgaris* L.) genotypes grown in a rainshelter at the Kellogg Biological Station in Hickory Corners, MI in 1995. Drought intensity index = 0.35.

Genotypes	Yield‡ Kg ha^{-1}	%yield reduction	Combined Yield§	Geometric mean	DSI	STI
Lef-2-RB	1863	30	1557 a*	1555	0.866	1.055
T3110-2	1739	34	1440 ab	1408	0.983	0.894
T3147-2	1550	31	1311 bc	1289	0.881	0.746
Sierra	1547	32	1303 bc	1280	0.901	0.737
Bat 477	1431	31	1208 bcd	1187	0.893	0.635
8-42-M-2	1393	36	1143 cd	1116	1.024	0.559
T3008-1	1337	46	1066 de	979	1.323	0.426
T3016-1	1057	36	869 e	849	1.016	0.322

* Different letters indicates significant difference among means within a column at $P \leq 0.05$ according to DMRT.

‡ Indicates yield under non-stress conditions.

§ Indicates combined stress and non-stress yield.

cultivars ranged from 849 to 1555 Kg ha^{-1}. Geometric mean was used to assess yield potential, an important factor since a genotype might be low yielding under sufficient moisture conditions, but have minimal yield reduction under stress. Such a genotype would be stress resistant but undesirable. The choice of GM to represent mean productivity is preferred because, when ranking genotypes, GM better accounts for large differences in performance between stress and nonstress environments than does the simple arithmetic mean used by Rosielle and Hamblin (1981). The genotype T3008-1 had the highest DSI and Lef-2-RB had the lowest (Table 2). According to this system, the resistant genotypes in order from most to least resistance were Lef-2-RB, T3147-2, Bat 477, Sierra, and T3110-2. The susceptible genotypes in order from most to least susceptible were T3008-1, T3016-1, and 8-42-M-2. STI ranged from 0.322 to 1.055 with the genotype Lef-2-RB having the highest value indicating the greatest resistance and highest yield potential and the genotype T3016-1 having the lowest value indicating susceptibility and low yield potential (Table 2). Arbitrarily using 0.6 as the STI cutoff between resistant and susceptible genotypes, STI and DSI agreed on the genotypes that would be assessed as resistant or susceptible, but the order within categories differs (Table 2).

The GM ranked Lef-2-RB, T3110-2, T3147-2, and Sierra in that order, as having the highest yield potential. These results were identical to those of STI. Bat 477 was used as the drought resistant check and the DII and STI both designated it as such, however, its yield potential was less than that of T3110-2 and T3147-2 and their parents, Lef-2-RB and Sierra. Previous work

(nonpublished) at MSU indicated that Bat 477 had a lower yield potential than Sierra and Lef-2-RB, but exhibited greater yield stability.

The GM, DSI, and STI were each analyzed to determine their degree of correlation with yield under stress conditions, yield under non-stress conditions, and combined yield of the two moisture treatments. The correlation of geometric mean and STI with yield under stress, non-stress, and combined moisture treatments was positive and highly significant, ranging from 0.98*** to 0.99*** (Table 3). As would be expected, the DSI was inversely correlated with all three yield categories but was only significantly correlated with yield in the stress treatment (-0.72*). The geometric mean and STI were more accurate than the DSI in selecting desirable genotypes based upon yield performance for 1995.

1996 field experiment

A significantly greater quantity of PAR was intercepted by the canopy of the nonstress treatment on 50, 78, and 92 DAP ($P \leq 0.01$, 0.05, and 0.05, respectively) (Figure 8). The difference in PAR intercepted by the canopy ranged from 656 in the stress treatment to 717 $\mu mol\ m^{-2}\ s^{-1}$ in the nonstress treatment. Leaf temperature ranged from 21 to 26.5 ^{0}C. The stress treatment had a significantly higher ($P \leq 0.10$) leaf temperature than the non-stress treatment at 71 and 85 DAP and the tendency was the same on all other sampling dates except 43 and 92 DAP (Figure 9). The non-stress treatment had a higher ($P \leq 0.10$) transpiration rate than the stress treatment at 92 DAP (Figure 10). The only difference in soil moisture between stress and non-stress

Table 3. Correlations of yield under stress, yield under non-stress, and combined yield for stress and non-stress treatment to geometric mean (GM), drought susceptibility index (DSI), and stress tolerance index (STI). Data from bean (*Phaseolus vulgaris* L.) plants grown at the Kellogg Biological Station in Hickory Corners, MI. In 1995.

	1995		
	GM	DSI	STI
Stress	0.99***	-0.72*	0.98***
Non-stress	0.98***	-0.46	0.98***
Combined	0.99***	-0.58	0.98***

***, * Indicates significance at $P \leq 0.001$ and 0.05, respectively, according to DMRT.

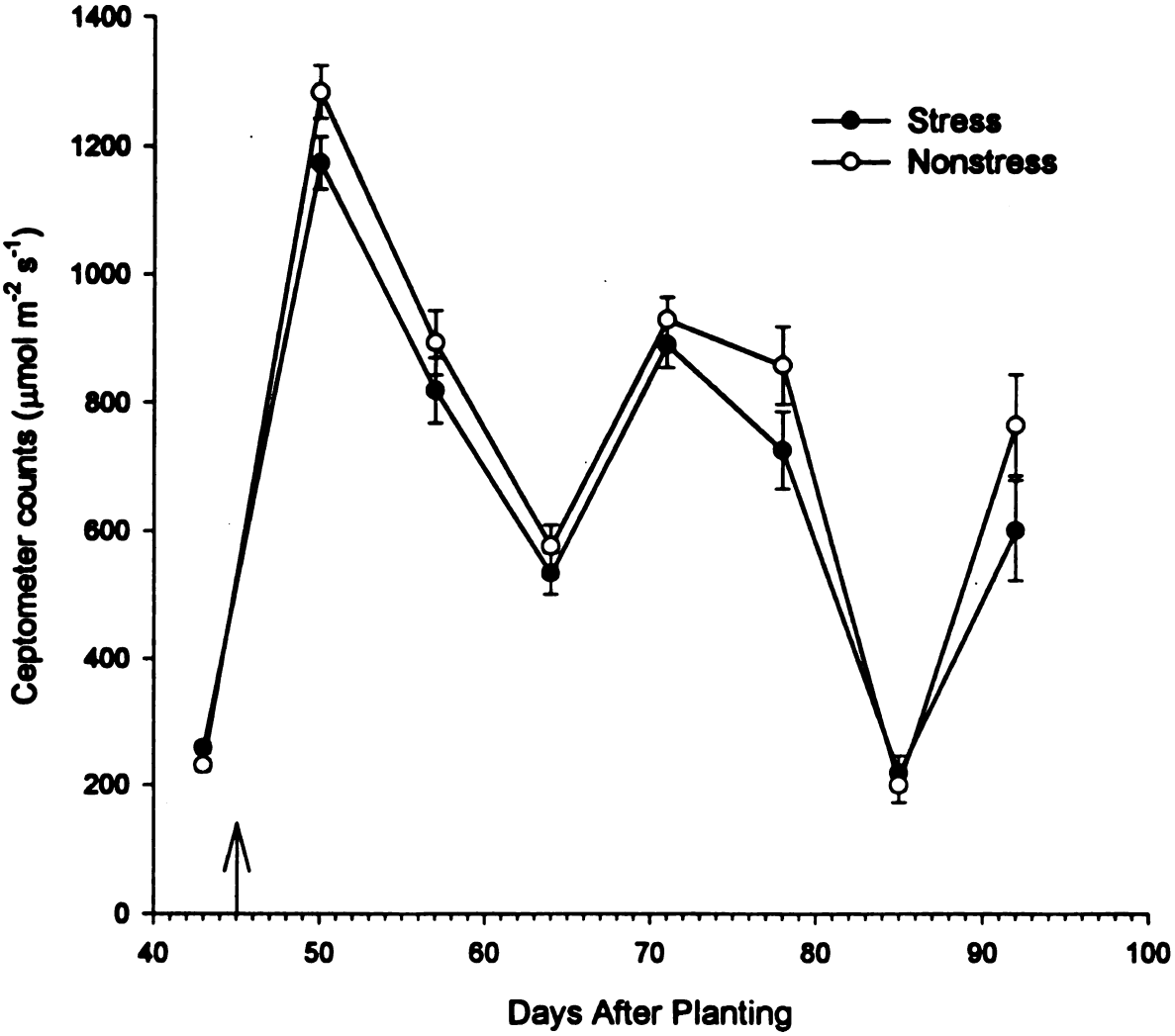

Figure 8. PAR intercepted by the canopy of eight genotypes of common bean grown under stress and nonstress moisture conditions at the Kellogg Biological Station, Hickory Corners, MI. in 1996.
Bars indicate standard error of the mean at $P \leq 0.05$.
Vertical arrow indicates when stress was induced.

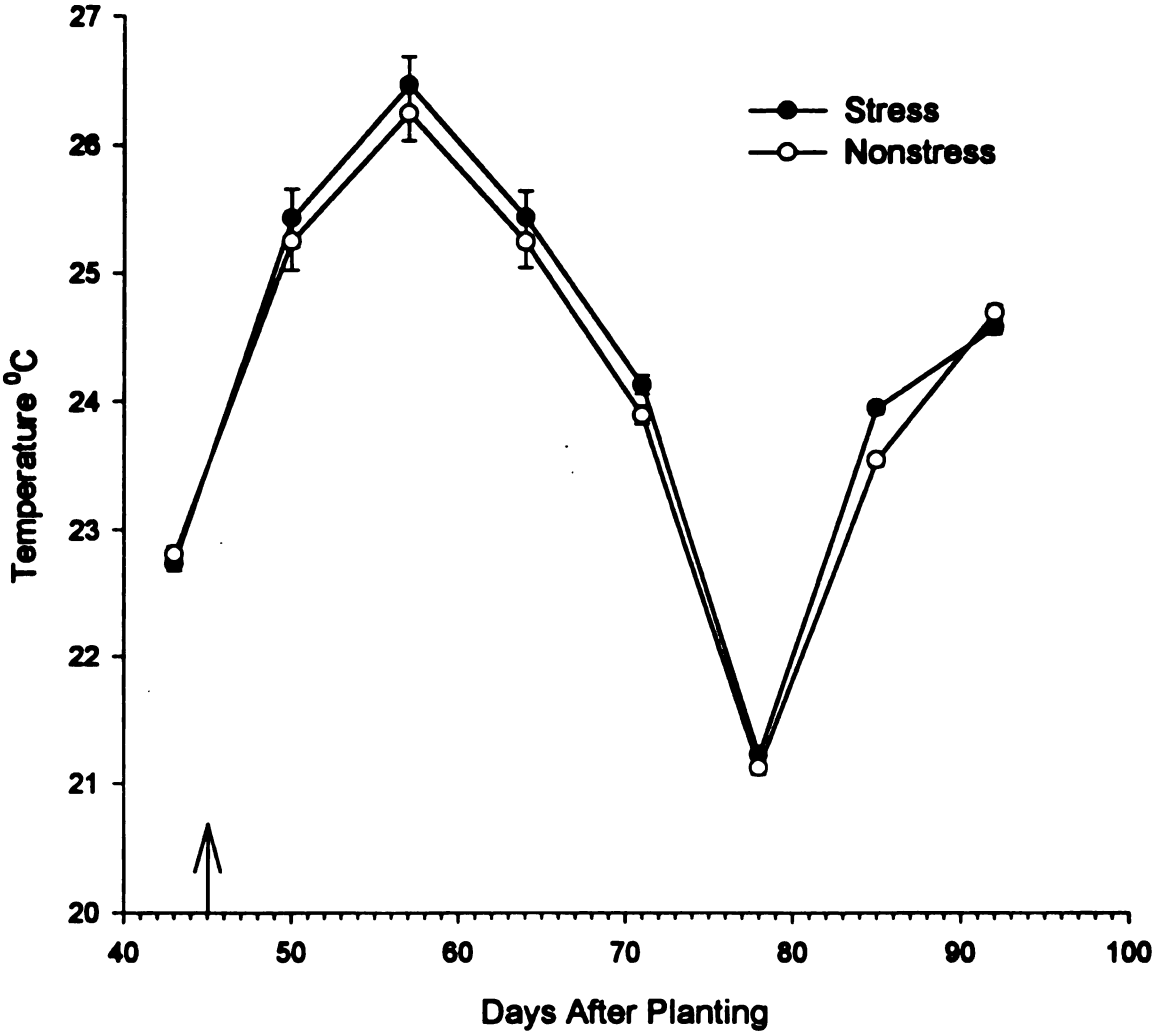

Figure 9. Leaf temperature of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1996. Bars indicate standard error of the mean at $P \leq 0.10$. Vertical arrow indicates when stress was inbduced.

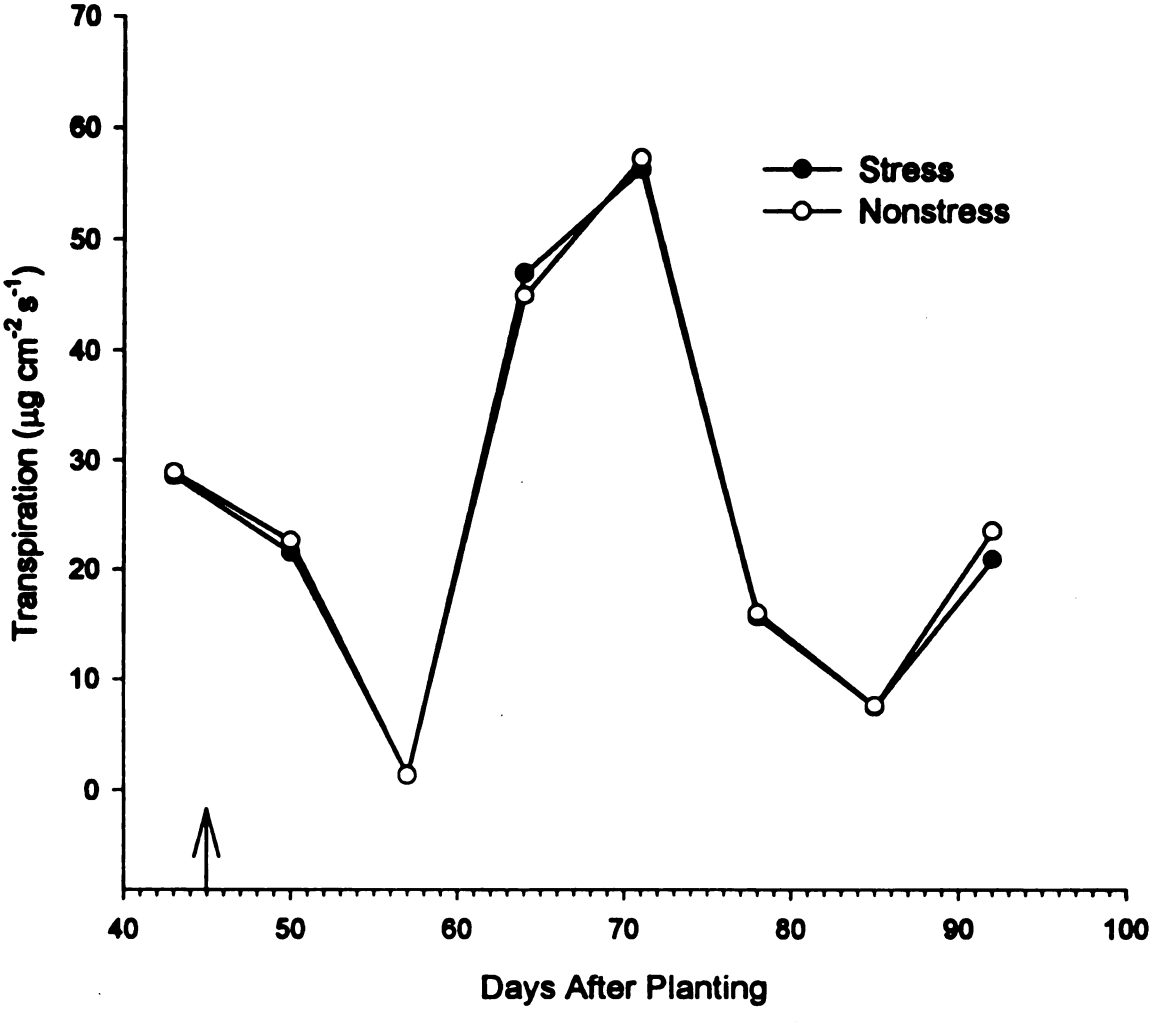

Figure10. Transpiration rate of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kelloggs Biological Station, Hickory Corners, MI. in 1996.
Bars indicate standard error of the mean at $P \leq 0.10$.
Vertical arrow indicates when stress was induced.

treatments occurred in the 1 to 33 cm depth at 78 DAP ($P \leq 0.05$) when the non-stress treatment had a significantly higher soil moisture content than the stress treatment (Figure 11). There was a tendency for higher soil moisture content in the non-stress treatment on all sampling dates for the 33 to 63.4 cm depth (Figure 12). There was no significant difference between the two treatments at the 63.5 to 91.4 cm depth (Figure 13). Average mean temperature ranged from 57.5 (minimum) to 80.4 (maximum) ^{0}F (Figure 7) and was higher in 1995 than in 1996.

The genotypic yield in 1996 ranged from 1151 to 1411 Kg ha^{-1} with a DII of 0.05, indicating no moisture stress (Table 4). Leaf temperature, transpiration, and neutron probe data supported the DII conclusion of no soil moisture stress in 1996. The lack of moisture stress in 1996 was attributed to consistent malfunctioning of the rainshelter throughout the growing season. The shelter did not close during precipitation and often had to be closed or kept open due to safety hazards associated with its operation. There was a numerical difference in yield between "stress" and "nonstress" treatments, but this was probably due to leaf injury symptoms resulting from sunscald and bronzing. The sunscald appeared to result from afternoon irrigation of the plants and subsequent opening of the rainshelter, subjecting moist leaves to bright sun and high temperatures. The bronzing was typical of ozone damage.

In 1996, visual data were colleted for sunscald, leaf bronzing, leaf yellowing, and brown veins. Plants were visually scored on a scale of 0 to 5, with 5 being severely damaged and 0 being no visual damage. The sunscald

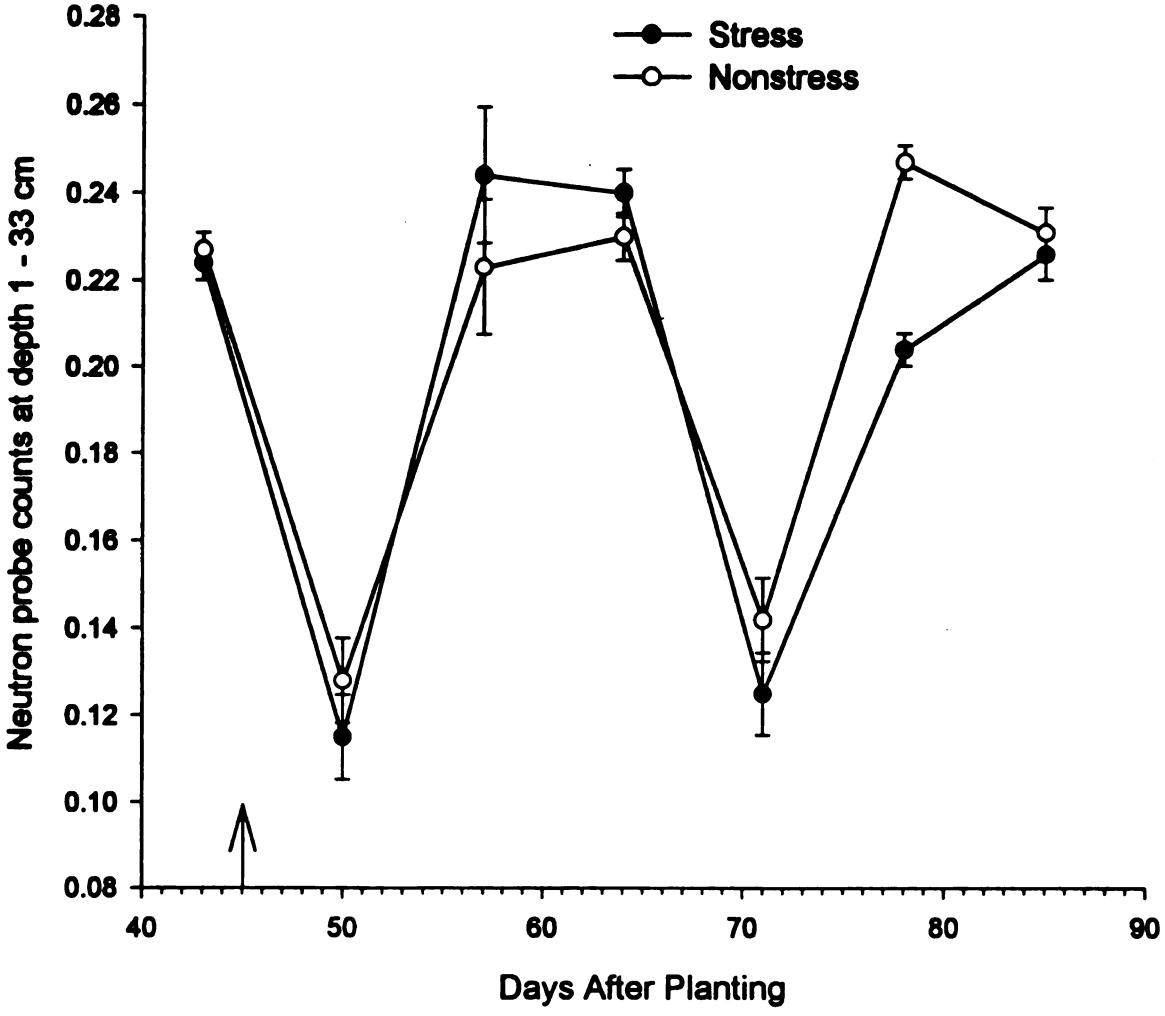

Figure 11. Neutron probe counts of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1996. Bars indicate standard error of the mean at $P \leq 0.05$. Vertical arrow indicates when stress was induced.

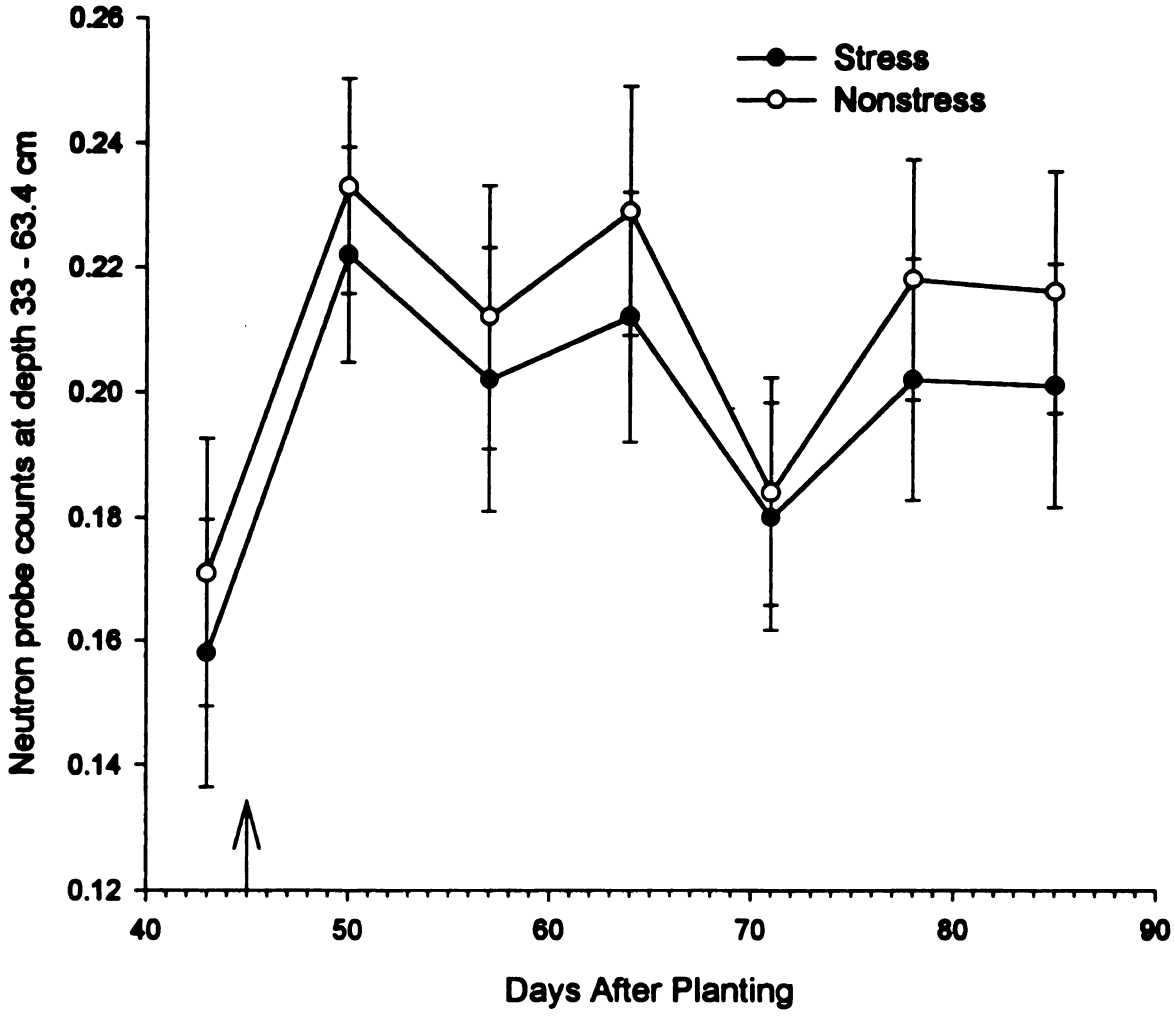

Figure 12. Neutron probe count of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1996.
Bars represent standard error of the mean.
Vertical arrow indicates when stress was induced.

Neutron probe counts at depth 63.5 - 91.4 cm

Fig

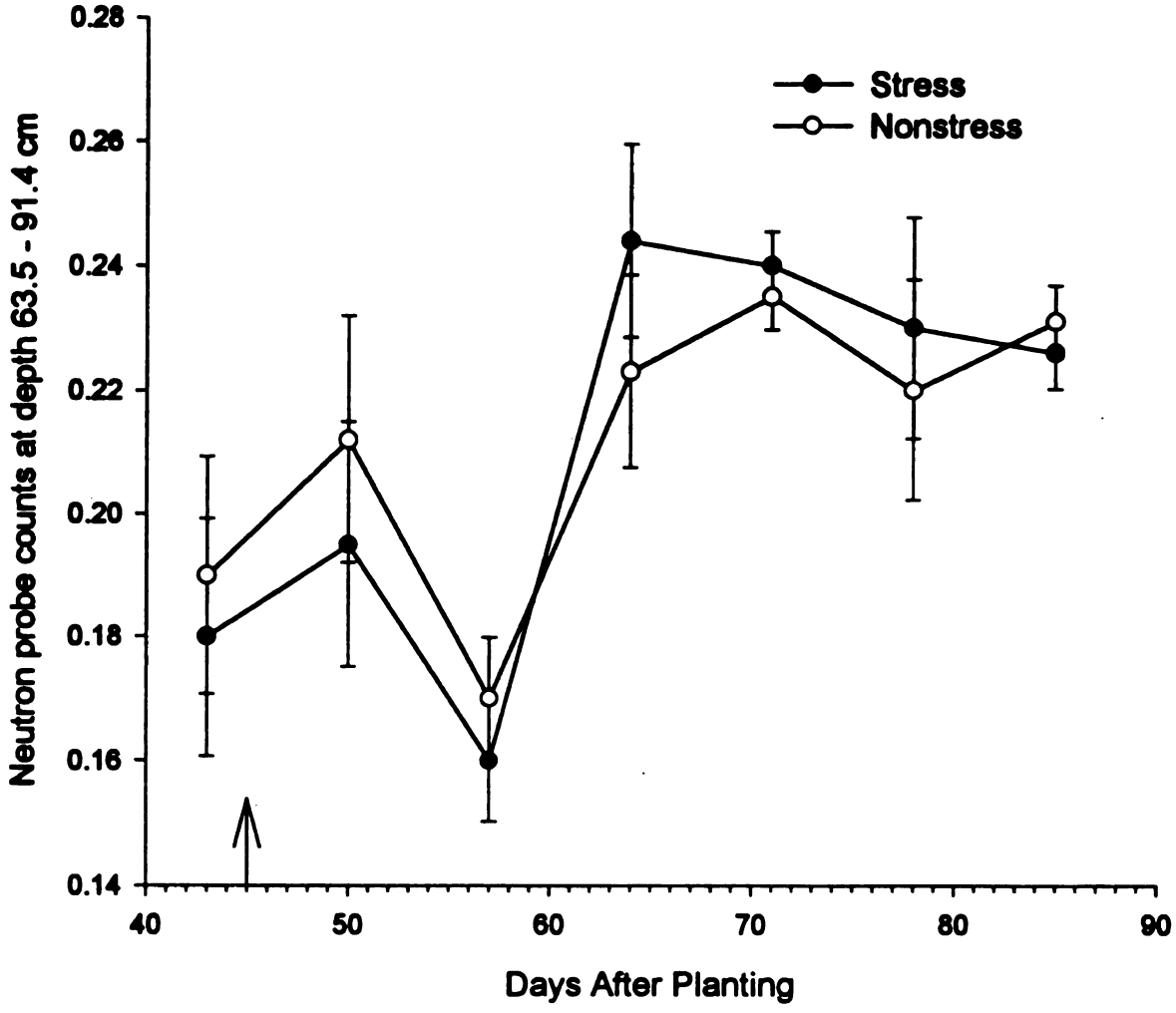

Figure 13. Neutron probe counts of eight genotypes of common bean grown under stress and nonstress moisture conditions in a rainshelter at the Kellogg Biological Station, Hickory Corners, MI. in 1996.
Bars represent standard error of the mean.
Vertical arrow indicates when stress was induced.

Table 4. Yield under stress and non-stress treatments, percent yield reduction, drought susceptibility index (DSI), geometric mean (GM), and stress tolerance index (STI) of bean (*Phaseolus vulgaris* L.) genotypes grown in a rainshelter at the Kellogg Biological Station in Hickory Corners, MI in 1996. Drought intensity index = 0.05.

Genotypes	Yield‡ Kg ha^{-1}	% reduction	Combined Yield§	Geometric Mean	DSI	STI
T3016-1	1501	12	1411 a*	1408	2.387	1.13
8-42-M-2	1440	10	1374 a	1369	1.935	1.07
T3147-2	1455	14	1353 a	1349	2.810	1.04
Sierra	1341	5	1310 ab	1309	0.952	0.98
T3110-2	1301	-2	1308 ab	1308	-0.229	-0.98
Lef-2-RB	1245	-5	1274 ab	1273	-0.927	-0.92
T3008-1	1140	-2	1152 b	1152	-0.408	-0.76
Bat 477	1176	4	1151 b	1151	0.844	0.76

* Different letters indicates significant difference among means within a column at $P \leq 0.05$ according to DMRT.
‡ Represents yield under non-stressed conditions.
§ Indicates combined yield from stress and non-stress treatments.

rating for 8-42-M-2 was significantly higher than that of T3147-2 and T3110-2. The genotype 8-42-M-2 had a significantly higher rating for leaf bronzing than all other genotypes except Lef-2-RB (Table 5). Leaf yellowing was significantly greater in T3016-1 than in Lef-2-RB, Sierra or T3110-2 (Table 5).

The genotypes, T3016-1, 8-42-M-2, and T3147-2 had a significantly higher yield than T3008-1 and Bat 477 (Table 4). Thus, the drought susceptible bean genotype, 8-42-M-2, had a significantly higher yield than the drought tolerant BAT 477 (Table 4). Although there was no moisture stress, the yield difference between the designated stress and non-stress treatments ranged from -5 to 14%, with a negative number indicating a higher yield in the designated stress than non-stress treatment (Table 4). The genotypes T3110-2 and T3008-1 had the least difference between yield in the two moisture treatments but T3147-2 had the greatest with a 14% yield reduction in the designated stress treatment. Even though the stress was not moisture related, the GM, DSI, and STI were still computed. The geometric mean ranked T3016-1, 8-42-M-2, T3147-2, and Sierra, in that order as having the highest yield potential. As in 1995, the STI produced the same ranking as the geometric mean with regard to drought resistance and yield potential. The DSI designated three of these same four genotypes as being susceptible, T3016-1, 8-42-M-2, and T3147-2. Ignoring the negative signs, the most tolerant lines, as designated by the DSI, were also the ones with the lowest yield potential. These data indicate that plants did experience a stress in 1996, that the genotypes were differentially affected by it, and the stress was not due to moisture deficit. As in 1995, the correlation of

Table 5. White mold, bronzing, and yellowing observed during the 1996 growing season at KBS.

Genotypes	Sunscald	Bronzing	Yellowing
8-42-M-2	4.1 a**	4.1 a**	1.3 abc**
T3008-1	3.9 ab	1.6 b	2.8 abc
BAT 477	3.4 ab	2.0 b	3.0 ab
T3016-1	2.9 abc	1.6 b	3.4 a
Lef-2-RB	2.7 abc	2.5 ab	0.9 bc
Sierra	2.6 abc	0.9 b	0.6 c
T3147-2	1.9 bc	1.3 b	1.8 abc
T3110-2	1.0 c	0.9 b	0.9 bc

** Different letters indicates significant difference among means within a column at $P \leq 0.01$ according to DMRT.

geometric mean and STI with yield from the stress, non-stress, and combined stress and non-stress treatments was positive and highly significant ranging from 0.85*** to 0.99*** , however, the correlation between GM and combined moisture was not valid because the data produced a 1.00 correlation (Table 6). Unlike, 1995, the correlation between yield and DSI was positive in all three yield categories and was significant for nonstress (0.82*) and combined moisture treatments (0.63†) (Table 6). T3147-2 and Sierra were among the four highest yielding varieties during both years.

Greater validity of 1995 data

Given the lack of moisture stress and the incidence of leaf injury in 1996, only the 1995 data could be construed as relating to moisture deficit. The 1995 data indicated that T3147-2, Sierra, Lef-2-RB, T3110-2, and BAT 477 were drought resistant and 8-42-M-2, T3016-1, and T3008-1 were drought susceptible. The designation of T3147-2 and T3110-2 was resistant are supported by the work of Schneider et al. (1997), while the designation of BAT 477 as resistant was supported by numerous studies (CIAT, 1984; Sponchiado et al., 1989; Singh, 1995). Similarly, the designation of Sierra and Lef-2-RB as drought resistant is supported by results of Ramirez-Vallejo (1992). However, the 1995 results categorized T3016-1 and T3008-1 as drought susceptible in contrast to the work of Schneider et al. (1997) which categorized them as drought resistant. The designation of 8-42-M-2 as susceptible was supported by the work of Acosta-Gallegos (1988). Genotypic differences in both GM and DSI

Table 6. Correlations of yield under stress, yield under non-stress treatment, and combined yield for moisture treatments to geometric mean (GM), drought susceptibility index (DSI), and stress tolerance index (STI). Data from bean (*Phaseolus vulgaris* L.) plants grown at the Kellogg Biological Station in Hickory Corners, MI. in 1996.

	1996		
	GM	DSI	STI
Stress	0.87**	0.16	0.85**
Non-stress	0.96***	0.82*	0.96***
Combined	-----	0.63†	0.99***

***, **, *, † Indicates significance at P ≤ 0.001, 0.01, 0.05, and 0.10, respectively, according to DMRT.

have been reported in common bean (Acosta-Gallegos, 1988; Acosta-Gallegos and Adams, 1991; White and Singh, 1991; Schneider et al., 1997) and in wheat (*Triticum aestivum*) (Clarke et al., 1992). White and Singh (1991) reported similar limitations in the use of DSI in common bean in that DSI did not differentiate between potentially drought resistant genotypes and genotypes with low yield potential.

Conclusion

T3147-2, Lef-2-RB, T3110-2, Sierra, and BAT 477 were drought resistant and T3016-1, T3008-1, and 8-42-M-2 were drought susceptible. Both GM and STI were better predictors than DSI of yield performance under limited moisture stress.

Literature cited

Acosta-Gallegos, J.A. 1988. Selection of common bean (*Phaseolus vulgaris* L.) genotypes with enhanced drought tolerance and biological nitrogen fixation. Ph.D. diss. Michigan State University, East Lansing, MI. U.S.A.

Acosta-Gallegos, J.A., and M.W. Adams. 1991. Plant traits and yield stability of dry bean (*Phaseolus vulgaris* L.) cultivars under drought stress. J. Agric. Sci. (Cambridge) 117:213-219.

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

CIAT (Centro Internacional de Agricultura Tropical). 1984. Annual report 1983. Bean Program CIAT, Cali, Columbia.

CIAT (Centro Internacional de Agricultura Tropical). 1988. Annual report 1987. Bean Program CIAT, Cali, Columbia.

Clarke, J.M., R.M. DePauw, and T.F. Townley-Smith. 1992. Evaluation of methods for quantification of drought tolerance in wheat. Crop Science 32:723-728.

Fairbairn, J.N. 1993. Evaluation of soils, climate and land use information at three scales: The case of low income bean farming in Latin America. Ph.D. diss. University of Reading, Reading, U.K.

Fernandez, C.J. G. 1993. Effective selection criteria for assessing plant stress tolerance. *In* Adaptation of food crops to temperature and water stress: Proceedings of an international symposium, Taiwan, 13-18 August, 1992. AVRDC. pp:257-270.

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

Food and Agriculture Organization (FAO). 1984. Food balance sheets, 1979-1981. FAO, Rome, Italy.

Kelly, J.D., M.W. Adams, A.W. Saettler, G.L. Hosfield, G.V. Varner, M.A. Uebersax, and J. Taylor. 1990. Registration of "Sierra" Pinto Bean. Crop Sci. 30:745-746.

Lynch, J.P. and J.J. van Beem. 1993. Growth and architecture of seedling roots of common bean genotypes. Crop Sci. 33:1253-1257.

Ramirez-Vallejo, P. 1992. Identification and estimation of heritabilities of drought related resistance traits in common bean (*Phaseolus vulgaris*). Ph.D. diss. Michigan State Univ., East Lansing (Diss. Abstr. 92-26240).

Rosielle, A.A. and J. Hamblin. 1981. Theoretical aspects of selection for yield in stress and non-stress environments. Crop Sci. 21:943-945.

Schneider, K.A., R. Rosales-Serna, F. Ibarra-Perez, B. Cazares-Enriquez, J.A. Acosta-Gallegos, P. Ramirez-Vallejo, N. Wassimi, and J.D. Kelly. 1997. Improving common bean performance under drought stress. Crop Science 37:43-50.

Schwartz, H.F., and M.A. Pastor-Corrales(eds.). 1989. Bean production problems in the tropics. 2nd ed. CIAT, Cali, Columbia.

Singh, S.P. 1982. A key for identification of different growth habits of *Phaseolus vulgaris* L. Bean Improvement Cooperative 25:92-95.

Singh, S.P. 1995. Selection for water-stress tolerance in interracial populations of common bean. Crop Science 35:118-124.

Sponchiado, B.N., J.W. White, J.A. Castillo, and P.G. Jones. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Exp. Agric. 25:249-257.

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

White J.W., and S.P. Singh. 1991. Breeding for adaptation to drought. p. 501-551. *In* A. van Schoonhoven and O. Voysest (ed.) Common beans: Research for crop improvement. C.A.B. International. wallingford, UK, and CIAT, Cali, Columbia.

Chapter 2

Bean seedling root growth as an indicator of field performance under moisture stress.

Introduction

Drought stress inhibits root growth (Robertson et al., 1990; Westgate and Boyer, 1985; Sharp, Silk, and Hsiao, 1988). Reports of increased root/shoot (R/S) ratio in droughted plants (Bradford and Hsiao, 1982; Sharp and Davies, 1979; Hubick et al., 1986) indicated that plants may respond to drought stress by preferentially maintaining root growth over shoot growth (Hsiao and Acevedo, 1974). Mild water stress promoted an increase in root elongation (Hsiao and Acevedo, 1974; Jupp and Newman, 1987; Watts et al., 1981). Blum (1988) found that root length density (RLD) and total root length per plant were greater in late maturing than in early maturing isogenic lines of sorghum (*Sorghum bicolor)* at most growth stages, yet when RLD was calculated versus leaf area per plant, the early lines had a greater RLD/unit leaf area. He interpreted this as meaning the early lines had an advantage in maintaining a higher leaf water potential at a given soil moisture potential and that this was a drought resistance attribute. Blum (1988) reported that the best yielding maize lines under stress had an improved root length density of 120 to 150 cm. Carrow (1996) concluded that high RLD in the 20 - 60 cm root zone and the ability to maintain

evapotranspiration in drying soil were important for drought resistance in tall fescue (*Festuca arundinaceae*).

The role of abscisic acid (ABA) in stomatal closure has been documented in many plants (Taiz and Zeiger, 1991), including cowpea (*Vigna unguiculata*) and cassava (*Manihot esculenta*). Less is known about the effects of ABA on root growth in water stressed environments, although ABA is believed to play a critical role in root elongation during drought stress (Robertson et al., 1990). ABA may have additional regulatory roles in the adaptation of plants to drought stress (Jones, 1978). ABA levels increased in the roots of water-stressed plants (Hubick et al., 1985; Lachno, 1984; Walton et al., 1976) and this increase did not depend on transport from the shoot (Walton et al., 1976). Similarly, Sharp et al. (1993) reported that ABA promoted root elongation and inhibited shoot elongation in maize (*Zea mays*) at low water potential. They also suggested that ABA is involved in the orientation of cell expansion in roots at low water potential.

Polyethylene glycol (PEG) has been used to simulate drought in plants. It induced a primary water stress by reducing water availability (Izzo, 1989). The most serious limitation of PEG as an osmoticum has been its toxicity (Izzo, 1989). Kaufman and Eckard (1971) concluded that PEG produced changes in plant water relations similar to those caused by drying soil at the same water potential. Such studies have been conducted utilizing many species, including maize (*Zea mays*) (Izzo et al., 1989), coleus (Krizek, D.T. and Semeniuk, P., 1979), white clover (*Trifolium repens*) (Robin et al., 1989), and *Capsicum annum*

(Schaefer et al., 1979). These studies all concluded that PEG has the potential to simulate a drought stress environment.

Historically, the soil medium has been the single greatest inhibitor to the advancement of knowledge about root growth and development (Waisel et al., 1996). Until recently, there were few suitable nondestructive methods for observing the growth and development of intact root systems. Nondestructive methods of root systems are limited to hydroponic and minirhizotron systems, which are expensive and limit the observation and measurement of the root system (Merhaut et al., 1989). In order to be useful to plant breeding programs, methods must be relatively inexpensive and must permit rapid evaluation of large numbers of germplasm (Brar et al., 1990). The growth pouch method outlined by McMichael et al. (1985) appears to meet this criteria with regard to screening for root growth. McMicheal et al. (1985) using small seeded legumes (alfalfa and clover) found that root growth in pouches correlated to root growth in minirhizotrons and in field grown plants.

The objectives of this study were to investigate root morphological response to ABA or PEG in *Phaseolus vulgaris* L. and to assess the feasibility of using root growth in pouches as a screening tool for drought resistance in common bean.

Materials and Methods:

Genotypes

The study used eight common bean genotypes which vary in their response to moisture stress:

1. Sierra, a bean developed in Michigan.
2. BAT 477, documented by CIAT (1984) to be drought resistant.
3. 8-42-M-2, a drought susceptible line developed at Michigan State University.
4. Lef-2-RB, a drought resistant line.
5. T3008-1, developed by the Michigan State University bean breeding program.
6. T3016-1, developed by the Michigan State University bean breeding program.
7. T3110-2, developed by the Michigan State University bean breeding program.
8. T3147-2, developed by the Michigan State University bean breeding program.

(Table 1).

Growth chamber study

Seedlings were grown in a growth chamber with 23/20^{0}C day/night temperatures and a 15 h photoperiod. Photosynthetically active radiation (PAR) measured 523 µmol m^{-2} s^{-1} at the top of the plant canopy using a Decagon Sunfleck Ceptometer (Pullman, Wash.). The experimental design was a split plot with solution (Half strength Hoagland's nutrient solution or deionized water) as the main plot, genotypes as the subplot, and four replications. Seeds were germinated four days prior to initiation of the experiment. Uniform sized seeds

Table 1. Characteristics of common bean genotypes grown in field experiments at Kellogg Biological Station, Hickory Corners, MI. in 1995 and 1996.

Genotypes	Pedigree	Origin£	Seed¥ Size	Seed Color	Plant‡ Type
Sierra	Not identified§	MSU	M	Pinto	II
T3110-2	Sierra X Lef-2-RB	MSU	M	Striped	III
T3147-2	Sierra X Lef-2-RB	MSU	M	Striped	III
Lef-2-RB	(Ver 10/Chis 143)/pue 144	INIFAP	M	Black (striped)	III
Bat 477	(51051 X ICA Bunsi) X (51012 X Cornell 49-242)	CIAT	M	Brown	II
8-42-M-2	N81017 X Lef-2-RB	MSU	M	Tan or Brown	III
T3016-1	Sierra X AC 1028	MSU	M	Tan or Brown	III
T3008-1	Sierra x AC 1028	MSU	M	Tan or Brown	III

£ MSU = Michigan State University

CIAT = Centro Internacional de Agricultura Tropical

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

¥ M=Medium.

‡ Type II = Indeterminate-bush, erect stem and branches

Type III = Indeterminate-bush, prostrate main stem and branches

§ Derived from crosses of Durango Race Pinto with Mesoamerican Race Black (Kelly et al., 1990).

were selected for inclusion and rinsed in a 1 μmol $CaSO_4$ solution for one hour before germination. Seeds were germinated four days prior to initiation of the experiment. Seedlings were transplanted to a CYG growth pouch measuring 15.24 cm x 16.51 cm (MEGA International, Minneapolis, Minn.) at one seed per pouch, an adaptation of a procedure used by McMichael et al. (1985). All pouches contained 50 cc of deionized water and were stapled to black cardboard and placed upright in a specially designed holder with 2.54 cm between pouches. Seedlings were covered with a clear plastic covering for two days. Plants were given four 50 cc applications of half strength Hoagland's nutrient solution, adjusted to pH 6.14, or deionized water from the sixth day after transplanting (DAT) to the fourteenth day when plants were sampled. Fresh weights were taken for roots, stems and leaves. Fresh roots were placed in a whirlpack bag and stored in 15% (v/v) methanol solution at 4^0 C. Leaves and stems were oven dried for 48 h at 60^0 C, weighed, and discarded. Roots were prepared for root imaging according to the procedure developed by Smucker et al. (1990). Root dry weight was then determined. Root quantification and processing was done using a Sun Ultra-based WR-RIPL; V. 3.0 at the root image processing laboratory, Michigan State University (Http://rootdig.css.msu.edu.). Statistical analysis was done with the aid of MSTAT.

Root statistics

Roots were divided into 5 classes, based upon root diameter. Root length was determined for each class and a summation was made of root length in all classes. The classes were Class 1 (0.2 mm), Class 2 (0.5 mm), Class 3 (0.9 mm), Class 4 (1.4 mm), and Class 5 (2.1 mm). Root classes 1, 2, and 3 comprised secondary roots and classes 4 and 5 comprised primary roots. Various ratios of secondary to primary roots were determined. The difference between control root length and root length under each treatment (ABA, -0.52 MPa PEG, and -1.07 MPa PEG) (delta value) was calculated. Some delta values were negative so a transformation of the data was done using a logarithmic scale ($\Delta^{1.2}$) for statistical analysis of the data. Data were analyzed across treatments to determine treatment effects.

ABA experiment

Plants were grown in a growth chamber with 23/20^{0}C day/night temperatures and a 15 h photoperiod. PAR measured 527 μmol $m^{-2}s^{-1}$ at the top of the plant canopy using a Decagon Sunfleck Ceptometer. The experimental design was a split plot with solution (ABA + deionized water or ABA + half strength Hoagland's nutrient solution) as the main plot, genotypes as the subplot, and four replications. Experimental procedures were the same as those of the control experiment. From 6 to 14 DAT, the solutions in the pouches were replaced four times. ABA (*cis-trans*, ± ABA, Sigma) was dissolved in deionized

water or nutrient solution for a final ABA concentration of 10^{-6} m.

PEG experiment

Two experiments were initiated with polyethylene glycol (PEG 600). The experimental design was a split plot with solution (PEG + deionized water or PEG + half strength Hoagland's nutrient solution) as the main plot, genotypes as the subplot, and four replications. Plants in the first PEG experiment were grown in a PEG solution with a water potential of -1.07 MPa. The water potential was -0.52 MPa in the second PEG experiment. Day/night temperature regimes for both experiments was 23/20^{0}C with a 15 h photoperiod. PAR measured 524 and 528 μmol $m^{-2}s^{-1}$ for the -1.07 MPa and -0.52 MPa experiments, respectively. Water stress was induced at six DAT by adding PEG 600 (Sigma Chemical Co., St. Louis, MO) at 25 ml/L (osmotic potential -1.07 MPa) or 18 ml/L (osmotic potential -0.52 MPa). Solutions were replaced four times between 6 and 14 DAT.

Greenhouse Study

Plants were grown in polyvinyl chloride tubes (PVC) for 40 days in a greenhouse at Michigan State University, in East Lansing, MI. The temperature regime was 28^{0}C ± 2^{0}C and a light intensity of 1241 μE $m^{-2}s^{-1}$ for the first experiment and a temperature regime of 25^{0}C ± 2^{0}C and a light intensity of 1200 μE $m^{-2}s^{-1}$ for the second experiment. Both experiments had a 15 h photoperiod.

Experiment 1 consisted of the medium-sized seeded genotypes, Sierra, T3008-1, T3147-2, and 8-42-M-2 and was planted on June 18, 1996. Experiment 2 also consisted of the medium-sized seeded genotypes T3016-1, Lef-2-RB, T3110-2, and, BAT 477 and was planted on September 16, 1996. The experimental design was a split plot with water (stressed and nonstressed) as the main plot, genotypes as the subplot, and four replications. The PVC tubes were 76.2 cm in length with a diameter of 30.5 cm. To determine root growth at different depths each PVC tube was cut into five 15.2 cm sections. The five individual sections were taped together to produce one 76.2 cm tube. The bottom section was filled with silica sand. The remainder of the PVC tube was filled with a Kalamazoo sandy loam soil (Typic Hapludalfs, fine-loamy, mixed, mesic) that had been sieved to remove all stones and packed to a bulk density of 1.31 g/cm^3. Five seeds per PVC tube were planted and thinned to one plant per PVC tube at 14 days after planting (DAP). Stress was initiated at 14 DAP by reducing the amount of water given to plants in the stress treatment. Plants in the stress treatment received 53% less water than plants in the nonstress treatment. Determination was done by visually observing plants and the soil in the stress environment. Plants were watered when the soil began to crack from lack of water and plants began to wilt. Stress plants were watered approximately once per week. Plants in the nonstress environment were watered approximately three times per week. Plants were sampled at 40 DAP. Stem, leaf and reproductive parts were weighed, and dried at 60^{0}C for 48 h, re-weighed, and discarded. Roots were extracted from each section by sieving the soil through 2

mm mesh wire. Roots were prepared for video imaging according to the procedure used by Smucker (1990). Root quantification and processing was done using a Sun Ultra-based WR-RIPL; V. 3.0 at the root image processing laboratory, Michigan State University (Http://rootdig.css.msu.edu.). After video imaging, roots were dried at 60°C for 48 h then weighed and discarded. Statistical analysis was done with the aid of MSTAT.

Correlations

Correlations were determined for each root class of the control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG experiments and with each root class of PVC experiments 1 and 2. Correlations were determined separately using pouch data from the water solution and pouch data from the nutrient solution and each of these was correlated separately against the stress and non-stress treatment of each PVC experiment. Correlations were determined separately for each soil depth of PVC experiments 1 and 2.

Results and Discussion

Root length: Control experiment

There were no significant genotypic differences for root classes 1 and 5, the smallest diameter of secondary roots measured by this procedure and the widest diameter of primary roots, respectively (Table 2). BAT 477, the resistant

Table 2. Total root length of eight common bean genotypes germinated in a germination chamber for 4 d at 25^{0}C and transplanted to an environmentally controlled growth chamber for 14 d in a control solution of half strength Hoagland's solution or deionized water at 23/20^{0}C day/night temperatures and a 15 h photoperiod. Roots are divided into 5 classes based on width diameter.

Genotypes	100 seed wt.(g)	Total root Lth§	Class1(0.2)‡	Class2(0.5)	Class3(0.9)	Class4(1.4)	Class5(2.1)
Sierra	40.35 a*	3.50 a*	0.50 ns	1.98 a*	1.00 a**	0.06 ab*	0.002 ns
T3147-2	38.46 ab	3.52 a	0.53	2.10 a	0.86 ab	0.04 abc	0.001
8-42-M-2	35.46 c	2.67 ab	0.49	1.45 ab	0.70 ab	0.03 bc	0.001
Lef-2-RB	32.39 d	2.73 ab	0.42	1.65 ab	0.64 ab	0.02 c	0.001
T3110-2	37.28 bc	2.90 ab	0.39	1.60 ab	0.83 ab	0.05 abc	0.002
T3008-1	39.50 a	3.21 a	0.41	1.77 a	1.00 a	0.07 a	0.005
T3016-1	36.14 c	3.60 a	0.40	2.04 a	0.96 a	0.07 a	0.004
BAT 477	28.00 e	1.96 b	0.32	1.10 b	0.52 b	0.02 c	0.001
C.V.	6	35	52	33	35	60	151

**, * Different letters indicates significance among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

§, ‡ Indicates root length in meters and diameter of each root class in millimeters, respectively.

check, had a significantly lower total root length than Sierra, T3147-2, T3008-1 and T3016-1. BAT 477 also had a lower seed weight than these genotypes (Table 2). Class 2 root length was significantly lower in BAT 477 than in Sierra, T3147-2, T3008-1, and T3016-1. Similarly, the root length for root classes 3 and 4 of BAT 477 were also lower than for Sierra, T3008-1, and T3016-1 (Table 2). Field performance of Sierra and T3147-2 designated them as resistant genotypes but their root length was significantly greater than that of BAT 477, the resistant check, which may be partly explained by their larger seed weight. Gregory's work (1989) showed that BAT 477 had a greater rooting depth than susceptible genotypes under stress but stress and rooting depth were not a part of this treatment. BAT 477 and 8-42-M-2, the susceptible check, did not differ significantly with regard to total root length or root length of any of the five root classes.

Fifty-two to 61% of the total root length consisted of class 2 roots, while the percentage of class 1 roots ranged from 11 to 17% of the total root length (Table 3). Secondary root classes 1 and 2 comprised 63 to 75% of the total root length and root classes 2 and 3 contained 82 to 86% of the total root length. Ninety-five% of the total root length was comprised of all secondary roots (classes 1-3,Table 3). There were no significant genotypic differences for class 5 roots (Table 3). Seed weight did not affect percentage of roots in the individual root classes.

The resistant check BAT 477 had a smaller percentage of its total roots as class 2 than did T3147-2 and Lef-2-RB, two other resistant genotypes, and

Table 3. Percentage of roots in individual root classes for eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d in half strength Hoagland's nutrient solution or deionized water at 23/20°C day/night temperatures and a 15 h photoperiod.

Genotypes	100seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Classes1+2	Classes2+3	Classes1+2+3
					%				
Sierra	40.35 a*	14 ns	56 ab+	28 ab*	1.60 ab*	0.07 ns	70 abc*	85 ns	98 ns
T3147-2	38.46 ab	14	61 a	24 b	1.10 b	0.03	75 a	84	99
8-42-M-2	35.46 c	17	55 b	27 ab	1.10 b	0.03	72 ab	82	99
Lef-2-RB	32.39 d	15	61 a	24 b	0.81 b	0.03	75 a	85	99
T3110-2	37.28 bc	13	55 b	31 a	1.60 ab	0.08	67 bc	86	98
T3008-1	39.50 a	11	52 b	32 a	2.60 a	0.12	63 c	84	95
T3016-1	36.14 c	13	57 ab	27 ab	2.00 ab	0.10	71 ab	85	98
BAT 477	28.00 e	14	54 b	30 a	1.60 ab	0.03	68 abc	84	98
C.V.	6	29	11	18	63	132	9	5	3

*, + Different letters indicate significant difference among means within a column at $P \leq 0.05$ and 0.10, respectively, according to DMRT.
ns Indicates no significant difference among means within a column.
‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

did not differ significantly from 8-42-M-2, the susceptible check, or the resistant genotype Sierra. The percentage of class 3 roots in BAT 477 was greater than that of T3147-2, but not different from that of 8-42-M-2 or Sierra. The control did not separate resistant and susceptible genotypes, and root growth in half strength Hoagland's solution did not differ from root growth in deionized water (Table 4).

ABA experiment root length

There were no significant genotypic differences for root classes 3, 4, and 5 (Table 5). The genotypes T3147-2 and Lef-2-RB had a significantly higher ($P \leq 0.01$) total root length than Sierra. Total root length of the resistant genotypes T3147-2 and BAT 477 did not differ significantly from that of the susceptible check 8-42-M-2. The class 1 root length of T3147-2 was significantly higher ($P \leq 0.05$) than that of all other genotypes except, 8-42-M-2 and Lef-2-RB (Table 5). The genotypes T3147-2, 8-42-M-2, and Lef-2-RB, had a significantly greater ($P \leq 0.05$) length of class 2 roots than Sierra, T3008-1, and BAT 477 (Table 5). BAT 477 had one of the lowest total root lengths in the control treatment, but was among the group with the highest total root length in the ABA treatment. Seed weight did not affect root length of plants in the ABA experiment. Total root length of plants in the ABA treatment was significantly greater than that of control plants and the same was true for all of the individual root classes (Table 6).

Significant genotypic differences existed for percentage of total roots in

Table 4. Root growth response to half strength Hoagland's nutrient solution versus deionized water.

Root Classes	Control£	ABA	-0.52 MPa PEG	-1.07 MPa PEG
Class 1	ns	ns	W < H^{+}	W < H^{+}
Class 2	ns	ns	W < H^{+}	W < H^{+}
Class 3	ns	ns	W < H*	W < H*
Class 4	ns	ns	W < H^{+}	ns
Class 5	ns	ns	ns	ns
Total	ns	ns	W < H^{+}	W < H^{+}
Classes 1 + 2	ns	ns	W < H*	W < H^{+}
Classes 1+2+3	ns	ns	ns	ns

*, + Indicates significant difference at $P \leq 0.05$ and 0.10, respectively.

ns Indicate non significant data.

W = Water

H = Hoagland's nutrient solution

£ Control solution contained half strength Hoagland's nutrient solution or deionized water.

ABA solution contained 10^{-6} m ABA dissolved in half strength Hoagland's nutrient solution or deionized water.

PEG solution contained 18 ml/L (-0.52 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution or 25 ml/L (-1.07 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution.

Table 5. Total root length of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d in 10^{-6} M ABA at 23/20°C day/night temperatures and a 15 h photoperiod. Roots were divided into 5 classes based upon root diameter.

Genotypes	100 seed wt.(g)	Total root Lth§	Class1 (0.2)‡	Class2 (0.5)	Class3 (0.9)	Class4 (1.4)	Class5 (2.1)
Sierra	40.35 a*	7.730 b**	3.23 d*	3.33 c*	0.93 ns	0.21 ns	0.04 ns
T3147-2	38.46 ab	15.12 a	7.25 a	6.44 ab	1.20	0.18	0.05
8-42-M-2	35.46 c	14.25 ab	5.92 abc	6.64 a	1.41	0.23	0.05
Lef-2-RB	32.39 d	14.73 a	6.29 ab	6.92 a	1.30	0.17	0.05
T3110-2	37.28 bc	8.719 ab	3.21 cd	4.25 bc	1.03	0.16	0.07
T3008-1	39.50 a	8.425 ab	3.13 d	3.99 c	1.10	0.16	0.05
T3016-1	36.14 c	11.19 ab	4.56 bcd	5.36 abc	1.10	0.16	0.04
BAT 477	28.00 e	9.013 ab	3.74 cd	4.05 c	1.00	0.17	0.07
C.V.	6	41.14	46.36	41.07	45.33	52.99	78.21

**,* Different letters indicates significant difference among means within a column at P≤ 0.01 and 0.05, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

§, ‡ Indicates root length in meters and diameter of each root class in millimeters, respectively.

Table 6. Comparison of root length of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod from the four treatments imposed. Roots were divided into 5 classes based upon root diameter.

Treatment£	Total root Lth§	Class1 (0.2)‡	Class2 (0.5)	Class3 (0.9)	Class4 (1.4)	Class5 (2.1)
Control	3.01 d**	0.44 d**	1.71 b**	0.81 b**	0.04 c**	0.002 c**
ABA	11.15 a	4.67 a	5.12 a	1.13 a	0.20 a	0.054 a
-0.52 MPa PEG	4.86 c	1.66 c	2.50 b	0.59 c	0.09 b	0.027 b
-1.07 MPa PEG	9.20 b	3.70 b	4.60 a	0.82 b	0.10 b	0.023 b
C.V.	51	64	50	47	61	101

** Different letters indicate significance among means within a column at $P \leq 0.01$, according to DMRT.

§,‡ Indicates root length in meters and root width classes in millimeters, respectively.

£ Control solution contained half strength Hoagland's nutrient solution or deionized water.
ABA solution contained 10^{-6} m ABA dissolved in half strength Hoagland's nutrient solution or deionized water.
PEG solution contained 18 ml/L (-0.52 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution or 25 ml/L (-1.07 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution.

root classes 1-4 of plants grown in exogenous ABA (Table 7). Unlike the control, 32 to 47% of the total root length was comprised of class 1 roots. Root classes 1 and 2 comprised 81 to 90% of the total root length. Root classes 1 through 3 comprised 95 to 99%, as they did in the control treatment. Percentage of total roots in class 1 was significantly greater in the plants from the ABA treatment than in control plants (Table 8). However, the percentage of root length in root classes 2 and 3 was greater in the control plants. Nevertheless, the increase in class 1 roots of ABA treated plants was so much greater than that of control plants that the combination of class 1 + 2 roots comprised a significantly greater percentage of the total root length in ABA treated plants than in control plants (86 vs 71%, respectively). Seed weight did not affect percentage of total roots in individual root classes. The ABA treatment stimulated the development of the finer secondary roots. Presumably such an occurrence during a moisture deficit would increase the root absorptive surface area, thereby permitting the plant to obtain more water. Simultaneously, a greater percentage of ABA treated plants was in class 5 in comparison to control plants (Table 8). This would permit the plant to obtain moisture that might be in the deeper soil depths. These results generated the working hypothesis that ABA provides information about a genotype's potential for root expansion during moisture stress. The data agree with other work indicating that ABA stimulates root growth (Creelman et al., 1990; Robertson et al., 1990; Sharp et al., 1993) and are exciting in their suggestion that ABA disproportionately induces development of fine secondary roots.

Table 7. Percentage of roots from individual root classes of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in 10^{-6} M ABA.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Classes$_{1+2}$	Classes$_{1+2+3}$	Classes$_{2+3}$
					%				
Sierra	40.4 a*	38 abc*	43 c*	14 ab*	4.00 a*	1.40 ns	81 b*	95 d+	57 ns
T3147-2	38.5 ab	47 a	43 bc	8 c	1.30 b	0.40	90 a	98 ab	52
8-42-M-2	35.5 c	41 ab	47 abc	10 bc	1.60 b	0.40	88 a	98 abc	57
Lef-2-RB	32.4 d	43 ab	47 abc	9 c	1.20 b	0.32	90 a	99 a	56
T3110-2	37.3 bc	32 c	49 a	16 a	2.80 ab	1.20	81 b	97 bcd	65
T3008-1	39.5 a	37 bc	48 ab	12 abc	1.80 b	0.61	85 ab	97 abc	60
T3016-1	36.1 c	40 abc	47 abc	10 bc	2.40 ab	0.90	87 ab	97 abcd	57
BAT 477	28.0 e	42 ab	43 c	11 abc	2.80 ab	1.60	85 ab	96 cd	54
C.V.	6	19	10	40	79	132	7	3	11

*, + Different letters indicate significance among means within a column at $P \leq 0.05$ and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 8. Comparison of percentage of roots from individual root classes of eight common bean genotypes from four treatments germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod.

Treatment £	Class1‡	Class2	Class3	Class4	Class5	Classes1+2	Classes1+2+3	Classes2+3
Control	14 c**	57 a**	27 a**	1.53 bc**	0.06 b**	71 d**	98 a**	84 a**
ABA	40 a	46 c	11 c	2.21 ab	0.83 a	86 b	97 b	57 c
-0.52 MPa PEG	30 b	51 a	15 b	2.82 a	0.32 ab	81 c	96 b	66 b
-1.07 MPa PEG	39 a	50 b	9 c	1.20 c	1.02 a	89 a	98 a	59 c
C.V.	23	11	31	78	150	7	2	9

** Different letters indicate significance among means within a column at $P \leq 0.01$ according to DMRT.

£ Control solution contained half strength Hoagland's nutrient solution or deionized water.

ABA solution was 10^{-6} m ABA dissolved in half strength Hoagland's nutrient solution or deionized water.

PEG solution contained 18 ml/L (-0.52 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution or 25 ml/L (-1.07 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

-0.52 MPa polyethylene experiment root length

Significant genotypic differences were observed for all root length classes in the -0.52 MPa treatment, except class 5 (Table 9). The total root length of T3147-2 was significantly higher ($P \leq 0.05$) than that of Lef-2-RB, T3110-2, and T3008-1 (Table 9). For class 1 roots, T3147-2 root length was significantly higher ($P \leq 0.05$) than 8-42-M-2, Lef-2-RB, T3110-2, and T3008-1 (Table 9). Class 2 root length for T3147-2 was significantly higher ($P \leq 0.05$) than that of Lef-2-RB and T3008-1 (Table 9). Sierra and BAT 477 had a significantly greater ($P \leq 0.01$) class 3 root length than T3008-1 (Table 9). Sierra, 8-42-M-2, T3110-2, and BAT 477 were among the group with the highest ($P \leq 0.10$) root length for class 4 roots (Table 9). Root length did not correspond with seed size.

As in the ABA treatment, BAT 477 was among the group of plants with the highest total root length when plants were grown in PEG at a ψ of -0.52 MPa and this was true for all root classes, except class 5 which had no significant genotypic differences (Table 9). Generally, the same situation applied for the resistant genotypes, Sierra and T3147-2. The genotype T3008-1 had a lower root length than BAT 477 for all root classes, except class 5. The susceptible check, 8-42-M-2 was among the group with the highest root length in all classes except class 1. Plants grown at a ψ of -0.52 MPa had a significantly greater total root length than the control plants and the same was true for all root classes, except Class 2 where the two were equal (Table 6). However, total root length of the -0.52 MPa-treated plants was significantly less than that of plants grown in ABA (Table 5), and the same was true for all root classes. Plants

Table 9. Total root length of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in a polyethylene glycol (PEG) solution of -0.52 MPa. Roots are divided into 5 classes based upon root diameter.

Genotypes	100 seed wt.(g)	Total root Lth§	Class1 (0.2)‡	Class2 (0.5)	Class3 (0.9)	Class4 (1.4)	Class5 (2.1)
Sierra	40.35 a*	6.3 abc*	2.2 abc*	3.1 ab*	0.83 a**	0.106 abc†	0.03 ns
T3147-2	38.46 ab	7.7 a	3.2 a	3.6 a	0.62 ab	0.083 bc	0.03
8-42-M-2	35.46 c	4.5 abcd	1.2 bc	2.4 abc	0.73 ab	0.135 a	0.03
Lef-2-RB	32.39 d	3.0 cd	0.9 bc	1.7 bc	0.40 ab	0.067 bc	0.03
T3110-2	37.28 bc	3.5 bcd	1.1 bc	1.9 abc	0.43 ab	0.091 abc	0.03
T3008-1	39.50 a	1.8 d	0.6 c	0.8 c	0.30 b	0.057 c	0.02
T3016-1	36.14 c	5.3 abcd	1.6 abc	2.9 ab	0.60 ab	0.068 bc	0.02
BAT 477	28.00 e	6.9 ab	2.4 ab	3.5 ab	0.82 a	0.117 ab	0.03
C.V.	6	70.26	92.48	67.23	54.60	60.45	80.66

**, *, † Different letters indicate significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicate no significant difference among means within a column.

§,‡ Indicate root length in meters and diameter of each root class in millimeters, respectively.

grown in -0.52 MPa PEG solution had a higher percentage of their roots in class 2 (46 to 56%) than in any other class (Table 10) and a larger percentage of roots in classes 1 + 2 than in classes 2 + 3. The percentage of total root length in class 1 was greater in the -0.52 MPa solution than in control plants but less than in the ABA-treated plants (Table 8). The percentage of total root length in class 2 roots equaled that of control plants and was greater than that of ABA-treated plants (Table 8). The percentage of total roots in secondary root classes 1 + 2 of plants in the -0.52 MPa treatment was intermediate to that of control and ABA-treated plants while the percentage of roots in classes 2 + 3 was less than that of control plants, but greater than that of ABA treated plants. The -0.52 MPa treatment was similar to the ABA treatment in that both stimulated the development of class 1 roots and total root length (RL). Percentage distribution in individual root classes did not correspond with seed weight (Table 10).

-1.07 MPa polyethylene glycol experiment

There were no genotypic differences for any of the root classes or for total root length in the -1.07 MPa treatment (Table 11). Total root length of plants grown in -1.07 MPa PEG was greater than that of control plants and than plants grown in -0.52 MPa PEG, but less than that of plants grown in ABA (Table 6). The same was true for class 1 roots. Root length of class 2 roots was equal to that of ABA-treated plants and greater than that of the other two treatments. Class 3 root length was equal to that of control plants but less than that of ABA-treated plants and greater than that of plants in the -0.52 MPa experiment. Root

Table 10. Percentage of roots from individual root classes of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in a polyethylene glycol (PEG 600) solution of -0.52 MPa.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Classes1+2	Classes1+2+3	Classes2+3
					%				
Sierra	40.4 a*	29 ns	48 cd*	18 ns	3.60 ns	1.60 ns	77 ns	95 ns	66 ab+
T3147-2	38.5 ab	37	49 bcd	11	2.30	0.70	86	97	60 b
8-42-M-2	35.5 c	25	54 abc	17	3.10	0.90	79	96	71 a
Lef-2-RB	32.4 d	26	56 a	14	2.80	1.10	82	96	70 a
T3110-2	37.3 bc	30	53 abc	14	3.10	0.90	83	97	66 ab
T3008-1	39.5 a	32	46 d	17	3.60	1.90	78	95	63 b
T3016-1	36.1 c	31	54 ab	12	1.50	0.60	85	97	67 ab
BAT 477	28.0 e	33	51 abcd	13	2.50	0.70	84	97	64 ab
C.V.	6	30	11	37	79	110	10	3	11

*, + Different letters indicate significant difference among means within a column at $P \leq 0.05$ and 0.10, respectively, according to DMRT.
ns Indicate no significant differences among means within a column.
‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 11. Total root length of eight bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in a polyethylene glycol (PEG) solution of -1.07 MPa. Roots are divided into 5 classes based upon root diameter.

Genotypes	100 seed wt.(g)	Total root Lth§	Class1 (0.2)‡	Class2 (0.5)	Class3 (0.9)	Class4 (1.4)	Class5 (2.1)
Sierra	40.35 a*	9.6 ns	4.3 ns	4.3 ns	0.96 ns	0.10 ns	0.01 ns
T3147-2	38.46 ab	9.0	3.6	4.5	0.72	0.09	0.02
8-42-M-2	35.46 c	8.3	3.0	4.3	0.91	0.12	0.04
Lef-2-RB	32.39 d	10.9	4.7	5.3	0.81	0.08	0.02
T3110-2	37.28 bc	7.6	2.6	4.1	0.76	0.09	0.03
T3008-1	39.50 a	8.8	3.2	4.5	0.85	0.10	0.02
T3016-1	36.14 c	11.1	4.4	5.6	0.93	0.13	0.03
BAT 477	28.00 e	8.1	3.6	3.8	0.64	0.08	0.02
C.V.	6	44	53	42	45	49	89

* Different letters indicate significant difference among means within a column at $P \leq 0.05$ according to DMRT.

ns Indicate no significant difference among means within a column.

§,‡ Indicates root length in meters and diameter of each root class in millimeters, respectively.

length of classes 4 and 5 was equal to that of plants grown in -0.52 MPa, less than that of ABA-treated plants, and greater than that of control plants (Table 6). BAT 477 had a greater percentage of its roots as class 1 roots than did 8-42-M-2, T3110-2, and T3008-1 (Table 12). The reverse was true for class 2 roots. BAT 477 had a greater percentage of its roots in classes 1 + 2 than did 8-42-M-2 while the reverse was true for classes 2 + 3 (Table 12). The resistant genotypes, Sierra and T3147-2, did not differ from 8-42-M-2 with regard to classes 1 + 2 and classes 2 + 3. Percentage distribution in individual root classes did not correspond with seed size.

The percentage of total root length in class 1 was equal to that of the ABA-treated plants and greater than that of the other two treatments. Percentage of total roots in class 2 was less than that of control plants and plants grown in -0.52 MPa PEG treatment (Table 8). The percentage of total root length in classes 1 and 2 was higher than that of any other treatment. While not identical, the distribution of roots in classes 1 through 5 and the total root length of plants grown in -1.07 MPa was more similar to that of plants grown in ABA than to plants in any of the other experiments. Class 1 root growth was stimulated by ABA and by both PEG concentrations (Table 8). No work in the literature was found comparing the effects of ABA and PEG on root length, but the data concur with previous work indicating that ABA increased root growth (Robertson et al., 1990).

Table 12. Percentage of roots from individual root classes of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d in a polyethylene glycol (PEG 600) solution of -1.07 MPa at 23/20°C day/night temperatures and a 15 h photoperiod.

Genotypes	Class1‡	Class2	Class3	Class4	Class5	Classes1+2	Classes1+2+3	Classes2+3
	%							
Sierra	43 ab**	45 c*	11 a*	1.20 ns	0.20 ns	88 bc*	99 ns	56 bc**
T3147-2	40 abc	49 abc	9 abc	1.20	0.20	89 abc	98	58 abc
8-42-M-2	35 bc	51 a	11 a	1.40	0.60	86 c	97	62 ab
Lef-2-RB	42 ab	49 abc	7 c	0.80	0.20	92 a	99	56 bc
T3110-2	33 c	54 a	11 a	1.20	0.50	87 bc	98	65 a
T3008-1	35 bc	53 a	10 abc	1.30	0.20	88 abc	98	63 ab
T3016-1	41 abc	50 ab	8 bc	1.10	0.30	91 ab	99	58 abc
BAT 477	45 a	46 bc	8 bc	1.20	0.40	91 ab	99	54 c

**, * Different letters indicate significant difference among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

ns Indicate no significant differences among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Ratios

Since there were distinct differences among experiments with regard to percentage of roots as primary or secondary roots, this raised a question about the existence of a pattern between primary and secondary roots among genotypes and across treatments. A number of possible ratios of primary to secondary roots were calculated and analyzed to determine if there was a pattern among the genotypes or across the four experiments (Table 13). Ratios were reported based on genotypic significance and a relatively low coefficient of variation. Several ratios had significant genotypic differences in both the ABA and -1.07 MPa experiments. These primarily involved the ratio of class 1 roots to other root classes and reflect the stimulatory effect that both ABA and -1.07 MPa PEG had on class 1 roots. Root ratios did not correspond with seed weight among the medium-sized seeds in this study.

Control ratios

No ratio distinguished between resistant and susceptible genotypes. BAT 477 did not differ from T3110-2, T3008-1, or T3016-1 in any of the ratios (Table 14).

ABA ratios

As with the ratios from the control experiment, none of the ABA ratios distinguished between resistant and susceptible genotypes. There was greater

Table 13. Various ratios of different root classes in plants grown in the growth chamber in control, ABA or PEG 600 (-0.52 or -1.07 MPa) solutions.

Ratios‡	Control	ABA	-0.52 MPa	-1.07 MPa
½	ns	*(26)	ns	*(23)
1/3	†(41)	ns	ns	**(37)
1/4	**(72)	**(66)	ns	ns
½+3	ns	**(29)	ns	**(24)
1/3+4	*(42)	ns	ns	**(38)
1/3+5	†(41)	ns	ns	**(38)
1/4+5	**(73)	ns	ns	**(38)
½+3+4	ns	**(29)	ns	**(24)
½+3+4+5	ns	**(29)	ns	**(25)
1+2/3+4	†(29)	ns	ns	*(31)
1+2/3+5	ns	ns	†(48)	*(31)
1+2/4+5	**(69)	ns	ns	ns
1+2+3/4+5	ns	*(58)	ns	ns
2/3	ns	ns	*(38)	*(28)
2/4	**(71)	*(54)	ns	ns
2/3+4	ns	ns	*(39)	ns
2/3+5	ns	ns	*(35)	†(28)
2/4+5	**(70)	ns	ns	ns
2/3+4+5	ns	ns	*(40)	ns

**, *, † Indicates significance at P ≤ 0.01, 0.05, and 0.10, respectively among means, according to DMRT. Number in parentheses is coefficient of variation.

ns Indicate no significant differences.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 14. Ratios of root classes that had significant genotypic differences in the control experiment of seedlings grown in growth pouches in a hydroponic solution that contained deionized water or half strength Hoagland's nutrient solution.

Genotypes	(1)/(3)‡	(1)/(4)	(1)/(3+4)	(1)/(3+5)	(1)/(4+5)
Sierra	0.49 bc†	11 bcd*	0.47 abc*	0.49 bc†	11 bc*
T3147-2	0.63 ab	18 abc	0.60 ab	0.63 ab	18 ab
8-42-M-2	0.71 a	22 ab	0.68 a	0.71 a	21 a
Lef-2-RB	0.63 ab	26 a	0.61 ab	0.63 ab	25 a
T3110-2	0.43 bc	8 cd	0.41 bc	0.43 bc	8 bc
T3008-1	0.40 c	6 d	0.34 c	0.36 c	6 c
T3016-1	0.50 bc	8 cd	0.46 abc	0.50 bc	8 bc
BAT 477	0.53 abc	11 bcd	0.51 abc	0.53 abc	11 bc
C.V.	41	72	42	41	73

Genotypes	(1+2)/(3+4)‡	(1+2)/(4+5)	(2)/(4)	(2)/(4+5)
Sierra	2.4 b†	0.63 ab**	52 bc*	52 ab
T3147-2	3.2 a	0.97 ab	81 ab	79 ab
8-42-M-2	2.7 ab	0.87 ab	66 abc	65 ab
Lef-2-RB	3.1 a	1.27 a	107 a	102 a
T3110-2	2.1 b	0.43 b	37 c	25 b
T3008-1	2.5 b	0.33 b	28 c	27 b
T3016-1	2.5 b	0.41 b	35 c	33 b
BAT 477	2.4 b	0.52 b	42 bc	41 b
C.V.	29	69	70	70

**, *, + Different letters indicate significant difference among means within a column at $P \leq 0.01$, 0.05, and 0.10, respectively, according to DMRT.

‡ Indicate root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively.

than a 10-fold ratio between secondary to primary roots (classes 1+2/classes 4 + 5) (Table 15 and 16).

-0.52 MPa ratios

Several of the ratios did separate T3147-2 from 8-42-M-2, but none separated 8-42-M-2 from BAT 477 (Table 17). Generally, T3147-2 and BAT 477 did not differ from each other and Sierra and BAT 477 did not differ (Table 17). There were no significant genotypic difference between susceptible and resistant genotypes with the ratios that produced significant genotypic differences in the control experiment, but there was a consistent pattern to the ratios of secondary to primary roots in which T3147-2 > BAT 477 > 8-42-M-2 (Table 18). Sierra was somewhat similar to BAT 477.

-1.07 MPa Ratios

Unlike root length (RL) in the -1.07 MPa experiment, the ratios exhibited significant genotypic differences (Table 19 and 20). The resistant genotypes T3147-2 and BAT 477 did not differ for any of the ratios with class 1 in the numerator while BAT 477 consistently had a higher ratio than the susceptible check 8-42-M-2. These ratios compared class 1 roots to other roots and illustrate the greater proportion of class 1 (fine) roots to other roots in the -1.07 MPa PEG experiment. The data suggest that such a ratio is indicative of a resistant genotype. Nevertheless, Sierra, the other genotype designated as

Table 15. Table of all ratios from ABA experiment that had genotypic significance.

Genotypes	(1)/(2)‡	(1)/(4)	(2)/(4)	(1)/(2+3)
Sierra	0.93 ab*	16 c*	17 c*	0.71 ab*
T3147-2	1.13 a	48 ab	41 ab	1.00 a
8-42-M-2	0.90 abc	31 abc	33 abc	0.75 ab
Lef-2-RB	0.97 ab	52 a	49 a	0.83 ab
T3110-2	0.66 c	18 c	25 bc	0.51 c
T3008-1	0.78 bc	28 bc	35 abc	0.63 bc
T3016-1	0.86 bc	31 abc	36 abc	0.71 ab
BAT 477	1.03 ab	22 c	22 bc	0.84 ab
C.V.	26	66	54	29

Genotypes	(1)/(2+3+4)‡	(1)/(2+3+4+5)	(1+2+3)/(4+5)
Sierra	0.66 ab**	0.65 bc*	32 b**
T3147-2	0.93 a	0.93 a	78 ab
8-42-M-2	0.73 ab	0.73 ab	58 ab
Lef-2-RB	0.81 ab	0.81 ab	88 a
T3110-2	0.50 b	0.49 c	38 b
T3008-1	0.62 ab	0.61 bc	46 ab
T3016-1	0.68 ab	0.67 bc	62 ab
BAT 477	0.80 ab	0.78 ab	39 b
C.V.	29	29	58

**, * Different letters indicate significance among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 16. Ratios from the ABA experiment that correspond to the control experiment ratios that had genotypic significance.

Genotypes	(1+2)/(3+4)‡	(1+2)/(4+5)	(1)/(3+4)	(1)/(3+5)	(1)/(3)
Sierra	5 ns	28 c*	3 ns	3 ns	3 ns
T3147-2	11	72 ab	8	6	7
8-42-M-2	8	52 abc	4	4	5
Lef-2-RB	11	81 a	5	6	6
T3110-2	5	33 c	2	2	3
T3008-1	12	41 bc	5	5	7
T3016-1	8	56 abc	4	4	5
BAT 477	7	35 c	4	4	5
C.V.	78	60	77	64	91

* Different letters indicate significant difference among means within a column at $P \leq 0.05$ according to DMRT.

ns Indicate no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 17. Table of ratios from polyethylene glycol (-0.52 MPa) experiment that have genotypic significance.

Genotypes	(2)/(3+5)‡	(2)/(3)	(2)/(3+4+5)	(1+2)/(3+5)	(2)/(3+4)
Sierra	3.14 bc*	3.28 b*	2.82 abc*	5.23 b†	2.92 abc*
T3147-2	4.91 a	5.24 a	4.17 ab	9.00 a	4.36 a
8-42-M-2	3.08 bc	3.22 b	2.63 bc	4.55 b	2.73 bc
Lef-2-RB	4.63 ab	5.01 ab	3.92 abc	7.55 ab	4.20 ab
T3110-2	3.95 abc	4.23 ab	3.27 abc	6.23 ab	3.42 abc
T3008-1	2.87 c	3.25 b	2.36 c	4.89 b	2.59 c
T3016-1	4.71 ab	4.90 ab	4.24 a	7.44 ab	4.38 a
BAT 477	4.34 abc	4.52 ab	3.77 abc	7.40 ab	3.89 abc
C.V.	38	38	40	48	39

*, † Different letters indicates significant difference among means within a column at $P \leq 0.05$ and 0.10, respectively, according to DMRT.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 18. Ratios from the -0.52 MPa PEG experiment that correspond to the control experiment ratios that had genotypic significance.

Genotypes	(1+2)/(3+4)‡	(1+2)/(4+5)	(1)/(3+4)	(1)/(3+5)	(1)/(3)
Sierra	4.86 ns	53.10 ns	1.96 ns	2.08 ns	2.15 ns
T3147-2	8.02	62.83	3.66	4.10	4.37
8-42-M-2	4.03	22.75	1.30	1.47	1.54
Lef-2-RB	6.96	32.61	2.76	2.29	3.30
T3110-2	5.40	40.20	1.98	2.27	2.43
T3008-1	4.42	21.51	1.83	2.02	2.26
T3016-1	6.94	57.39	2.56	2.73	2.86
BAT 477	6.63	47.05	2.74	3.05	3.17
C.V.	51	74	74	69	72

ns Indicate no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 19. Table of all ratios from polyethylene glycol (-1.07 MPa) experiment that have genotypic significance.

Genotypes	(1+2)/(3+5)‡	(1+2)/(3+4)	(1)/(3+5)	(1)/(2+3+4+5)	(1)/(3+4)	(2)/(3+5)
Sierra	8.8 bc*	8.1 bc*	4.42 ab**	0.79 ab**	4.1 ab**	4.0 d†
T3147-2	10.9 abc	10.0 abc	5.00 ab	0.69 abc	4.5 ab	5.4 abc
8-42-M-2	8.00 c	7.2 c	3.30 b	0.55 bc	3.0 b	4.3 cd
Lef-2-RB	12.6 a	11.8 a	5.80 ab	0.74 abc	5.4 a	6.4 a
T3110-2	8.8 bc	8.3 bc	3.50 ab	0.51 c	3.2 ab	5.0 abcd
T3008-1	8.9 bc	8.1 bc	3.53 ab	0.55 bc	3.2 ab	4.8 bcd
T3016-1	11.8 ab	10.7 ab	5.44 ab	0.70 abc	4.9 ab	5.8 ab
BAT 477	11.9 ab	10.8 ab	6.10 a	0.83 a	5.5 a	5.3 abcd
C.V.	31	31	38	25	38	28

**, *, † Different letters indicate significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 19. continued.

Genotypes	(1)/(2)‡	(2)/(3)	(1)/(3)	(1)/(3+4)	(1)/(2+3+4)	(1)/(2+3)
Sierra	0.99 a*	4.5 c*	4.5 ab**	0.80 ab**	0.79 ab**	0.80 ab**
T3147-2	0.83 ab	6.1 abc	5.1 ab	0.70 abc	0.69 abc	0.70 abc
8-42-M-2	0.69 bc	4.9 bc	3.4 b	0.57 bc	0.55 bc	0.57 bc
Lef-2-RB	0.87 ab	7.0 a	6.0 ab	0.76 abc	0.75 abc	0.76 abc
T3110-2	0.62 c	5.6 abc	3.6 b	0.52 c	0.51 c	0.52 c
T3008-1	0.67 bc	5.4 abc	3.6 b	0.57 bc	0.56 bc	0.57 bc
T3016-1	0.82 abc	6.6 ab	5.6 ab	0.72 abc	0.70 abc	0.72 abc
BAT 477	1.00 a	6.1 abc	6.4 a	0.86 a	0.84 a	0.86 a
C.V.	23	28	37	24	24	24

**, * Different letters indicate significant difference among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 20. Ratios from the -1.07 MPa PEG experiment that correspond to the control experiment ratios that had genotypic significance.

Genotypes	(1+2)/(3+4)‡	(1+2)/(4+5)	(1)/(3+4)	(1)/(3+5)	(1)/(3)
Sierra	8.09 bc*	105.31 ns	0.80 ab**	4.42 ab**	4.50 ab**
T3147-2	10.01 abc	98.70	0.70 abc	5.00 ab	5.10 ab
8-42-M-2	7.24 c	50.13	0.57 bc	3.30 b	3.40 b
Lef-2-RB	11.80 a	106.21	0.77 abc	5.80 ab	6.00 ab
T3110-2	8.26 bc	72.44	0.52 c	3.50 ab	3.61 b
T3008-1	8.06 bc	72.56	0.57 bc	3.54 ab	3.62 b
T3016-1	10.72 ab	79.66	0.72 abc	5.44 ab	5.60 ab
BAT 477	10.30 ab	91.10	0.86 a	6.10 a	6.37 a
C.V.	31	62	24	38	37

**, * Different letters indicate significant difference among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

ns Indicate no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

resistant, usually did not differ from 8-42-M-2.

Deltas values

ABA Deltas

The greatest numerical increase of ABA-treated plants over control plants for all genotypes occurred with class 1 roots followed by class 2 roots (Table 21). Class 2 roots in Sierra increased less than class 2 roots of 8-42-M-2 and Lef-2-RB. BAT 477 was in the group of genotypes with the lowest increase in root length of class 1 and class 3 roots, although its class 2 roots did not differ from the group of genotypes with the greatest increase in root length (Table 21). The increase in total root length of BAT 477 with ABA was intermediate to that of the other genotypes, with T3147-2 and 8-42-M-2 at the high and Sierra at the low end.

-0.52 MPa PEG Deltas

The PEG concentration of -0.52 MPa increased total root length of all genotypes except T3008-1, which decreased (Table 22). The increase in total root length in T3147-2 and BAT 477 was significantly greater than that of all other genotypes (Table 22). With the -0.52 MPa treatment, T3008-1 decreased its root length in comparison to the control for roots in classes 2, 3, and 4 (Table 22). There was a decrease in class 3 roots in all genotypes except 8-42-M-2 and BAT 477(Table 22), where 8-42-M-2 maintained its class 3 RL and BAT 477

Table 21. Mean difference between ABA and control (delta) for each root class. All numbers represents ABA experiment individual root classes minus the appropriate root class from the control treatment.

Genotypes	Total root	Class1‡	Class2	Class3§	Class4	Class5
Sierra	4.23 b*	2.73 d*	1.35 b**	-0.07 c†	0.15 ns	0.05 ns
T3147-2	11.60 a	6.72 a	4.35 ab	0.34 abc	0.14	0.05
8-42-M-2	11.60 a	5.44 abc	5.20 a	0.72 a	0.20	0.05
Lef-2-RB	12.00 a	5.87 ab	5.30 a	0.70 a	0.20	0.05
T3110-2	5.85 b	2.82 d	2.64 ab	0.20 abc	0.12	0.07
T3008-1	5.21 b	2.71 d	2.22 ab	0.11 bc	0.10	0.05
T3016-1	7.62 ab	4.07 bcd	3.31 ab	0.12 bc	0.10	0.03
BAT 477	7.05 ab	3.43 cd	3.00 ab	0.50 bc	0.15	0.07
C.V.	55	51	60	10	72	80

**, *, † Different letters indicate significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicate no significant difference among means within a column.

§ Level of statistical significance obtained after transformation of data using a logarithmic scale ($\Delta^{1.2}$).

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 22. Polyethylene glycol (-0.52 MPa) delta conversions. All numbers represents polyethylene glycol (0.52 MPa) experiment individual root classes minus the appropriate root class from the control treatment.

Genotypes	Total root§	‡Class1§	Class2§	Class3§	Class4§	Class5
Sierra	2.81 b*	1.69 ab*	1.17 ab*	-0.17 abc*	0.05 ab*	0.03 ns
T3147-2	4.14 a	2.64 a	1.55 a	-0.24 bc	0.04 ab	0.02
8-42-M-2	1.79 b	0.71 ab	0.91 ab	0.03 ab	0.11 a	0.03
Lef-2-RB	0.28 b	0.50 b	0.01 b	-0.26 bc	0.05 ab	0.03
T3110-2	0.68 b	0.72 ab	0.28 ab	-0.40 bc	0.05 ab	0.02
T3008-1	-1.42 b	0.19 b	-0.96 b	-0.69 c	-0.01 b	0.02
T3016-1	1.70 b	1.15 ab	0.90 ab	-0.37 bc	-0.002 b	0.02
BAT 477	4.96 a	2.11 a	2.43 a	0.30 a	0.09 a	0.03
C.V.	133	43	9	9	1.2	87

* Different letters indicates significant difference among means within a column at $P \leq 0.05$ according to DMRT.

§ Level of statistical significance obtained after transformation of data using a logarithmic scale.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

increased.

-1.07 MPa PEG Deltas

There were no significant genotypic differences in the increase over the control in total root length or in root classes when plants were grown in -1.07 MPa PEG (Table 23). Five of the 8 genotypes had a decrease in class 3 roots when plants were grown in -1.07 MPa PEG (Table 23).

Polyvinyl-chloride Experiment 1.

Significant genotypic differences were only observed in root class 1 and total root length (Table 24) for the 1 to 15.2 cm depth. In total root length and root class 1, T3147-2 had a significantly higher root length ($P \leq 0.10$) than the other three genotypes. The stress treatment had a significantly lower ($P \leq 0.001$) root length of class 3 roots than the non-stress treatment and the same was true for class 5 ($P \leq 0.10$) roots (Table 25).

In the 15.3 to 30.5 cm depth, significant genotypic differences occurred for total root length and for root classes 2, 3, and 5 (Table 24). In root classes 2 and 3, T3147-2 had a significantly higher ($P \leq 0.05$ and 0.01, respectively) root length than 8-42-M-2 but was not significantly higher than Sierra and T3008-1. For class 5, T3147-2 had a significantly higher ($P \leq 0.01$) root length than Sierra and 8-42-M-2 (Table 24). For total root length 8-42-M-2 had a significantly lower ($P \leq 0.10$) root length than Sierra and T3147-2 but was not significantly different

Table 23. Polyethylene glycol (-1.07 MPa) delta conversions. All numbers represents polyethylene glycol (-1.07 MPa) experiment individual root classes minus the representative root class from the control treatment.

Genotypes	Total root	Class1‡	Class2	Class3	Class4	Class5
Sierra	6.07 ns	3.71 ns	2.32 ns	-0.04 ns	0.04 ns	0.01 ns
T3147-2	5.50	3.11	2.46	-0.13	0.05	0.02
8-42-M-2	5.64	2.47	2.83	0.25	0.09	0.04
Lef-2-RB	8.22	4.30	3.70	0.18	0.06	0.02
T3110-2	4.74	2.21	2.54	-0.06	0.04	0.02
T3008-1	5.54	2.82	2.80	-0.14	0.03	0.02
T3016-1	7.52	3.86	3.60	-0.03	0.06	0.03
BAT 477	6.16	3.30	2.67	0.12	0.06	0.02
C.V.	65	60	69	8	89	95

ns Indicate no significance difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 24. Total root length of four common bean genotypes grown in 0.7 m PVC tubes of 30 cm diameter in a greenhouse for 40 d at 28^{0}C ± 2 day/night temperatures and a 15 h photoperiod in stress and non-stress conditions. PVC Experiment 1.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡	Class2	Class3	Class4	Class5
				1-15.2 cm			
Sierra	40.35 a*	37.5 b†	21.8 b†	12.5 ns	2.6 ns	0.4 ns	0.05 ns
T3008-1	39.50 a	37.2 b	23.0 b	11.5	2.3	0.3	0.04
T3147-2	38.46 a	46.5 a	29.4 a	14.2	2.5	0.3	0.04
8-42-M-2	35.46 b	32.9 b	20.1 b	10.0	2.0	0.7	0.06
				15.24-30.5 cm			
Sierra	40.35 a*	55.2 a†	30.7 ns	20.9 a*	3.3 a**	0.2 ns	0.03 b**
T3008-1	39.50 a	45.7 ab	28.2	15.1 ab	2.2 ab	0.2	0.05 ab
T3147-2	38.46 a	51.3 a	28.6	19.2 a	3.1 a	0.3	0.09 a
8-42-M-2	35.46 b	32.0 b	21.2	9.60 b	1.1 b	0.1	0.03 b

Table 24. Continued.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡	Class2	Class3	Class4	Class5
			30.5-45.7 cm				
Sierra	40.35 a*	54.4 a†	27.0 ns	23.6 a**	3.6 a**	0.2 ns	0.06 ab†
T3008-1	39.50 a	49.3 a	27.7	18.8 ab	2.6 ab	0.1	0.07 a
T3147-2	38.46 a	50.8 a	25.9	21.3 a	3.4 a	0.2	0.07 a
8-42-M-2	35.46 b	25.9 b	16.3	8.57 b	1.0 b	0.1	0.03 b
			45.8-61.0 cm				
Sierra	40.35 a*	57.8 ns	28.6 ns	25.1 ns	3.8 a**	0.2 ns	0.10 a*
T3008-1	39.50 a	47.4	23.5	20.7	3.0 ab	0.2	0.03 b
T3147-2	38.46 a	36.3	18.0	15.4	2.6 ab	0.1	0.03 b
8-42-M-2	35.46 b	29.3	15.6	12.4	1.2 b	0.1	0.09 a

Table 24. Continued.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡	Class2	Class3	Class4	Class5
				61.0-76.2 cm			
Sierra	40.35 a*	2.6 ns	1.0 ns	1.2 ns	0.4 ns	0.02 ns	0.00 ns
T3008-1	39.50 a	2.2	0.8	1.1	0.3	0.02	0.01
T3147-2	38.46 a	6.4	2.7	2.9	0.7	0.10	0.01
8-42-M-2	35.46 b	3.5	1.6	1.6	0.3	0.01	0.00

**, *, † Different letters indicate significant difference among means within acolumn at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

§ Indicate root length in meters.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 25. Statistical analysis of root growth under stress and non-stress conditions of the PVC 1 experiment. Data presented for actual root length in each class and for percentage of total root length in each class.

Classes	"A"	"B"	"C"	"D"	"E"	Total
			RL			
Class 1	ns	ns	S > N*	ns	ns	S > N†
Class 2	ns	ns	S > N*	ns	ns	S > N†
Class 3	S < N***	ns	ns	ns	ns	ns
Class 4	ns	ns	ns	ns	ns	ns
Class 5	S < N†	ns	ns	ns	ns	ns
Total	ns	ns	S > N**	ns	ns	S > N†
Root dw	ns	ns	S > N*	S > N†	ns	ns
			Percentages			
Class 1	S > N*	ns	ns	ns	ns	ns
Class 2	S < N*	ns	ns	ns	ns	ns
Class 3	ns	S < N†	S < N*	ns	ns	S < N†
Class 4	ns	ns	ns	ns	ns	S < N†
Class 5	ns	ns	ns	ns	ns	ns
Class1+2	S > N†	ns	S > N*	ns	ns	S > N†
Class2+3	S < N**	ns	S < N†	ns	ns	S < N*

***, **, *, † Indicates significant difference at P ≤ 0.001, 0.01, 0.05, and 0.10, respectively.

ns Indicate non significant data.

S = Stress treatment, N= Non-stress treatment, RL = root length

Depth "A" =1-15.2 cm, "B" = 15.3-30.5 cm, "C" = 30.6-45.7 cm, "D" = 45.8-61 cm, "E" = 61.1-76.2 cm.

from T3008-1 (Table 24). Moisture status had no affect on root length for roots at the 15.2 to 30.5 cm depth (Table 25).

Significant genotypic differences were observed for total root length and for root classes 2, 3, and 5 at a depth of 30.6 to 45.7 cm (Table 24). In root classes 2 and 3 ($P \leq 0.01$), 8-42-M-2 had a significantly lower root length than Sierra and T3147-2 (Table 24). Class 5 root length of 8-42-M-2 was significantly lower ($P \leq 0.10$) than that of T3008-1 and T3147-2 (Table 24). Total root length of 8-42-M-2 was significantly lower ($P \leq 0.10$) than that of the other three genotypes (Table 24). At this depth, root length of class 1 and class 2 roots was significantly higher ($P \leq 0.05$) under the stress treatment than under the non-stress treatment (Table 25). The same was true for total root length ($P \leq 0.01$) and root dry weight at this depth (Table 25).

At a depth of 45.8 to 61 cm, the only significant genotypic differences occurred in root classes 3 and 5 (Table 24). In root class 3, 8-42- M-2 had a significantly lower ($P \leq 0.01$) root length than Sierra but did not differ from T3008-1 and T3147-2 (Table 24). However, in root class 5, 8-42-M-2 and Sierra were significantly higher ($P \leq 0.05$) than T3008-1 and T3147-2 (Table 24). Root dry weight at this depth was significantly greater ($P \leq 0.10$) under stress (Table 25).

There were no significant genotypic differences in total root length or in any of the five root classes for depth 61.1 to 76.2 cm (Table 24), and moisture stress did not affect root length at this depth (Table 25).

Across the five depths, genotypic differences occurred for total root length

and for root classes 2 and 3 (Table 26). The genotype 8-42-M-2 had a significantly lower total root length and lower class 2 root length ($P \leq 0.05$) than the other three genotypes (Table 26). In class 3, 8-42-M-2 was significantly lower ($P \leq 0.01$) than Sierra and T3147-2 (Table 26). The genotype 8-42-M-2 had a significantly lower seed weight than the other genotypes, suggesting that TRL corresponded to seed weight (Table 26). Across all depths, stress increased ($P \leq 0.10$) total root length and root length in classes 1 and 2 (Table 25).

No significant genotypic differences existed for percentages of root length in any of the root classes at depth 1 to 15.2 cm (Table 27), but 58 to 61% of all roots at this depth were class 1 roots and 31 to 33% were class 2 roots (Table 27). At this depth, the stress treatment had a greater percentage ($P \leq 0.05$) of total roots as class 1 roots than the non-stress treatment and the reverse ($P \leq 0.05$) was true for class 2 roots. The percentage of class 1 plus class 2 roots was greater ($P \leq 0.10$) under stress (Table 25).

For the 15.3 to 30.5 cm depth, significant genotypic differences were observed for percentage of total roots in classes 1, 2, and 3 and in classes 1 + 2 and classes 2 + 3 (Table 27). Root classes 1 + 2 comprised 93 to 96% of the total root length (Table 27). The genotype 8-42-M-2 had a significantly higher ($P \leq 0.05$) percentage of total roots in class 1 than Sierra and T3147-2 (Table 27), but a lower percentage of roots in classes 2 and 3 than Sierra and T3147-2. Consequently, 8-42-M-2 had a significantly higher percentage ($P \leq 0.05$) of total roots in classes 1 + 2 than Sierra and T3147-2 and a significantly lower

Table 26. Cumulative total root length of four common bean genotypes grown in 0.7 m PVC tubes of 30 cm diameter in a greenhouse for 40 d at 28^{0}C±2 day/night temperatures and a 15 h photoperiod in a stress and non-stress treatment. PVC Experiment 1.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡	Class2	Class3	Class4	Class5
Sierra	40.35 a*	207.46 a†	109.25 ns	83.31 a*	13.64 a**	1.02 ns	0.24 ns
T3008-1	39.50 a	181.73 a	103.12	67.21 a	10.35 ab	0.86	0.20
T3147-2	38.46 a	191.21 a	104.61	73.10 a	12.30 a	1.01	0.24
8-42-M-2	35.46 b	123.57 b	74.77	42.14 b	5.50 b	0.97	0.21

**, *, † Different letters indicate significant differences among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

§ Indicates root length in meters.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 27. Percentage of root length for individual sections of four common bean genotypes grown in 0.7 m PVC tubes of 30 cm diameter in a greenhouse for 40 d at 28°C ± 2 day/night temperatures and a 15 h photoperiod in stress and non-stress conditions. Experiment 1.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
	1-15.2 cm								
Sierra	40.35 a*	58 ns	33 ns	7 ns	1 ns	0.40 ns	92 ns	99 ns	40 ns
T3008-1	39.50 a	61	31	7	1	0.11	92	99	38
T3147-2	38.46 a	63	31	5	1	0.10	94	99	36
8-42-M-2	35.46 b	61	31	6	2	0.21	92	98	37
	15.2-30.5 cm								
Sierra	40.35 a*	56 b*	37 a*	6.1 a**	0.40 ns	0.09 ns	93 b*	99.5 ns	43.1 a*
T3008-1	39.50 a	60 ab	34 ab	5.0 ab	0.50	0.10	94 ab	99.0	39.2 ab
T3147-2	38.46 a	54 b	38 a	6.5 a	0.60	0.20	93 b	99.0	45.0 a
8-42-M-2	35.46 b	65 a	31 b	3.4 b	0.30	0.10	96 a	99.5	34.5 b

Table 27. Continued.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
	30.5-45.7 cm								
Sierra	40.35 a*	50 b**	44 a**	7 a*	0.33 ns	0.12 ns	93 b*	99.5 ns	50 a**
T3008-1	39.50 a	54 b	40 a	6 a	0.22	0.20	94 b	99.6	46 a
T3147-2	38.46 a	50 b	42 a	7 a	0.41	0.14	92 b	99.5	49 a
8-42-M-2	35.46 b	63 a	33 b	4 b	0.30	0.14	96 a	99.6	36 b
	45.7-61.0 cm								
Sierra	40.35 a*	45 b†	47 ns	8 a*	0.30 ns	0.163 b**	92 b*	99.5 ns	54 a†
T3008-1	39.50 a	48 ab	45	7 a	0.30	0.059 b	92 b	99.6	52 a
T3147-2	38.46 a	49 ab	43	7 a	0.44	0.093 b	92 b	99.5	50 ab
8-42-M-2	35.46 b	52 a	43	5 b	0.22	0.467 a	95 a	99.3	48 b

Table 27. Continued.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
	61.0-76.2 cm								
Sierra	40.35 a*	20 ns	22 ns	7 ns	0.30 ns	0.0 ns	44 ns	51 ns	29 ns
T3008-1	39.50 a	14	18	5	0.38	0.2	32	37	23
T3147-2	38.46 a	30	42	13	1.91	0.2	72	85	55
8-42-M-2	35.46 b	33	34	8	0.39	0.0	67	75	42

**, *, † Different letters indicate significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

percentage ($P \leq 0.05$ and 0.01, respectively) of total roots in classes 2 + 3 than Sierra and T3147-2 (Table 27). Percentage distribution among root classes did not correspond to genotypic seed weight. Stress decreased the percentage of total roots in class 3 ($P \leq 0.10$) (Table 25).

For depth 30.6 to 45.7 cm, percentage of roots in class 1 ranged from 50 to 63% with 8-42-M-2 having a significantly higher ($P \leq 0.01$) percentage than the other three genotypes (Table 27), corresponding with the lower seed weight of 8-42-M-2 in comparison with the other three genotypes. Percentage of total roots as class 2 ranged from 33 to 44%, with 8-42-M-2 having a significantly lower ($P \leq 0.01$) percentage than the other three genotypes (Table 27). Root classes 1 + 2 comprised 92 to 96% of the total root length and was significantly higher for 8-42-M-2 than for the other three genotypes (Table 27). Root classes 1 through 3 comprised 99% of all roots.

Percentage of total roots in Class 1 at the 45.8 to 61 cm depth ranged from 45 to 52% with 8-42-M-2 having a significantly higher ($P \leq 0.10$) percentage than Sierra. The genotype 8-42-M-2 had a significantly lower percentage ($P \leq 0.01$) of total roots in classes 2+3 at this depth than all other genotypes except T3147-2 (Table 27). However, the greater percentage of class 1 roots in 8-42-M-2 was such that 8-42-M-2 had a higher percentage of roots in classes 1+2 ($P \leq 0.05$) than the other three genotypes (Table 25), again corresponding with the lower seed weight of 8-42-M-2 in comparison to the other three genotypes.

At a depth of 61.1 to 76 cm, only 14 to 33% of the total roots were class 1 roots and root classes 1+2 only comprised 32 to 67% of all roots (Table 27).

There were no genotypic differences.

When data for all depths of the 0.7 m PVC column were combined, 8-42-M-2 had a higher ($P \leq 0.05$) percentage of its roots in classes 1 and 5 than the other three genotypes and a lower percentage ($P \leq 0.05$) in classes 2 and 3 (Table 28). Consequently, 8-42-M-2 had the highest percentage of roots in classes 1+2 and the lowest in classes 2+3.

Stress increased ($P \leq 0.10$) the percentage of total root length in classes 1+2 and decreased ($P \leq 0.10$) the percentage in classes 3 and 4 (Table 25). In the pouch experiments, ABA and PEG increased total root length and percentage of roots in class 1 during these treatments, which were designed to simulate moisture stress, and also decreased the percentage of class 2 roots, yet had a greater percentage of all roots in classes 1+2. In PVC Experiment 1, moisture stress did exactly that in the top 15 cm of the soil profile. Furthermore, stress increased ($P \leq 0.05$) the percentage of class 1+2 roots in the 30.5 to 45.7 cm soil depth and when all soil depths were combined (Table 25). With regard to actual root length, stress increased RL in root classes 1 and 2 and total root length ($P \leq 0.01$) at the 30.5 to 45.7 cm depth. The same was true for class 1, class 2, and total root length across all depths (Table 25).

The susceptible check, 8-42-M-2, had a greater root length of class 1 roots and of classes 1+2 than the other three genotypes. If stress increases the roots in classes 1+2, the data indicate that 8-42-M-2 was experiencing a greater degree of stress than the other three genotypes and this may be further evidence of its drought susceptibility in the severe moisture stress of PVC

Table 28. Percentages of roots in individual root classes when data was combined for all depths of a 0.7 m PVC tubes of 30 cm diameter for four common bean genotypes. Plants were grown in a greenhouse for 40 d at 28°C±2 day/night temperatures and a 15 h photoperiod in a stress and non-stress treatment. Experiment 1.

Genotypes	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
Sierra	52 b*	40 a*	7 a*	0.504 ns	0.121 b†	92 b†	99 ns	47 a**
T3008-1	55 b	38 a	6 a	0.472	0.107 b	93 b	99	44 ab
T3147-2	54 b	38 a	7 a	0.552	0.126 b	92 b	99	45 ab
8-42-M-2	61 a	34 b	4 b	0.642	0.192 a	95 a	99	38 b

**, *, † Different letters indicate significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Experiment 1. However, the data may simply reflect the lower seed weight of 8-42-M-2 in comparison with the other three genotypes, although all four are medium-sized seeds.

PVC Experiment 1 ratios

Root class ratios across all soil depths showed that 8-42-M-2 exceeded the other three genotypes with regards to ratio of class 1/Class 3, Class 1/classes 3+4, and classes 1+2/classes 3+4 (Table 29). This suggest that 8-42-M-2 had a greater proportion of its roots as the smaller secondary roots in comparison to the other three genotypes, again possibly suggesting that the genotype was experiencing stress and providing further evidence of the drought susceptibility of this genotype or simply reflecting the smaller seed weight of 8-42-M-2.

Polyvinyl-chloride experiment 2.

Rooting Pattern

None of the genotypes in PVC Experiment 2 had roots that reached deeper than 61 cm (Table 30). This experiment was conducted in greenhouse temperatures that were cooler than that of PVC Experiment 1. Thus, these plants experienced a milder moisture stress and that may have been reflected in the more shallow root growth of the plants in PVC Experiment 2 and in the different rooting patterns of PVC Experiment 1 and PVC Experiment 2.

Table 29. Ratios of total root length across all soil depths of PVC Experiment 1 and which correspond to the control experiment ratios (Pouch study) that had genotypic significance.

Genotypes	(1)/(3)‡	(1)/(3+4)	(1)/(3+5)	(1+2)/(3+4)	(1+2)/(4+5)	(1+2+3)/(4+5)
Sierra	8.1 b**	7.5 b**	8.0 b**	13.1 b**	154.9 ns	166.1 ns
T3008-1	9.6 b	8.9 b	9.4 b	14.8 b	169.5	180.8
T3147-2	9.3 b	8.8 b	9.1 b	14.5 b	183.5	194.7
8-42-M-2	15.8 a	14.4 a	15.1 a	22.1 a	189.4	196.7

** Different letters indicates significant difference among means within a column at $P \leq 0.01$ according tp DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 30. Percentage of total root length at each soil depth in two different experiments using 0.7 m PVC tubes. Plants in PVC Experiment 1 were planted in June 1996 and grown at 28 ± 2°C. Plants in PVC Experiment 2 were planted in September 1996 and grown at 25 ± 2°C.

Treatment	1 - 15.2 cm	15.3 - 30.5 cm	30.6 - 45.7 cm	45.8 - 61 cm	61.1 - 76.2 cm
	PVC Expt 1				
Stress	21 ns	23 b*	29 a*	26 ns	2 ns
Nonstress	26	29 a	22 b	20	3
	PVC Expt 2				
Stress	68 a†	25 b*	6 ns	1 ns	0
Nonstress	57 b	34 a	7	2	0

*, † Different letters indicate significant difference among means within a column at $P \leq 0.05$ and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

The total root length of PVC Experiment 1 was fairly evenly divided throughout the first four depths of the study, 1 - 61 cm (Table 30). Stress decreased ($P \leq 0.05$) the percentage of roots at the 15 to 30.5 cm depth and increased ($P \leq 0.05$) it at the 30.6 to 45.7 cm depth (Table 30). The moisture stress of PVC Experiment 1 was designated as severe due to fairly high temperature of 28 ± 2^0C and high intensity of sunlight during growth of plants from June 18 through July. Plants in the stress treatment received 53% less water than plants in the nonstress treatment. In contrast, total root length of PVC Experiment 2 was concentrated in the top two depths of the study, the first 30 cm (Table 30). As in PVC Experiment 1, stress decreased ($P \leq 0.05$) the percentage of roots at the 15 to 30.5 cm depth. It increased ($P \leq 0.10$) the percentage of roots in the top 15 cm (Table 30). The moisture stress of PVC Experiment 2 was designated as mild due to low temperatures of 25 ± 2^0C and lower sunlight intensity during plant growth from September 18 through October. Plants in the stress treatment received 53% less water than plants in the nonstress treatment. The same amount of total water was given to plants in both PVC experiments.

The resistant check, BAT 477, had a lower ($P \leq 0.10$) total root length than T-3110-2 in the top 15 cm (Table 31). Lef-2-RB and BAT 477 had a significantly lower ($P \leq 0.10$) root length of class 1 roots than T3110-2 and a significantly lower ($P \leq 0.10$) root length of class 3 roots than T3016-1 (Table 31). At this depth, stress significantly increased ($P \leq 0.01$) the percentage of class 1 roots, and significantly decreased the percentage of roots in class 2 ($P \leq 0.05$) and class 3 ($P \leq 0.10$) (Table 32). Stress increased ($P \leq 0.10$) the

Table 31. Total root length of four common bean genotypes grown in 0.7 m PVC tubes of 30 cm diameter in a greenhouse for 40 d at 25°C ± 2 day/night emperatures and a 15 h photoperiod in stress and non-stress conditions. PVC Experiment 2.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡	Class2	Class3	Class4	Class5
			1-15.2 cm				
T3016-1	36.14 a**	87.01 ab†	51.20 ab†	31.32 ns	4.04 a†	0.40 ns	0.08 ns
Lef-2-RB	32.39 b	84.80 ab	48.74 b	32.44	3.20 b	0.30	0.16
BAT 477	28.00 c	72.00 b	42.34 b	26.45	2.82 b	0.30	0.07
T3110-2	37.28 a	98.44 a	61.80 a	33.09	3.31 ab	0.24	0.05
			15.2-30.5 cm				
T3016-1	36.14 a**	45.10 ns	19.83 b†	21.31 ns	3.60 ns	0.30 ns	0.05 ns
Lef-2-RB	32.39 b	35.80	16.42 b	17.30	2.00	0.10	0.04
BAT 477	28.00 c	45.51	21.15 b	21.30	2.80	0.26	0.05
T3110-2	37.28 a	74.00	40.90 a	29.51	3.28	0.25	0.05

Table 31. Continued.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡	Class2	Class3	Class4	Class5
				30.5-45.7 cm			
T3016-1	36.14 a**	18.80 ns	8.82 ns	8.41 ns	1.43 ns	0.10 ns	0.03 ns
Lef-2-RB	32.39 b	3.84	1.60	2.00	0.34	0.01	0.00
BAT 477	28.00 c	8.11	4.03	3.61	0.42	0.04	0.01
T3110-2	37.28 a	24.20	12.05	10.70	1.30	0.14	0.04
				45.7-61.0 cm			
T3016-1	36.14 a**	3.96 ns	2.10 ns	1.64 ns	0.25 ns	0.01 ns	0.01 ns
Lef-2-RB	32.39 b	2.01	0.87	1.00	0.20	0.01	0.01
BAT 477	28.00 c	0.00	0.00	0.00	0.00	0.00	0.00
T3110-2	37.28 a	8.32	3.44	4.21	0.62	0.04	0.01

**, † Different letters indicates significant difference among means within a column at P ≤ 0.01 and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

§ Indicates root length in meters.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 32. Statistical analysis of root growth under stress and non-stress conditions of the PVC 2 experiment. Data presented for actual root length of each class and for percentage of total root length in each class.

Classes	"A"	"B"	"C"	"D"	"E"	Total
	RL					
Class1	ns	S > N†	ns	ns	ns	ns
Class2	ns	S > N†	ns	ns	ns	ns
Class3	S < N†	S < N†	ns	ns	ns	ns
Class4	ns	S < N†	ns	ns	ns	ns
Class5	ns	ns	ns	ns	ns	ns
Total	ns	S < N†	ns	ns	ns	ns
Root dw	ns	S < N†	ns	ns	ns	ns
	Percentages					
Class1	S > N**	ns	S < N†	ns	ns	S > N*
Class2	S < N*	ns	S < N†	ns	ns	S < N*
Class3	S < N†	S < N†	ns	ns	ns	S < N*
Class4	ns	ns	ns	ns	ns	S < N†
Class5	ns	ns	S < N*	ns	ns	ns
Class1+2	ns	S > N*	S < N†	ns	ns	S > N*
Class2+3	S < N**	ns	S < N†	ns	ns	S < N*

**, *, † Indicates significant difference at P ≤ 0.01, 0.05, and 0.10, respectively.

ns Indicate non significant data.

S= Stress treatment, N= Non-stress treatment, RL = root length

Depth "A" =1-15.2 cm, "B" = 15.3-30.5 cm, "C" = 30.6-45.7 cm, "D" = 45.8-61 cm, "E" = 61.1-76.2 cm.

percentage of total roots at the top 15 cm (Table 31).

For the 15.2 to 30.5 cm depth T3110-2 had a significantly higher root length of class 1 roots ($P \leq 0.10$) than the other three genotypes (Table 31). Stress decreased ($P \leq 0.10$) the percentage of class 3 roots, and the percentage of roots in classes 1+2 was significantly greater ($P \leq 0.05$) under stress (Table 32).

There were no significant genotypic differences at any of the other depths (Table 31). At the 30.6 to 45.7 cm depth, stress decreased the percentage of roots in classes 1 ($P \leq 0.10$), 2 ($P \leq 0.10$), and 5 ($P \leq 0.05$) (Table 32).

Cumulative total root length across all depths indicated that T3110-2 had a significantly higher total root length and class 1 root length ($P \leq 0.10$ and 0.05, respectively) than Lef-2-RB and BAT 477 (Table 33). Seed weight of T3110-2 was also significantly higher than that of Lef-2-RB and BAT 477, whereas T3110-2 seed weight, TRL and length of class 1 roots did not differ from T3016-1.

With regard to percentage of roots in each class at each soil depth, there were no significant genotypic differences at any of the root depths except 15 to 30 cm (Table 34). At this depth, T3110-2 had a greater percentage of its roots in class 1 than the other three genotypes, a lower percentage in class 2 ($P \leq 0.05$) than T3016-1 and Lef-2-RB, and a lower percentage in class 3 than T3016-1 (Table 34). The percentage of roots in classes 1+2 was greater ($P \leq 0.01$) in T3110-2 than in T3016-1 and lower ($P \leq 0.05$) in root classes 2+3 for T3110-2 than for the other three genotypes (Table 34).

Table 33. Cumulative total root length of four common bean genotypes grown in 0.7 m PVC tubes of 30 cm diameter in a greenhouse for 40 d at 25°C±2 day/night temperatures and a 15 h photoperiod in a stress and non-stress treatment. PVC Experiment 2.

Genotypes	100 seed wt.(g)	Total roots§	Class1‡.	Class2	Class3	Class4	Class5
T3016-1	36.14 a**	154.82 ab†	81.90 ab*	62.70 ns	9.32 ns	0.78 ns	0.16 ns
Lef-2-RB	32.39 b	126.42 b	67.63 b	52.60	5.60	0.40	0.20
Bat 477	28.00 c	125.60 b	67.52 b	51.34	6.00	0.57	0.13
T3110-2	37.28 a	204.90 a	118.11 a	77.50	8.50	0.67	0.16

**, *, † Different letters indicate significant differences among means within a column at P ≤ 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

§ Indicates root length in meters.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 34. Percentage of root length for individual sections of four common bean genotypes grown in 0.7 m PVC tubes of 30 cm diameter in a greenhouse for 40 d at 25°C ± 2 day/night temperatures and a 15 h photoperiod in stress and non-stress conditions. Experiment 2.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
					1-15.24 cm				
T3016-1	36.14 a**	58 ns	36 ns	5 ns	0.50 ns	0.10 ns	94 ns	99 ns	41 ns
Lef-2-RB	32.39 b	58	38	4	0.30	0.20	96	99	42
Bat 477	28.00 c	59	37	4	0.40	0.10	96	99	41
T3110-2	37.28 a	62	35	4	0.30	0.10	96	99	39
					15.24-30.48 cm				
T3016-1	36.14 a**	43 b*	48 a*	8.456 a**	0.50 ns	0.10 ns	91 b**	99 ns	57 a*
Lef-2-RB	32.39 b	44 b	50 a	5.597 ab	0.30	0.10	94 ab	99	56 a
Bat 477	28.00 c	46 b	47 ab	6.233 ab	0.50	0.10	93 ab	99	53 a
T3110-2	37.28 a	53 a	43 b	4.447 b	0.30	0.10	96 a	99	46 b

Table 34. Continued.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
				30.49-45.72 cm					
T3016-1	36.14 a**	27 ns	29 ns	6 ns	0.40 ns	0.10 ns	56 ns	62 ns	35 ns
Lef-2-RB	32.39 b	21	24	5	0.10	0.01	45	50	29
Bat 477	28.00 c	29	28	4	0.50	0.10	57	61	32
T3110-2	37.28 a	43	40	5	0.40	0.10	83	88	45

**, *, † Different letters indicate significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Percentages of total root length in each soil depth showed that classes 1 + 2 comprised 93 to 96% of the total roots with the genotypes Lef-2-RB and T3110-2 having a higher ($P \leq 0.10$) percentage than T3016-1 but not significantly higher than BAT 477 (Table 35). Class 1 comprised 54 to 57%, of total root length, class 2 comprised 38 to 41%, and class 3 comprised 4 to 6% with T3016-1 having a higher percentage of its roots in class 3 than Lef-2-RB and T3110-2 (Table 35).

Percentage wise across all soil depths, stress increased ($P \leq 0.05$) the percentage of roots in class 1, decreased ($P \leq 0.05$) the percentage in classes 2 and 3, decreased ($P \leq 0.10$) the percentage in class 4, increased ($P \leq 0.05$) the percentage in classes 1+2, and decreased ($P \leq 0.05$) the percentage in classes 2+3 (Table 32).

Ratios

Genotypic differences for PVC Experiment 2 revealed that T3110-2 had a higher ($P \leq 0.10$) ratio than the other three genotypes with regard to classes 1 +2/classes 4+5 and classes 1+2+3/classes 4+5 (Table 36), indicating a greater proportion of secondary to primary roots and agreeing with the data for root length and percentage of class 1 roots in T3110-2. Root growth of T3110-2 performed as would be expected of a susceptible genotype, however, its 1995 field performance suggested that it is resistant. The 1995 field performance indicated that T3110-2, Lef-2-RB, BAT 477, and T3110-2 were resistant, yet T3110-2 produced a greater class 1 root length at the top two depths than the

Table 35. Percentages of roots in individual root classes when data was combined for all depths of a 0.7 m PVC tubes of 30 cm diameter for four common bean genotypes. Plants were grown in a greenhouse for 40 d at 25^{0}C±2 day/night temperatures and a 15 h photoperiod in a stress and non-stress treatment. Experiment 2.

Genotypes	100 seed wt.(g)	Class1‡	Class2	Class3	Class4	Class5	Class1+2	Class1+2+3	Class2+3
T3016-1	36.14 a**	54 ns	40 ns	6 a†	0.44 ns	0.10 ns	92.6 b†	99 ns	46 ns
Lef-2-RB	32.39 b	54	41	4 b	0.30	0.13	95.3 a	99	45
BAT 477	28.00 c	54	41	5 ab	0.43	0.10	94.7 ab	99	46
T3110-2	37.28 a	57	38	4 b	0.29	0.10	95.5 a	99	43

† Different letters indicate significant difference among means within a column at P ≤ 0.10 according to DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

Table 36. Comparison of all ratios with genotypic significance from the control treatment in the pouch study to the same ratios from PVC Experiment 2.

Genotypes	(1)/(3)‡	(1)/(3+4)	(1)/(3+5)	(1+2)/(3+4)	(1+2)/(4+5)	(1+2+3)/(4+5)
T3016-1	10.6 ns	10 ns	10.5 ns	16.8 ns	245 b†	259 b†
Lef-2-RB	13.1	12	12.7	21.5	256 b	267 b
BAT 477	12.1	11	11.9	19.3	215 b	225 b
T3110-2	14.5	14	14.3	22.5	402 a	417 a

† Different letters indicates significant difference among means within a column at P ≤ 0.10 according tp DMRT.

ns Indicates no significant difference among means within a column.

‡ Indicates root width classes 1-5 in millimeters (0.2, 0.5, 0.9, 1.4, and 2.1, respectively).

other two genotypes. Several plausible explanations exist. One is that more credence should be given to the 1996 field data. Including this data would remove T3110-2 from the resistant genotype category, however response of T3110-2 from work of Schneider et al. (1997) support the 1995 results of this study and the designation of T3110-2 as resistant. Another possible explanation is that the root architecture resulting from the mild stress of PVC Experiment 2 was different from the root architecture resulting from the severe moisture stress of PVC Experiment 1. The degree of difference in rooting pattern was unexpected and warrants further study.

Correlations

PVC Experiment 1.

When significant ($P \leq 0.05$) correlations occurred, all were high, 0.91 or greater. Expectations were for class 1 roots of the ABA and PEG treatments to correlate positively with the stress treatment of PVC Experiments 1 and 2 and possibly inversely with the nonstress treatments. In actuality, correlations were diverse and included all root classes and the control, ABA, and both PEG experiments. Caution was used in interpreting the high correlations obtained for root classes 4 and 5 because the root length was extremely low in these root classes in both the pouch and PVC and statistics indicate that when very small numbers are correlated against each other, a falsely high correlation may be obtained (Dr. Oliver Schabenberger, personal communication). Nevertheless,

the data appeared to be valid because of the number of instances of low or no correlation involving root classes 4 and 5. Correlation of pouch experiments (control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG) to PVC Experiment 1 varied with soil depth (Table 37 - 41).

Correlations of root classes from the ABA, control, -0.52 MPa PEG and -1.07 MPa PEG growth pouch experiments with corresponding root classes from the five depths of PVC Experiment 1 suggested that root growth in pouches may assist in predicting plant root growth up to 40 DAP. However, additional work must be done to further test this hypothesis. Numerically, there were more correlations between root growth in the PVC tubes and root growth in the pouches when plants in the pouches were grown in half-strength Hoagland's nutrient solution (Tables 37 - 41); thus, it would be prudent for future studies to only include half-strength Hoagland's nutrient solution. Only the correlations involving the half-strength nutrient solution are discussed below.

At the 1 - 15.2 cm PVC depth, length of root classes 2 and 3 of the nonstress treatment correlated highly (0.95* and 0.99***, respectively) with length of root classes 2 and 3 of the -0.52 MPa PEG treatment (Table 37). At the 15.3 - 30.5 cm depth, class 2 root length and total RL of all root classes of the PVC stress (0.95* and 0.98*, respectively) and nonstress (0.97* and 0.98*, respectively) treatments were highly correlated with the corresponding root classes in the control pouch study containing nutrient solution (Table 38). At the 30.6 - 45.7 cm PVC depth, root classes 1, 2 and total RL of the nonstress treatment correlated highly (0.98**, 0.98** and 0.94*) with the -1.07 MPa pouch

Table 37. Correlations of root classes from control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 1- 15.2 cm. PVC Experiment 1.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
ABA Class 1	0.55	0.87†	0.42	0.41
ABA Class 4	0.81	-0.51	-0.89†	0.91†
ABA Class 5	0.83	0.08	-0.91†	0.19
ABA Total	0.42	0.92*	0.04	0.31
Control Class 2	0.97*	0.50	0.78	0.81
Control Class 4	0.88†	-0.88†	0.99*	-0.70
Control Total	0.91†	0.39	0.48	0.47
-0.52 MPa PEG Class 1	0.22	0.69	0.55	0.91†
-0.52 MPa PEG Class 2	-0.32	0.57	0.36	0.95*
-0.52 MPa PEG Class 3	-0.44	0.87†	-0.01	0.99***
-0.52 MPa PEG Class 4	-0.98**	0.69	-0.35	0.82
-0.52 MPa PEG Total	-0.16	0.57	0.42	0.90†
-1.07 MPa PEG Class 1	0.85	0.99**	-0.30	-0.05
-1.07 MPa PEG Class 5	-0.94*	0.20	-0.72	0.87†
-1.07 MPa PEG Total	0.90†	0.75	-0.16	-0.07

***, **, *, † Significant at 0.001, 0.01, 0.05, and 0.10 probability levels, respectively.

Table 38. Correlations of root classes from control, -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 15.3- 30.5 cm. PVC Experiment 1.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
Control Class 1	-0.75	-0.94*	-0.37	0.76
Control Class 2	0.79	0.49	0.95*	0.97*
Control Class 3	0.53	0.37	0.91*	0.81
Control Total	0.47	0.33	0.98**	0.98**
-0.52 MPa PEG Class 4	-0.40	-0.27	-0.97*	-0.47
-0.52 MPa PEG Class 5	0.49	-0.25	-0.94*	0.34
-1.07 MPa PEG Class 2	0.01	-0.37	0.76	0.92*

**, * Significant at 0.01 and 0.05 probability levels, respectively.

Table 39. Correlations of root classes from control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 30.6 – 45.7 cm. PVC Experiment 1.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
ABA Class 1	-0.14	-0.26	-0.36	-0.93*
Control Class 1	-0.61	-0.93*	0.34	0.90+
Control Class 2	0.87+	0.32	0.84	0.90+
Control Total	0.81	0.12	0.75	0.94*
-0.52 MPa PEG Class 4	-0.37	0.30	-0.90+	0.22
-0.52 MPa PEG Class 5	-0.13	0.14	-0.60	0.98**
-1.07 MPa PEG Class1	0.40	-0.04	0.24	0.98**
-1.07 MPa PEG Class 2	0.16	-0.54	0.69	0.98**
-1.07 MPa PEG Total	0.43	-0.27	0.33	0.94*

**, *, + Significant at 0.01, 0.05, and 0.10 probability levels, respectively.

Table 40. Correlations of root classes from control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 45.8 – 61.0 cm. PVC Experiment 1.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
ABA Class 1	-0.72	-0.18	-0.93*	-0.90+
ABA Class 2	-0.86+	-0.35	-0.86+	-0.92*
ABA Class 3	0.72	0.79	-0.83	-0.97*
ABA Class 4	0.88+	0.46	-0.96*	-0.34
ABA Class 5	0.98**	0.20	-0.99**	-0.00
ABA Total	-0.71	-0.21	-0.91+	-0.92*
Control Class 1	-0.95*	-0.88+	0.47	0.92*
Control Class 3	0.87+	0.68	0.87+	0.99**
Control Total	0.33	-0.09	0.53	0.94*
-0.52 MPa PEG Class 4	-0.88+	-0.00	-0.46	-0.17
-0.52 MPa PEG Class 5	-0.81	0.48	0.70	0.98**
-1.07 MPa PEG Class 1	-0.35	-0.00	0.67	0.98**
-1.07 MPa PEG Class 2	-0.09	-0.67	0.62	0.98**
-1.07 MPa PEG Class 5	-0.99**	-0.05	-0.54	0.53
-1.07 MPa PEG Total	-0.31	-0.43	0.62	0.94*

**, *, + Significant at 0.01, 0.05, and 0.10 probability levels, respectively.

Table 41. Correlations of root classes from -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 61.1 – 76.2 cm. PVC Experiment 1.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
-0.52 MPa PEG Class 2	0.93*	0.05	0.59	0.51
0.52 MPa PEG Class 3	0.93*	-0.45	0.97*	-0.34
0.52 MPa PEG Class 4	0.37	0.23	0.95*	-0.67
0.52 MPa PEG Total	0.88+	0.17	0.45	0.59
-1.07 MPa PEG Class 1	-0.13	0.97*	-0.24	-0.25
1.07 MPa PEG Class 3	0.38	-0.81	0.18	-0.99**
1.07 MPa PEG Class 4	-0.49	0.53	0.77	-0.95*
1.07 MPa PEG Total	-0.11	0.96*	-0.16	-0.36

**, *, + Significant at 0.01, 0.05, and 0.10 probability levels, respectively.

study (Table 39).

The largest number of significant correlations between PVC Experiment 1 and the pouch experiments occurred at the 45.8 - 61 cm depth (Table 40). At this depth, there were significant correlations involving the ABA, Control, and -1.07 MPa PEG studies. The correlations involving ABA were negative and the others were positive. Length of class 1 roots of the PVC stress treatment was negatively correlated with the class 1 RL of the ABA treatment (-0.93*). Length of ABA root classes 2, 3 and total RL were negatively correlated (-0.92*, -0.97*, and -0.92*) with the corresponding root classes of the nonstress PVC treatment. Root length of classes 1, 3, and total RL of the control were correlated (0.92*, 0.99**, and 0.94*) with the nonstress PVC treatment at this depth. Similarly, length of root classes 1, 2, and total RL of the -1.07 MPa PEG treatment correlated with the nonstress PVC treatment (0.98**, 0.98** and 0.94*, respectively) at this depth.

At the 61.1 - 76.2 cm depth, class 3 RL of the -0.52 MPa PEG treatment correlated with the stress PVC treatment and class 3 RL of the -1.07 MPa PEG treatment correlated (-0.99**) with the nonstress PVC treatment. The -1.07 MPa treatment had a larger number of significant correlations with root growth in the deeper soil depths. ABA had significant negative correlations to the PVC stress treatment at the 45.8 - 61.0 cm depths. One interpretation is that increased root growth in response to ABA indicated a lessened ability of plant root growth in moisture stress environments.

PVC Experiment 2

As with PVC Experiment 1, PVC Experiment 2 had more significant correlations between the growth pouch experiments conducted in half-strength Hoagland's nutrient solution than in deionized water (Table 42 and 43). At the 1 - 15.2 cm depth, control class 1 correlated with the nonstress PVC treatment (0.91*) and class 3 with the stress PVC treatment (0.92*). Similarly, -1.07 MPa PEG treatment correlated negatively with the class 1 RL of the PVC stress treatment (-0.97*) while RL of class 2 roots correlated positively with class 2 RL of the nonstress treatment (0.94*). At the 15.3 - 30.5 cm depth, -1.07 MPa PEG class 1, class 2 and total RL correlated negatively with the nonstress PVC treatment (-0.98**, -0.93*, and -0.97*, respectively). There were minimal correlations between the ABA pouch study and the mild moisture stress of PVC Experiment 2. The -1.07 MPa pouch treatment had the largest number of correlations in the top two depths where over 90% of the roots were located in the mild moisture stress treatment of PVC Experiment 2.

Conclusion

Field performance of Sierra and T3147-2 designated them as resistant genotypes but their root length was significantly greater than that of BAT 477, the resistant check in the control pouch treatment, although the root length data may be partially attributable to the greater seed weight of Sierra and T3147-2 in comparison to BAT 477. Gregory's work (1989) showed that BAT 477 had a

Table 42. Correlations of root classes from control, -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 1 – 15.2 cm. PVC Experiment 2.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
Control Class 1	-0.43	-0.51	0.10	0.91*
Control Class 2	-0.23	0.69	0.23	0.90+
Control Class 3	0.91+	0.64	0.92*	0.78
Control Class 4	0.76	0.38	0.93*	0.61
Control Class 5	0.44	-0.96*	0.92*	-0.49
Control Total	-0.04	0.56	0.18	---
-0.52 MPa PEG Class 2	-0.50	0.93*	-0.74	-0.41
-1.07 MPa PEG Class 1	-0.59	0.24	-0.97**	-0.74
-1.07 MPa PEG Class 2	-0.10	0.99**	-0.51	0.94*
-1.07 MPa PEG Class 3	0.56	0.95*	0.94*	0.37
-1.07 MPa PEG Class 4	0.92*	0.69	0.95*	0.84
-1.07 MPa PEG Total	-0.37	0.76	-0.87+	0.32

**, *, + Significant at 0.01, 0.05, and 0.10 probability levels, respectively.

Table 43. Correlations of root classes from control, -0.52 MPa PEG, and -1.07 MPa PEG (pouch study) containing deionized water or half strength Hoagland's nutrient solution with the corresponding root classes of plants grown in a 0.76 m PVC tube at depth 15.3 – 30.5 cm. PVC Experiment 2.

Root Class	Water "vs" PVC		Nutrients "vs" PVC	
	Stress	Nonstress	Stress	Nonstress
ABA Class 5	-0.92*	0.70	-0.31	0.48
Control Class 2	0.95*	-0.45	0.74	-0.48
Control Class 3	0.90+	0.17	0.79	-0.32
Control Class 4	0.83	0.23	0.96*	-0.11
Control Class 5	0.24	0.63	0.90+	-0.20
-0.52 MPa PEG Class 2	0.58	-0.92*	-0.07	-0.01
-0.52 MPa PEG Class 3	0.95*	0.10	-0.11	0.31
-1.07 MPa PEG Class 1	-0.71	-0.72	-0.75	-0.98**
-1.07 MPa PEG Class 2	0.51	-0.79	0.56	-0.93*
-1.07 MPa PEG Class 4	0.96*	0.08	0.91+	-0.60
-1.07 MPa PEG total	-0.10	-0.76	-0.22	-0.97*

**, *, + Significant at 0.01, 0.05, and 0.10 probability levels, respectively.

greater rooting depth than susceptible genotypes under stress but stress and rooting depth were not a part of the growth pouch study. BAT 477 and 8-42-M-2, the susceptible check, did not differ significantly with regard to total root length, although both were the smaller of the medium-sized seeds in this study. No ratio distinguished between resistant and susceptible genotypes. BAT 477 did not differ from T3110-2, T3008-1, or T3016-1 in any of the ratios, again reflecting the lack of correspondence between seed weight and percentage distribution among root classes.

In the ABA-treated plants, the genotypes T3147-2 and Lef-2-RB had a significantly higher ($P \leq 0.01$) total root length than Sierra. Total root length of the resistant genotypes T3147-2 and BAT 477 did not differ significantly from that of the susceptible check 8-42-M-2. As with the ratios from the control experiment, none of the ABA ratios distinguished between resistant and susceptible genotypes.

When plants were grown in PEG at a ψ of -0.52 MPa, BAT 477 was among the group of plants with the highest total root length. Generally, the same situation applied for the other resistant genotypes, Sierra and T3147-2. The genotype T3008-1 had a lower root length than BAT 477. The susceptible check, 8-42-M-2 was among the group with the highest root length. Several of the ratios did separate T3147-2 from 8-42-M-2, but none separated 8-42-M-2 from BAT 477. Generally, T3147-2 and BAT 477 did not differ from each other and Sierra and BAT 477 did not differ. There were no significant genotypic differences between susceptible and resistant genotypes with the ratios that

produced significant genotypic differences in the control experiment, but there was a consistent pattern in which T3147-2 > BAT 477 > 8-42-M-2 (Table 18). Sierra was somewhat similar to BAT 477.

Total root length of plants grown in -1.07 MPa PEG was greater than that of control plants and than plants grown in -0.52 MPa PEG, but less than that of plants grown in ABA. Unlike root length (RL), the ratios exhibited significant genotypic differences. The resistant genotype BAT 477 consistently had a higher ratio than the susceptible check 8-42-M-2. Sierra and T3147-2, the other genotypes designated as resistant, usually did not differ from 8-42-M-2.

Analysis of the delta values supports the working hypothesis that the 10^{-6} M ABA treatment measured the genetic potential for root length expansion. Root length increased in the -1.07 MPa (PEG) treatment more than in the -0.52 MPa (PEG) treatment and both were less than the ABA treatment. They did not differentiate among genotypes.

None of the genotypes in PVC Experiment 2 had roots that reached deeper than 61 cm. This experiment was conducted in greenhouse temperatures that were cooler than that of PVC Experiment 1. Thus, these plants experienced a milder moisture stress and that may have been reflected in the more shallow root growth of the genotypes and in the different rooting patterns exhibited in the two experiments.

The total root length of PVC Experiment 1 was fairly evenly divided throughout the first four depths of the study, 1 - 61 cm. Approximately 23% of the total roots were in the top 15 cm; 26% at the 15 to 30.5 cm depth; 26% at the

30.6 to 45.7 cm depth; 23% at the 45.8 to 61 cm depth and 2.5% at the 61.1 to 76 cm depth. This may be partly explained by the larger seed weight of genotypes in PVC 1 in comparison to PVC 2. Stress decreased the percentage of roots at the 15 to 35.5 cm depth and increased it at the 30.6 to 45.7 cm depth. The moisture stress of PVC Experiment 1 has been designated as severe due to a fairly high temperature of 28 ± 2^{0}C and high intensity of sunlight during growth of plants from June 18 through July.

In contrast, total root length of PVC Experiment 2 was concentrated in the top two depths of the study, the first 30 cm. Approximately, 64% of the total roots were in the top 15 cm; 30% at the 15.3 to 30.5 cm depth; 6.5% at the 30.6 to 45.7 cm depth; 1.5% at the 45.8 to 61 cm depth, and 0% below 61 cm. As in PVC Experiment 1, stress decreased the percentage of roots at the 15 to 30.5 cm depth and increased the percentage of roots in the top 15 cm. The moisture stress of PVC Experiment 2 was designated as mild due to low temperatures of 25 ± 2^{0}C and lower sunlight intensity during plant growth from September 18 through October.

Results suggest that root length of the control and the -1.07 MPa PEG treatments may correlate more closely with the shallower soil depths under mild moisture stress, a situation where the roots are concentrated in the upper soil horizons. Under more severe moisture stress where the roots penetrate more deeply into the soil horizon, the control correlated more closely with the intermediate soil depths and the -0.52 and -1.07 MPa PEG with the deeper soil depths. The data also suggest that seed weight may be an important factor in

total root length until at least 40 DAP, may affect root length distribution among the individual root classes, and that root length comparisons among genotypes should only be made among genotypes that have a similar seed weight.

Literature cited

Blum, A. 1988. Plant breeding for stress environments. CRC Press, Boca Raton, Fla.

Bradford, K.C. and T.C. Hsiao. 1982. Physiological responses to moderate water stress. In: O.L. Lange, P.S. Nobel, C.B. Osmond, H. Ziegler, Eds., Encyclopedia of Plant Physiology (New Series), Vol 12B. Physiological Plant Ecology II. Springer-Verlag, Berlin, pp 263-324.

Brar, G.S., A.G. Matches, H.M. Taylor, B.L. McMichael, and J.F. Gomez. 1990. Two methods for characterizing rooting depth of forage-legume seedlings in the field. Crop Science 30:413-417.

Carrow, R. 1996. Drought avoidance characteristics of diverse tall fescue cultivars. Crop Science 36:371-377.

Gregory, P.J. 1989. The role of root characteristics in moderating the effects of drought. P. 141-150. *In*: F.W.G. Baker (ed.) Drought resistance in cereals. C.A.B. Int., Wallingford, England.

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

Hubick, K.T., J.S. Taylor, D.M. Reid. 1985. The effect of drought on levels of abscisic acid, cytokinins, gibberellins, and ethylene in aeroponically grown sunflower plants. Plant Growth Regul. 16(2):234-241.

Izzo, R., F. Navari-Izzo, and M.F. Quartacci. 1989. Growth and mineral contents of roots and shoots of maize seedlings in response to increasing water deficits induced by PEG solutions. Journal of Plant Nutrition, 12:1175-1193.

Jones, H.G. 1978. How plants responds to stress. Nature 271:610.

Jupp, A.P., and E.I. Newman. 1987. Morphological and anatomical effects of severe drought on the roots *Lolium perenne* L. The New Physiologist, 105:393-402.

Kaufman, M.R. and A.N. Eckard. 1971. Evaluation of water stress control with polyethylene glycols by analysis of guttation. Plant Physiol. 47:453-456.

Kelly, J.D., M.W. Adams, A.W. Saettler, G.L. Hosfield, G.V. Varner, M.A. Uebersax, and J. Taylor. 1990. Registration of "Sierra" Pinto Bean. Crop Sci. 30:745-746.

Krizek, D.T. and P. Semeniuk. 1979. Differential sensitivity of eleven cultivars of coleus to water stress following application of polyethylene glycol 600. HortScience 14(3): 404 (Abstract).

Lachno, D.R. 1984. Abscisic acid and indole-3-acetic acid in maize roots subjected to water, salt, and mechanical stress. News bulletin: Br Pl Gr Reg Gr Mono 6:16.

McMichael, B.L., J.J. Burke, J.D. Berlin, J.L. Hatfield, and J.E. Quisenberry. 1985. Root vascular bundle arrangement among cotton strains and cultivars. Environ. and Exp. Bot. 25:23-30.

Merhaut, D.J.F., J.G. Latimer, and J.W. Daniell. 1989. Use of transparent polyethylene rhizo-bags to study growth of peach roots. HortScience, 24(6):1038.

Robertson, J.M., K.T. Hubick, E.C. Yeung, and D.M. Ried. 1990. Developmental responses to drought and abscisic acid in sunflower roots. I. Root growth, apical anatomy, and osmotic adjustment. Journal of Experimental Botany 41:325-337.

Robin, C., L. Shamsun-Noor, and A. Guckert. 1989. Effect of potassium on the tolerance to PEG-induced water stress of two white clover varieties (*Trifolium repens* L.). Plant and Soil 120:153-158.

Schaefer, R.L., D.T. Krizek, and C.W. Reynolds. 1979. Relationship between leaf water potential and leaf conductance in *Capsicum annuum* 'Yolo Wonder'. HortScience 14:404 (Abstract).

Schneider, K.A., R. Rosales-Serna, F. Ibarra-Perez, B. Cazares-Enriquez, J.A. Acosta-Gallegos, P. Ramirez-Vallejo, N. Wassimi, and J.D. Kelly. 1997. Improving common bean performance under drought stress. Crop Science 37:43-50.

Sharp, R.E. and W.J. Davies. 1979. Solute regulation and growth by roots and shoots of water stressed maize plants. Planta 147:43-49.

Sharp, R.E., W.K. Silk, and T.C. Hsiao. 1988. Growth of the primary root at low water potentials.1. Spatial distribution of expansive growth. Plant Physiology, 87:50-57.

Sharp, R.E., G.S. Voetberg, I.N. Saab, and N. Bernstein. 1993. Role of abscicic acid in the regulation of cell expansion in roots at low water potentials. *In:* T.J. Close and E.A. Bray (eds), Plant responses to cellular dehydration during environmental stress. Current topics in plant physiology: An

American Society of Plant Physiologists Series, 10:57-65.

Smucker, A.J.M., A.K. Srivastava, M.W. Adams, and B.D. Knezek. 1991. Secondary tillage and traffic compaction modifications of the growth and production of dry edible beans and soybeans. Applied engineering in agriculture 7(2):149-157.

Taiz, L. and E. Zeiger. 1991. Plant Physiology. The Benjamin/Cummings Publishing Company, Inc. Redwood City, California.

Waisel, Y., A. Eshel, and U. Kafkafi. 1996. Plant Roots: The hidden half. Marcel Dekker, Inc., New York, New York. pp. 541-545.

Walton, D.C., M.A. Harrison, and P. Cote. 1976. The effects of water stress on abscisic acid levels and metabolism in roots of *Phaseolus vulgaris* L. And other plants. Planta 147:43-49.

Watts, S., J.L. Rodriguez, S.E. Evans, and W.J. Davies. 1981. Root and shoot growth of plants treated with abscisic acid. Annals of Botany, 47:595-602.

Westgate, M.E. and J.S. Boyer. 1985. Osmotic adjustment and the inhibition of leaf, root, stem and silk growth at low water potentials in maize. Planta 164:540-549.

Chapter 3

The effect of ABA, PEG, and water stress on above ground growth

Introduction

Growth and development in most crops proceeded completely unimpaired and crop yield was maximal only when high water status was maintained throughout the life of the crop (Laing et al., 1984). While the ultimate effect of drought was limitation of growth and yield, specific physiological effects of water stress varied depending on the history of the crop, and timing and intensity of stress (White and Castillo, 1989).

In bean, the most sensitive phase of development to water stress was from flowering to early pod set (Dubetz and Mahalle, 1969; Laing et al., 1983 and 1984; Halterlein, 1983; Sheriff and Muchow, 1984). Prolonged stress before flowering restricted canopy development, which in turn limited yield (Laing et al., 1984). The relative sensitivity of different stages of development to stress varied with the degree of stress (Begg and Turner, 1976).

The most common effect of water deficit during bean growth was reduction in plant size and yield (Kramer, 1983). Drought stress affected many physiological and morphological characteristics associated ultimately with seed yield. The phenological stage of the crop at the time of the stress as well as the intensity and duration of the water stress determined the amount of damage

done to the crop and therefore yield (Acosta-Gallegos and Adams, 1991). When drought stress was imposed at the beginning of the reproductive phase in dry bean, seed yield was reduced twice as much as the reduction observed when the stress was imposed at the vegetative phase (Acosta-Gallegos and Shibata, 1989). Stem length, number of branches, pods per plant, seeds per pod and yield were all reduced.

Root characteristics were of primary importance in determining drought response of common bean (White and Castillo, 1989). Under conditions of water stress, root growth in the soil surface layer was relatively slow while the growth of new roots in the deeper, wetter layers was hastened (Garay and Wilhelm, 1983; Sponchiado et al., 1989;Trejo and Davis, 1991).

Early water deficits reduced the rate of leaf expansion and hence, leaf area accumulation. Reduction of leaf area in common bean was associated with smaller size of individual leaves rather than decreased leaf number (Bonnano and Mack, 1983). Leaf senescence, on the other hand, was considered to be a drought avoidance mechanism that allowed the plant to survive dry periods (Kramer, 1983). Rapid senescence rates, however, may be detrimental to final yield.

Abscisic acid (ABA) has been suggested to be one metabolic signal involved in responses to environmental stresses (Zhang and Davies, 1987). ABA is known to regulate stomatal closure (Zeevaart and Creelman, 1988) and has shown to reduce the rate of leaf growth of *Phaseolus* (Van Volkenburgh and Davies, 1983). Shoot responses to root hypoxia have been reported to be

mediated both by changes in leaf water status (Schildwacht, 1989) and by ABA transported from the roots (Zhang and Davies, 1987). Sharp and Davies (1989) have suggested that root signals and shoot water status act together to modulate shoot responses to root stresses. They concluded that in plants with hypoxic roots, leaf expansion rates and stomatal conductance are limited by leaf water status or shoot signals depending on the rate of water loss from the leaves at the time of the imposition of the stress.

The objectives of this study were to investigate shoot response *P. Vulgaris* to ABA, PEG and moisture deficit.

Materials and Methods:

Genotypes

The study used eight common bean genotypes which vary in their response to moisture stress:

1. Sierra, a bean developed in Michigan.
2. BAT 477, documented by CIAT (1984) to be drought resistant.
3. 8-42-M-2, a drought susceptible line developed at Michigan State University.
4. Lef-2-RB, a drought resistant line.
5. T3008-1, developed by the Michigan State University bean breeding program.
6. T3016-1, developed by the Michigan State University bean breeding program.
7. T3110-2, developed by the Michigan State University bean breeding program.
8. T3147-2, developed by the Michigan State University bean breeding program.

(Table 1).

Growth chamber study

Seedlings were grown in a growth chamber with 23/20^{0}C day/night temperatures and a 15 h photoperiod. Photosynthetically active radiation (PAR) measured 523 µmol m^{-2} s^{-1} at the top of the plant canopy using a Decagon Sunfleck Ceptometer (Pullman, Wash.). The experimental design was a split plot with solution (Half-strength Hoagland's nutrient solution or deionized water) as the main plot, genotypes as the subplot, and four replications. Seeds were germinated four days prior to initiation of the experiment. Uniform sized seeds were selected for inclusion and rinsed in a 1 µmol $CaSO_4$ solution for one hour before germination. Seeds were germinated four days prior to initiation of the experiment. Seedlings were transplanted to a CYG growth pouch measuring 15.2 cm x 16.5 cm (MEGA International, Minneapolis, Minn.) at one seed per pouch, an adaptation of a procedure used by McMichael et al. (1985). All pouches contained 50 cc of deionized water and were stapled to black cardboard and placed upright in a specially designed holder with 2.54 cm between pouches. Seedlings were covered with a clear plastic covering for two days. Plants were given four 50 cc applications of half strength Hoagland's nutrient solution, adjusted to pH 6.14, or deionized water from the sixth day after transplanting (DAT) to the fourteenth day when plants were sampled. Fresh weights were taken for roots, stems and leaves. Fresh roots were placed in a whirlpack bag and stored in 15% (v/v) methanol solution at 4^{0}C. Leaves and

Table 1. Characteristics of common bean genotypes grown in field experiments at Kellogg Biological Station, Hickory Corners, MI. in 1995 and 1996.

Genotypes	Pedigree	Origin£	Seed¥ Size	Seed Color	Plant‡ Type
Sierra	Not identified§	MSU	M	Pinto	II
T3110-2	Sierra X Lef-2-RB	MSU	M	Striped	III
T3147-2	Sierra X Lef-2-RB	MSU	M	Striped	III
Lef-2-RB	(Ver 10/Chis 143)/pue 144	INIFAP	M	Black (striped)	III
Bat 477	(51051 X ICA Bunsi) X (51012 X Cornell 49-242)	CIAT	M	Brown	II
8-42-M-2	N81017 X Lef-2-RB	MSU	M	Tan or Brown	III
T3016-1	Sierra X AC 1028	MSU	M	Tan or Brown	III
T3008-1	Sierra x AC 1028	MSU	M	Tan or Brown	III

£ MSU = Michigan State University

CIAT = Centro Internacional de Agricultura Tropical

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

¥ M=Medium.

‡ Type II = Indeterminate-bush, erect stem and branches

Type III = Indeterminate-bush, prostrate main stem and branches

§ Derived from crosses of Durango Race Pinto with Mesoamerican Race Black (Kelly et al., 1990).

stems were oven dried for 48 h at 60^0 C, weighed, and discarded. Root dry weight was obtained after the root imaging process was completed. Statistical analysis was done with the aid of MSTAT.

ABA experiment

Plants were grown in a growth chamber with $23/20^0$C day/night temperatures and a 15 h photoperiod. PAR measured 527 μmol $m^{-2}s^{-1}$ at the top of the plant canopy using a Decagon Sunfleck Ceptometer. The experimental design was a split plot with solution (ABA + deionized water or ABA + half strength Hoagland's nutrient solution) as the main plot, genotypes as the subplot, and four replications. Experimental procedures were the same as those of the control experiment. From 6 to 14 DAT, the solutions in the pouches were replaced four times. ABA (*cis-trans*, ± ABA, Sigma) was dissolved in deionized water or nutrient solution to a final ABA concentration of 10^{-6} m.

PEG experiment

Two experiments were conducted using polyethylene glycol (PEG 600). The experimental design was a split plot with solution (PEG + deionized water or PEG + half strength Hoagland's nutrient solution) as the main plot, genotypes as the subplot, and four replications. Plants in the first PEG experiment were grown in a PEG solution with a water potential of -1.07 MPa. The water potential was -0.52 MPa in the second PEG experiment. Day/night temperature regimes for

both experiments was 23/20°C with a 15 h photoperiod. PAR measured 524 and 528 μmol $m^{-2}s^{-1}$ for the -1.07 MPa and -0.52 MPa experiments, respectively. Water stress was induced at six DAT by adding PEG 600 (Sigma Chemical Co., St. Louis, MO) at 25 ml/L (osmotic potential -1.07 MPa) or 18 ml/L (osmotic potential -0.52 MPa). Solutions were replaced four times between 6 and 14 DAT.

Greenhouse Study

Plants were grown in polyvinyl chloride tubes (PVC) for 40 days in a greenhouse at Michigan State University, in East Lansing, MI. The temperature regime was 28°C ± 2°C and a light intensity of 1241 μE $m^{-2}s^{-1}$ for the first experiment and a temperature regime of 25°C ± 2°C and a light intensity of 1200 μE $m^{-2}s^{-1}$ for the second experiment. Experiment 1 consisting of genotypes Sierra, T3008-1, T3147-2, and 8-42-M-2 was planted on June 18. Experiment 2 consisting of genotypes T3016-1, Lef-2-RB, BAT 477, and T3110-2 was planted on September 16, 1996. The experimental design was a split plot with water (stress and nonstress) as the main plot, genotypes as the subplot, and four replications. The PVC tubes were 76.2 cm in length with a diameter of 30.5 cm and cut into five individual sections measuring 15.2 cm. The bottom section was filled with silica sand. The remainder of the PVC tube was filled with a Kalamazoo sandy loam soil (Typic Hapludalfs, fine-loamy, mixed, mesic) that had been sieved to remove all stones and packed to a bulk density of 1.31 g/cm^3. Five seeds per PVC tube were planted but plants were then thinned to

one plant per PVC tube at 14 days after planting (DAP). Stress was initiated at 14 DAP by reducing the amount of water given to plants in the stress treatment. Plants in the stress treatment received 53% less water than plants in the nonstress treatment. Drought stress determination was done by visually observing plants and the soil in the stress environment. Plants were watered when the soil began to crack from lack of water and plants began to wilt. Stress plants were watered approximately once per week. Plants in the nonstress environment were watered approximately three times per week. Plants were sampled at 40 DAP. Stem, leaf and reproductive parts were weighed, and dried at 60^{0}C for 48 h, re-weighed, and discarded. Roots were extracted from each section by sieving the soil through 2 mm mesh wire. After video imaging, roots were dried at 60^{0}C for 48 h then weighed and discarded. The difference between control shoot growth and shoot growth under each treatment (ABA, -0.52 MPa PEG, and -1.07 MPa PEG) (delta value) was calculated. Some delta values were negative so a transformation of the data was done using a logarithmic scale ($\Delta^{1.2}$) for statistical analysis of the data. Statistical analysis was done with the aid of MSTAT.

Results and Discussion

Control treatment: Leaf, stem, and root dry weight

Significant genotypic differences were observed for leaf, stem, and root dry weight ($P \leq 0.01$). The genotype BAT 477 had significantly lower leaf dry

weight than T3110-2 (a resistant genotype), T3008-1, and T3016-1 (Table 2). However, there was no significant difference in leaf dry weight between BAT 477, a tolerant genotype, and 8-42-M-2, a susceptible genotype (Table 2) and no significant leaf dry weight differences between the resistant genotypes, BAT 477, Sierra and T3147-2. BAT 477 had a significantly lower stem dry weight than T3110-2 (resistant) and T3008-1 (Table 2). Again, there was no significant difference between BAT 477 and 8-42-M-2 or between BAT 477 and the resistant genotypes Sierra, T3147-2, and Lef-2-RB (Table 2). BAT 477 had a significantly lower shoot dry weight than Sierra, T3147-2, T3110-2, T3008-1, and T3016-1 ($(P \leq 0.05)$ Table 2). BAT 477 had a significantly lower root dry weight than Sierra, T3008-1, and T3016-1 (Table 2). The genotypes Sierra and 8-42-M-2 had a significantly higher R/S ratio ($P \leq 0.05$) than T3110-2, T3008-1, and BAT 477 suggesting that the former genotypes imparted a greater percentage of their carbohydrates into root production in comparison to the latter (Table 2).

All of the genotypes produced seed in the medium size seed class, although there were significant differences in seed weight among the genotypes (Table 2). Generally, leaf, stem, shoot, and root dry weight and R/S ratio did not follow a pattern with regard to seed weight. For example, both Sierra and T3008-1 had one of the largest seed weight, yet Sierra produced a high R/S ratio due to a relatively lower shoot dry weight in comparison to the genotypes. In contrast, T3008-1 produced a relatively large shoot and root dry weight, resulting in a lower R/S ratio. BAT 477 had the smallest seed weight of the genotypes in the study and one of the lowest shoot and root dry weights, but

according to DMRT.

Table 2. Dry weight (g) of leaves, stems, shoots, and roots and root/shoot ratio and 100 seed weight of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in a control solution of half strength Hoagland's solution or deionized water.

Genotypes	100 Seed wt.(g)	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	40.35 a*	0.148 bc**	0.080 bc**	0.228 bc*	0.089 a*	0.410 a*
T3147-2	38.46 ab	0.139 bc	0.091 bc	0.230 bc	0.072 ab	0.324 ab
8-42-M-2	35.46 c	0.106 c	0.070 c	0.176 cd	0.066 ab	0.410 a
Lef-2-RB	32.39 d	0.106 c	0.067 c	0.174 d	0.061 ab	0.367 ab
T3110-2	37.28 bc	0.172 ab	0.095 ab	0.267 b	0.072 ab	0.265 b
T3008-1	39.50 a	0.205 a	0.117 a	0.322 a	0.085 a	0.268 b
T3016-1	36.14 c	0.178 ab	0.093 bc	0.271 b	0.093 a	0.352 ab
BAT 477	28.00 e	0.110 c	0.058 c	0.168 d	0.046 b	0.276 b

**, * Different letters indicates significant difference among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

produced a R/S ratio that was no different from that of some of the genotypes with a significantly larger seed weight.

ABA treatment: Leaf, stem, and root dry weight

Significant genotypic differences were observed for leaf, stem, shoot, and root dry weight ($P \leq 0.05$, 0.10, 0.01 and 0.05), respectively (Table 3). The genotypes, Sierra and BAT 477, had a significantly lower leaf dry weight than all of the other genotypes (Table 3). The genotypes, T3147-2, 8-42-M-2, T3008-1, and T3016-1 had a significantly higher stem dry weight than Sierra and BAT 477 (Table 3). Consequently, BAT 477 and Sierra had a significantly lower ($P \leq 0.01$) shoot weight (Table 3) than all other genotypes. BAT 477 had a significantly lower root dry weight than all other genotypes except Sierra and T3110-2 (Table 3). Sierra had a significantly higher root/shoot ratio ($P \leq 0.05$) than all other genotypes except BAT 477 (Table 3), suggesting that a higher proportion of carbohydrates was partitioned to the roots of these two genotypes under ABA than in the other genotypes. BAT 477 had a significantly higher R/S ratio than T3110-2 but there was no significant difference between BAT 477 and T3147-2 (resistant), Lef-2-RB (resistant), and the susceptible genotype 8-42-M-2 (Table 3). However, Sierra and T3147-2 (both resistant) differed in their R/S ratio. Seed weight was not a factor in the affect of ABA on leaf, stem, shoot, and root dry weight or R/S ratio of the medium size seeds used in this study.

Table 3. Dry weight (g) of leaves, stems, shoots, and roots and root/shoot ratio and 100 seed weight of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in a solution of 10^{-6} M ABA.

Genotypes	100 seed wt.(g)	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	40.35 a*	0.102 b*	0.090 c†	0.192 b**	0.092 ab*	0.536 a*
T3147-2	38.46 ab	0.203 a	0.142 a	0.344 a	0.118 a	0.381 bc
8-42-M-2	35.46 c	0.224 a	0.146 a	0.370 a	0.122 a	0.341 bc
Lef-2-RB	32.39 d	0.208 a	0.118 abc	0.326 a	0.106 a	0.349 bc
T3110-2	37.28 bc	0.224 a	0.127 ab	0.351 a	0.087 ab	0.261 c
T3008-1	39.50 a	0.230 a	0.136 a	0.367 a	0.098 a	0.277 bc
T3016-1	36.14 c	0.247 a	0.136 a	0.383 a	0.102 a	0.275 bc
BAT 477	28.00 e	0.111 b	0.101 bc	0.212 b	0.062 b	0.441 ab

**, *, † Indicates significance at $P \leq 0.01$, 0.05, and 0.10, respectively, according to DMRT, among means within a column.

Deltas

Significant genotypic differences were observed for leaf, shoot, and root dry weights, however, there were no genotypic differences for stem dry weight and R/S ratio (Table 4). Sierra was the only genotype in which ABA decreased leaf and shoot dry weight in comparison to the control (Table 4). ABA increased shoot dry weight in BAT 477, primarily through an increase in stem weight. The ABA induced change in shoot dry weight of Sierra was significantly lower ($P \leq 0.05$) than that of T3147-2, 8-42-M-2, Lef-2-RB, T3016-1, and Bat 477 (Table 4). 8-42-M-2 had a significantly higher increase in ($P \leq 0.01$) root dry weight than Sierra but was not significantly higher than the other genotypes (Table 4).

-0.52 MPa PEG treatment: Leaf, stem, and root dry weight

A significantly lower ($P \leq 0.01$) leaf dry weight was obtained for Lef-2-RB and T3008-1 than for Sierra, T3016-1, and BAT 477 (Table 5). Sierra, 8-42-M-2, and T3008-1 (Table 5). 8-42-M-2 had a significantly higher ($P \leq 0.05$) shoot dry weight than Lef-2-RB and T3008-1 but was significantly lower than T3016-1 (Table 5). The genotype T3008-1 had a significantly lower ($P \leq 0.10$) root dry weight than all other genotypes except Lef-2-RB and T3110-2 (Table 5). Lef-2-RB had a significantly higher ($P \leq 0.05$) R/S ratio than Sierra, T3110-2, and T3016-1 (Table 5). BAT 477, 8-42-M-2, and T3147-2 were among the group with the highest R/S ratio.

Table 4. Mean difference between ABA treatment and control (delta) for leaf, stem, shoot, root, and root/shoot ratio for eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod.

Genotypes	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	-0.046 c**	0.01 ns	-0.036 b*	0.003 b**	0.13 ns
T3147-2	0.064 ab	0.05	0.115 a	0.045 ab	0.06
8-42-M-2	0.118 a	0.08	0.194 a	0.056 a	-0.07
Lef-2-RB	0.101 a	0.05	0.152 a	0.045 ab	-0.02
T3110-2	0.052 ab	0.03	0.084 ab	0.015 ab	-0.01
T3008-1	0.025 abc	0.02	0.045 ab	0.012 ab	0.01
T3016-1	0.069 ab	0.04	0.112 a	0.009 ab	-0.08
BAT 477	0.001 bc	0.18	0.168 a	0.016 ab	0.03

**, * Different letters indicates significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

Table 5. Dry weight (g) of leaves, stems, shoots, roots, and root/shoot ratio of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in polyethylene glycol 600 solution of -0.52 MPa.

Genotypes	100 seed wt.(g)	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	40.35 a*	0.160 a**	0.105 a†	0.265 ab*	0.071 a†	0.248 bc*
T3147-2	38.46 ab	0.136 ab	0.081 abc	0.217 bc	0.070 a	0.342 ab
8-42-M-2	35.46 c	0.119 ab	0.106 a	0.225 b	0.069 a	0.311 abc
Lef-2-RB	32.39 d	0.080 b	0.052 c	0.132 c	0.047 ab	0.360 a
T3110-2	37.28 bc	0.109 ab	0.105 a	0.214 bc	0.045 ab	0.230 c
T3008-1	39.50 a	0.081 b	0.061 bc	0.142 c	0.036 b	0.272 abc
T3016-1	36.14 c	0.183 a	0.090 ab	0.273 a	0.065 a	0.233 c
BAT 477	28.00 e	0.160 a	0.090 ab	0.250 ab	0.073 a	0.285 abc

**, *, † Different letters Indicates significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

Delta

Significant genotypic differences were observed for -0.52 MPa PEG induced differences in leaf, stem, shoot, and root dry weight and for R/S ratio. The leaf dry weight increased for T3147-2 was significantly higher ($P \leq 0.01$) than for T3110-2, T3008-1, and T3016-1 but did not differ from the other three genotypes (Table 6). 8-42-M-2 had a significantly higher ($P \leq 0.05$) stem dry weight than T3110-2, T3008-1, and T3016-1 but not significantly higher than Sierra, T3147-2, Lef-2-RB, and BAT 477 (Table 6). Nevertheless, the shoot dry weight of T3147-2 was only significantly higher ($P \leq 0.01$) than that of T3110-2 and T3008-1 (Table 6). Root dry weight showed that the genotype, 8-42-M-2 had a significantly higher ($P \leq 0.10$) root dry weight than T3110-2, T3008-1, and T3016-1 but not significantly higher than the other genotypes (Table 6). The genotype T3008-1 had a significantly higher ($P \leq 0.01$) R/S ratio than Sierra, 8-42-M-2, and Lef-2-RB (Table 6).

In comparison to the control, the -0.52 MPa PEG treatment increased shoot and decreased root dry weight of Sierra, decreased shoot and root dry weight of Lef-2-RB and T3110-2, increased shoot and root dry weight of T3008-1 and BAT 477. Shoot and root response were independent of the significant differences in seed weight among these genotypes in the medium size seed class.

Table 6. Mean difference between -0.52 MPa PEG treatment and control (delta) for leaf, stem, shoot, root, and root/shoot ratio for eight common bean genotypes germinated in a germination chamber for 4 d at 25^{0}C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20^{0}C day/night temperatures and a 15 h photoperiod.

Genotypes	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	0.032 abc*	0.012 abc*	0.044 abc**	-0.016 abc†	-0.142 b**
T3147-2	0.132 a	0.005 abcd	0.137 a	-0.011 abc	-0.094 ab
8-42-M-2	0.068 ab	0.045 a	0.113 ab	0.015 a	-0.133 b
Lef-2-RB	0.007 abc	0.029 ab	0.036 abc	-0.012 abc	-0.119 b
T3110-2	-0.085 bc	-0.013 bcd	-0.098 bc	-0.021 bc	0.041 ab
T3008-1	-0.103 c	-0.040 d	-0.143 c	-0.025 bc	0.077 a
T3016-1	-0.050 bc	-0.022 cd	-0.073 abc	-0.038 c	-0.062 ab
BAT 477	-0.012 abc	0.005 abcd	-0.007 abc	-0.001 ab	0.029 ab

**, *, † Different letters indicates significant difference among means within a column at P ≤ 0.01, 0.05, and 0.10, respectively, according to DMRT.

-1.07 MPa PEG treatment: Leaf, stem, and root dry weight

There were no genotypic differences for leaf, stem, shoot, and R/S (Table 7).

Deltas

There was no genotypic difference for leaf, stem, shoot, and root dry weight or for R/S ratio (Table 8). Although not significant, the -1.07 MPa treatment increased shoot and root dry weight in Lef-2-RB and BAT 477, the two genotypes with the lowest seed weight. Response to ABA varied among the genotypes, but the response exhibited no pattern with regard to seed weight.

Comparison across experiments

There were significant differences among the control, ABA, -0.52 MPa, and -1.07 MPa experiments for leaf, stem, shoot, and root dry weight and for R/S ratio (Table 9). The ABA experiment had a significantly higher ($P \leq 0.01$) leaf, shoot, and root dry weight than the other three experiments. It also had a significantly higher ($P \leq 0.01$) stem dry weight than the control and -0.52 MPa PEG experiment. The -0.52 MPa PEG experiment had a lower R/S ratio than the control and ABA experiments (Table 9).

ABA increased both shoot and root dry weights, while the -0.52 and -1.07 PEG experiments did not significantly differ from the control experiment with regard to root or shoot dry weights (Table 9). This was surprising since root

Table 7. Dry weight of leaves, stems, shoots, and roots and root/shoot ratio and 100 seed weight of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod in polyethylene glycol 600 solution of -1.07 MPa.

Genotypes	100 seed wt.(g)	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	40.35 a*	0.132 ns	0.102 ns	0.233 ns	0.078 ns	0.370 ns
T3147-2	38.46 ab	0.130	0.102	0.232	0.074	0.311
8-42-M-2	35.46 c	0.131	0.122	0.253	0.079	0.320
Lef-2-RB	32.39 d	0.144	0.102	0.246	0.086	0.347
T3110-2	37.28 bc	0.141	0.126	0.267	0.071	0.281
T3008-1	39.50 a	0.179	0.127	0.306	0.075	0.255
T3016-1	36.14 c	0.170	0.113	0.282	0.097	0.347
BAT 477	28.00 e	0.108	0.097	0.205	0.064	0.315

* Different letters indicates significant difference among means within a column at $P \leq 0.05$, according to DMRT.

ns no significant difference among means within a column.

Table 8. Mean difference between -1.07 MPa PEG treatment and control (delta) for leaf, stem, shoot, root, and root/shoot ratio for eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod.

Genotypes	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	-0.02 ns	0.02 ns	0.01 ns	-0.01 ns	-0.04 ns
T3147-2	-0.01	0.01	0.01	0.01	-0.01
8-42-M-2	0.03	0.05	0.08	0.01	-0.09
Lef-2-RB	0.04	0.04	0.07	0.03	-0.02
T3110-2	-0.03	0.03	0.01	-0.01	0.01
T3008-1	-0.03	0.01	-0.02	-0.01	-0.01
T3016-1	-0.01	0.02	0.01	0.01	-0.01
BAT 477	-0.01	0.04	0.04	0.02	0.04

ns Indicates no significant difference among means within a column.

Table 9. Comparison of leaf, stem, shoot, root dry weight and root/shoot ratio of eight common bean genotypes germinated in a germination chamber for 4 d at 25°C and transplanted to an environmentally controlled growth chamber for 14 d at 23/20°C day/night temperatures and a 15 h photoperiod from the four treatments imposed.

Treatment£	Leaf (g)	Stem (g)	Shoot (g)	Root (g)	R/S ratio
Control	0.146 b**	0.084 b**	0.229 b**	0.073 bc**	0.334 a*
ABA	0.194 a	0.140 a	0.334 a	0.098 a	0.341 a
-0.52 MPa PEG	0.144 b	0.086 b	0.230 b	0.060 c	0.284 b
-1.07 MPa PEG	0.142 b	0.111 ab	0.253 b	0.078 b	0.318 ab
C.V.	56	63	45	39	33

**, * Different letters indicate significance among means within a column at P ≤ 0.01 and 0.05, respectively, according to DMRT.

£ Control solution contained half strength Hoagland's nutrient solution or deionized water.

ABA solution contained 10^{-6} m ABA dissolved in half strength Hoagland's nutrient solution or deionized water.

PEG solution contained 18 ml/L (-0.52 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution or 25 ml/L (-1.07 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution.

length data (Chapter 2, Table 5) indicated that total root length of the ABA and PEG experiments was significantly greater than that of the control. However, the root length data also indicated that the increase was primarily that of class 1 roots, often with a corresponding decrease in root classes 2 and 3 (Chapter 2, Table 7). Since class 1 roots are smaller in diameter and dry weight than class 2 and 3 roots, the root dry weight results were reasonable. The -0.52 MPa PEG experiment had a lower R/S ratio than the control and ABA experiments, primarily due to the lower numerical root dry weight in comparison to the control and ABA experiments.

The lower R/S ratio of the -0.52 MPa PEG experiment and the lack of significant difference among R/S ratio of control, ABA, and -1.07 MPa PEG experiments was unexpected since ABA and moisture stress treatment, simulated dy both PEG experiments, reportedly increase root growth and inhibit shoot growth. An increased R/S ratio had been hypothesized. Nevertheless, the data does reflect increased total root length under ABA and both PEG experiments (Chapter 2). Again, the increased root length was in the smaller diameter class 1 roots which would be expected to have a lower dry weight than the class 2 and 3 roots which were decreased in the ABA and PEG experiments. BAT 477 maintained a fairly consistent leaf dry weight across all four treatments and its value was almost identical for the control, ABA and -1.07 MPa PEG treatment. The resistant genotype, T3147-2, was second to BAT 477 with regard to consistency of leaf weight across experiments.

Effects of Nutrient Solution Versus Water

Leaf dry weight of all experiments was significantly greater ($P \leq 0.05$) when plants were grown in the nutrient solution, while there was no significant difference for stem dry weight in any of the experiments (Table 10). Shoot dry weight was greater in all treatments except -1.07 MPa PEG when plants were grown in nutrient solution (Table 10). Consequently, the R/S was significantly greater ($P \leq 0.05$) in the water solution. Similar to the control experiment, leaf and shoot dry weight of the ABA experiment were significantly greater ($P \leq 0.05$ and 0.10, respectively) in nutrient solution (Table 10). Consequently, R/S ratio was significantly greater ($P \leq 0.05$) in the water solution of the control and ABA experiments (Table 10). Leaf ($P \leq 0.01$), shoot ($P \leq 0.05$), and root ($P \leq 0.05$) dry weight of the -0.52 MPa PEG experiment were significantly greater when plants were grown in nutrient solution. Thus, R/S ratio was greater in water than in nutrient solution for the control and ABA experiments (Table 10). Leaf (($P \leq 0.05$) and root ($P \leq 0.10$) dry weight were greater in nutrient solution in the -1.07 MPa PEG experiment, but stem and overall shoot dry weight did not differ between nutrient solution and water. As a result, the R/S ratio did not differ between nutrient solution and water treatments.

Insufficient nutrients, as indicated by the water treatment, decreased leaf dry weight in all experiments and decreased shoot dry weight in all experiments except the -1.07 MPa PEG experiment (Table 10). Insufficient nutrients did not affect stem dry weight in any of the experiments. Insufficient nutrients only reduced root dry weight in the PEG experiments while insufficient nutrients

Table 10. Leaf, stem, shoot, and root and R/S ratio growth response to half strength Hoagland's nutrient solution versus deionized water.

Root Classes	Control£	ABA	-0.52 MPa PEG	-1.07 MPa PEG
Leaf dry wt.	W < H*	W < H*	W < H**	W < H*
Stem dry wt.	ns	ns	ns	ns
Shoot dry wt.	W < H*	W < H+	W < H*	ns
Root dry wt.	ns	ns	W < H*	W < H+
R/S ratio.	W > H*	W > H*	ns	ns

**, *, + Indicates significant difference at P ≤ 0.01, 0.05, and 0.10, respectively.

ns Indicate non significant data.

W = Water

H = Hoagland's nutrient solution

£ Control solution contained half strength Hoagland's nutrient solution or deionized water.

ABA solution contained 10^{-6} m ABA dissolved in half strength Hoagland's nutrient solution or deionized water.

PEG solution contained 18 ml/L (-0.52 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution or 25 ml/L (-1.07 MPa) v/v of PEG 600 and deionized water or half strength Hoagland's nutrient solution.

increased R/S ratio in the control and ABA experiments. Results suggest that lack of sufficient nutrients reduce leaf dry weight during sufficient and insufficient moisture status, as simulated by PEG, and reduce root growth during moisture stress. Both are undesirable, but the latter would have a compounding effect during moisture stress. BAT 477 maintained a fairly consistent leaf dry weight across all four treatments and the value was almost identical for ABA and the -1.07 MPa PEG treatment (Table 10). Another resistant genotype, T3147-2, was second to BAT 477 with regard to consistency of leaf dry weight across experiments (Table 10).

Polyvinyl-chloride experiment 1

Leaf, stem, and root dry weight

The four genotypes used in this experiment were Sierra, T3008-1, T3147-2, and 8-42-M-2. There were no significant differences among the genotypes for leaf, stem, reproductive, and shoot dry weight or for R/S ratio. The susceptible genotype, 8-42-M-2, had a significantly lower ($P \leq 0.10$) root dry weight than the other three genotypes (Table 11). This corresponds with the greater percentage of class 1 roots in 8-42-M-2 than in the other three genotypes and the lower percentage of roots in classes 2 and 3 of 8-42-M-2 in comparison with the other three genotypes (Chapter 2). It is logical to expect the class 1 roots to have a lower dry weight than roots in classes 2 and 3.

Table 11. Dry weight of leaves, stems, shoots, and roots and root/shoot ratio of four common bean genotypes grown in a greenhouse for 40 d at 28°C±2°C and a 15 h photoperiod in a polyvinyl-chloride tube measuring 76.2 cm in length and 30.5 cm in diameter. PVC Experiment 1.

Genotypes	100 seed wt.(g)	Leaf (g)	Stem (g)	Reproductive (g)	Shoot (g)	Root (g)	R/S ratio
Sierra	40.35 a*	6.5 ns	3.6 ns	0.3 ns	10.3 ns	1.186 a†	0.12 ns
T3008-1	39.50 a	6.2	3.4	0.2	9.8	1.123 a	0.12
T3147-2	38.46 a	6.5	3.7	0.3	10.4	1.175 a	0.12
8-42-M-2	35.46 b	5.5	2.3	0.2	8.0	0.792 b	0.11

*, † Different letters indicates significance among means within a column at $P \leq 0.05$ and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

Polyvinyl-chloride experiment 2

Leaf, stem, and root dry weight

The four genotypes used in this experiment were Lef-2-RB, BAT 477, T3016-1, and T3110-2. As with the PVC 1 experiment, there were no significant differences among the genotypes for leaf, stem, reproductive, and shoot dry weight or for R/S ratio. The genotype, T3110-2, had a significantly higher ($P \leq 0.10$) root dry weight than BAT 477 and Lef-2-RB but was not significantly higher than T3016-1 (Table 12). Similar to PVC experiment 1, the root dry weight data corresponds well with the root length data from Chapter 2. The total root length of T3110-2 was significantly greater than that of Lef-2-RB and BAT 477 (Chapter 3, Table 29) but not than T3016-1 and the same was true for class 1 roots. There were no significant differences among genotypes for percentage of class 1 roots but there was a trend for T3110-2 to be higher than the rest (Chapter 2, Table 31).

Effects of water stress

Moisture stress decreased ($P \leq 0.10$) stem dry weight in PVC experiment 1 and leaf dry weight in PVC experiment 2 and increased R/S ratio in both PVC experiment 1 ($P \leq 0.01$) and PVC experiment 2 ($P \leq 0.10$) (Table 13).

Correlations

The two PVC experiments correlated poorly with the four growth pouch

Table 12. Dry weight of leaves, stems, shoots, and roots and root/shoot ratio of four common bean genotypes grown in a greenhouse for 40 d at 25°C±2°C and a 15 h photoperiod in a polyvinyl-chloride tube measuring 76.2 cm in length and 30.5 cm in diameter. PVC Experiment 2.

Genotypes	100 seed wt.(g)	Leaf (g)	Stem (g)	Reproductive (g)	Shoot (g)	Root (g)	R/S ratio
T3016-1	36.14 a**	2.81 ns	1.23 ns	0.10 ns	4.13 ns	0.878 ab†	0.25 ns
Lef-2-RB	32.14 b	2.21	0.97	0.10	3.30	0.601 c	0.20
BAT 477	28.00 c	2.71	0.94	0.10	3.74	0.642 bc	0.20
T3110-2	37.28 a	3.64	1.60	0.15	5.40	0.931 a	0.20

**, † Different letters indicates significance among means within a column at P ≤ 0.01 and 0.10, respectively, according to DMRT.

ns Indicates no significant difference among means within a column.

Table 13. Leaf, stem, shoot, reproductive, and root and R/S ratio growth response to stress and nonstress moisture conditions of plants grown in a greenhouse for 40 d at 28 ± 2°C (PVC Expt. 1) and 25 ± 2°C (PVC Expt. 2) day/night temperatures and a 15 h photoperiod in PVC tubes.

Root Classes	"A"	"B"	"C"	"D"	"E"	Total
PVC Experiment 1						
Leaf dry wt.	ns	ns	ns	ns	ns	ns
Stem dry wt.	ns	ns	ns	ns	ns	S < N+
Shoot dry wt.	ns	ns	ns	ns	ns	ns
Repro. dry wt.	ns	ns	S < N*	S < N+	ns	ns
Root dry wt.	ns	ns	ns	ns	ns	ns
R/S ratio.	ns	ns	ns	ns	ns	S > N**
PVC Experiment 2						
Leaf dry wt.	ns	ns	ns	ns	ns	S < N+
Stem dry wt.	ns	ns	ns	ns	ns	ns
Shoot dry wt.	ns	ns	ns	ns	ns	ns
Repro. dry wt.	ns	ns	ns	ns	ns	ns
Root dry wt.	ns	S < N+	ns	ns	ns	ns
R/S ratio.	ns	ns	ns	ns	ns	S > N+

**, *, + Indicates significant difference at P ≤ 0.01, 0.05, and 0.10, respectively.

ns Indicate non significant data.

S = Stress

N = Nonstress

Depth "A" =1-15.2 cm, "B" = 15.3-30.5 cm, "C" = 30.6-45.7 cm, "D" = 45.8-61 cm, "E" = 61.1-76.2 cm.

experiments and that was true for leaf, stem, shoot, and root dry weight data, and for R/S ratios (Tables 14 and 15).

Conclusion

In the control treatment, there was no significant differences between the resistant genotype BAT 477 and the susceptible genotype 8-42-M-2 for leaf, stem, and root dry weight, but there were significant leaf dry weight differences between the resistant genotypes, BAT 477, and Sierra and T3147-2. The genotypes Sierra and 8-42-M-2 had a significantly higher R/S ratio than T3110-2, T3008-1, and BAT 477 suggesting that the former genotypes imparted a greater percentage of their carbohydrates into root production in comparison to the latter.

For the ABA treatment, significant genotypic differences were observed for leaf, stem, shoot, and root dry weight. Sierra, a resistant genotype, had a significantly higher R/S ratio than all other genotypes except BAT 477, suggesting that a higher proportion of carbohydrates was partitioned to the roots. There was no significant difference between BAT 477 and T3147-2 (both resistant) and the susceptible genotype 8-42-M-2. Sierra and T3147-2 (both resistant) differed in their R/S ratio.

In the -0.52 MPa PEG treatment, there was no significant difference between BAT 477 and 8-42-M-2 for leaf, stem, shoot, and root dry weight and R/S ratio. BAT 477 and 8-42-M-2 were among the group with the highest R/S ratio.

There were no genotypic differences for leaf, stem, shoot, and R/S in the

Table 14.Correlation coefficient for leaf, stem, shoot, and R/S ratio among control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG experiments for common bean in a greenhouse for 40 d at 28 ± 2°C day/night temperatures and a 15 h photoperiod in PVC tubes. PVC Experiment 1.

Treatment	Leaf	Stem	Shoot	Root	R/S ratio
	Score				
			Stress		
Control	0.56	-0.82	-0.63	0.36	0.44
ABA	-0.60	-0.39	-0.70	-0.70	-0.35
-0.52 MPa PEG	-0.16	0.52	-0.07	-0.89†	0.30
-1.07 MPa PEG	0.05	-0.40	-0.70	-0.06	-0.14
			Non-stress		
Control	-0.56	0.01	0.1	0.64	0.07
ABA	0.82	-0.63	0.36	-0.38	0.42
-0.52 MPa PEG	0.51	-0.40	-0.77	0.26	0.25
-1.07 MPa PEG	-0.29	-0.08	0.25	0.47	-0.42
			Combined		
Control	0.43	-0.47	-0.5	0.72	-0.25
ABA	-0.25	-0.44	-0.37	-0.63	0.55
-0.52 MPa PEG	-0.16	0.54	-0.22	-0.72	-0.118
-1.07 MPa PEG	0.00	-0.13	-0.45	-0.65	0.23

† Significant at 0.10 probability level.

Table 15.Correlation coefficient for leaf, stem, shoot, and R/S ratio among control, ABA, -0.52 MPa PEG, and -1.07 MPa PEG experiments for common bean in a greenhouse for 40 d at 25 ± 2°C day/night temperatures and a 15 h photoperiod in PVC tubes. PVC Experiment 2.

Treatment	Leaf	Stem	Shoot	Root	R/S ratio
	Score				
	Stress				
Control	0.98**	-0.75	-0.56	0.73	0.50
ABA	-0.57	0.75	-0.56	0.11	0.47
-0.52 MPa PEG	0.49	0.14	0.61	0.70	0.65
-1.07 MPa PEG	0.55	-0.69	-0.35	0.10	-0.31
	Non-stress				
Control	0.11	-0.41	0.24	0.70	0.66
ABA	-0.91†	0.47	-0.98**	0.27	0.29
-0.52 MPa PEG	-0.78	0.57	0.18	-0.60	0.50
-1.07 MPa PEG	-0.38	0.17	0.07	0.91†	0.12
	Combined				
Control	0.72	-0.64	-0.23	0.75	0.59
ABA	-0.80	0.64	-0.87†	0.17	-0.34
-0.52 MPa PEG	-0.62	0.24	0.47	0.74	-0.04
-1.07 MPa PEG	0.03	-0.44	-0.30	0.20	0.66

**, † Significant at 0.01 and 0.10 probability level, respectively.

-1.07 MPa PEG treatment.

Comparison across treatments showed that the ABA experiment had a significantly higher leaf, shoot, and root dry weight than the other three experiments and a significantly higher stem dry weight than the control and -0.52 MPa PEG experiment but was not significantly higher than the -1.07 MPa PEG experiment.

ABA increased both shoot and root dry weights, while the -0.52 and -1.07 MPa PEG experiments did not significantly differ from the control experiment with regard to root or shoot dry weights. This was surprising since root length data indicated that total root length of ABA and both PEG experiments was significantly greater than that of the control. The -0.52 MPa PEG experiment had a lower R/S ratio than the control and ABA experiments, primarily due to the lower numerical root dry weight in comparison to the control.

BAT 477 maintained a fairly consistent leaf dry weight across all four treatments and the value was almost identical for control, ABA and -1.07 MPa PEG treatment. Another resistant genotype, T3147-2, was second to BAT 477 with regard to consistency of leaf weight across treatments.

Leaf and shoot dry weight of the control experiment were significantly greater in the nutrient solution than in deionized water, while there was no significant difference for stem or root dry weight. Insufficient nutrients, as indicated by the water treatment decreased leaf dry weight in all experiments and decreased shoot dry weight in all experiments except the -1.07 MPa PEG experiment, while insufficient nutrients did not affect stem dry weight in any of

the experiments. Insufficient nutrients only reduced root dry weight in the PEG experiments while insufficient nutrients increased R/S ratio in the control and ABA experiments.

In PVC Experiment 1 there were no significant differences among the genotypes for leaf, stem, reproductive, and shoot dry weight or for R/S ratio. The susceptible genotype, 8-42-M-2, had a significantly lower root dry weight than the other three genotypes.

In PVC Experiment 2 there were no significant differences among the genotypes for leaf, stem, reproductive, and shoot dry weight or for R/S ratio. The genotype, T3110-2, had a significantly higher root dry weight than BAT 477 and Lef-2-RB but was not significantly higher than T3016-1.

Moisture stress decreased stem dry weight in PVC experiment 1 and leaf dry weight in PVC experiment 2 and increased R/S ratio in both PVC experiment 1 and PVC experiment 2.

The two PVC experiments correlated poorly with the four growth pouch experiments and that was true for leaf, stem, shoot, and root dry weight data, and for R/S ratios.

Literature cited

Acosta-Gallegos, J.A., and J.K. Shibata. 1989. Effect of water stress on growth and yield of indeterminate dry bean (*Phaseolus vulgaris* L.) Cultivars. Field Crops Res. 20:81-93.

Acosta-Gallegos, J.A., and M.W. Adams. 1991. Plant traits and yield stability of dry bean (*Phaseolis vulgaris* L.) cultivars under drought stress. J. Agric. Sci. (Cambridge) 117:213-219.

Begg, J.E. and N.C. Turner. 1976. Crop water deficits. Adv. Agron. 28:161-217.

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

CIAT (Centro Internacional de Agricultura Tropical). 1984. Annual report 1983. Bean Program CIAT, Cali, Columbia.

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

Dubetz, S. and P.S. Mahalle. 1969. Effect of soil water stress on bush beans (*Phaseolus vulgaris* L.) At three stages of growth. J. Amer. Hortic. Sci. 94:479-481.

Garay, A.F., and W.W. Wilhelm. 1983. Root system characteristics of two soybean isolines undergoing water stress conditions. Agro. J. 75:973-975.

Halterlein, A.J. 1983. Bean water requirements, root system, irrigation, drought behavior in kidney beans. *In*: Crop-water relations. I.D. Tesar and M.M. Peet (Eds). John Wiley Press, New York.

Kelly, J.D., M.W. Adams, A.W. Saettler, G.L. Hosfield, G.V. Varner, M.A. Uebersax, and J. Taylor. 1990. Registration of "Sierra" Pinto Bean. Crop Sci. 30:745-746.

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

Laing, D.R., P.J. Kretchmer, S. Zuluaga, and P.G. Jones. 1983. Field bean. In: W.H. Smith and S.J. Banta (Eds), Symposium on potential productivity of field crops under different environments. Los Banos, Phillippines, 1980 (Proceedings) IRRI pp.227-248.

Laing, D.R., P.G. Jones, and J.H.C. Davis. 1984. Common bean (*Phaseolus vulgaris* L.) In: P.R. Goldsworthy and N.M. Fisher (Eds), The physiology of tropical crops. John Wiley & Sons Ltd. Pp.305-351.

McMichael, B.L., J.J. Burke, J.D. Berlin, J.L. Hatfield, & J.E. Quisenberry. 1985. Root vascular bundle arrangement among cotton strains and cultivars. Environ. and Exp. Bot. 25:23-30.

Schildwacht, P. 1989. Is a decreased water potential after withholding oxygen to roots the cause of the decline of leaf elongation rates in *Zea mays* and *Phaseolus vulgaris* L.? Ibid 177:178-184.

Sharp, R.E., and W.J. Davies. 1989. Regulation of growth and development of plants growing with a restricted supply of water. *In:* H.G. Jones, T.L. Flowers, and M.B. Jones (eds). Plants under stress. Cambridge University Press. London. Pp:72-93.

Sheriff, D.W. and R.C. Muchow. 1984. The water relations of crops. In: P.R. Goldsworthy and N.M. Fisher (Eds.), The physiology of tropical field crops. John Wiley & Sons Ltd. Pp.39-83.

Sponchiado, B.N., J.W. White, J.A. Castillo, and P.G. Jones. 1989. Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. Expl. Agric. 25:249-257.

Trejo, C.J. and W.J. Davis. 1991. Drought induced closure of *Phaseolus vulgaris* L. Stomata precedes leaf water deficit and any increase in xylem ABA concentration. J. Expt. Botany 42:1507-1515.

Van Volkenburgh, E., and W.J. Davies. 1983. Inhibition of light stimulated leaf expansion by ABA. Journal of Experimental Botany 34:835-845.

White, J.W. and J.A. Castillo. 1989. Relative effect of root and shoot genotypes on yield of common bean under drought stress. Crop Sci. 29:360-362.

Zeevaart, J.A., and R.A. Creelman. 1988. Metabolism and physiology of abscisic acid. Annual Review Plant Physiology Plant Molecular Biology 39:439-473.

Zhang, J., and W.J. Davies. 1987. ABA in roots and leaves flooded plain plants. Ibid. 37:649-659.

Summary and conclusion

Geometric mean and STI were better predictors than DSI of yield performance under limited moisture. The yield performance of T3147-2, Sierra, Lef-2-RB, T3110-2, and BAT 477 under moisture stress conditions in the field met the criteria for categorization as drought resistant while 8-42-M-2, T3008-1, and T3016-1 were categorized as drought susceptible.

ABA increased total root length and root length of all root classes except class 2 when plants were grown in 15.2 x 16.5 cm growth pouches. The -0.52 and -1.07 MPa PEG experiments increased total root length and root length of root classes 1, 3, 4, and 5. ABA and both PEG experiments shifted the percentage of total roots heavily towards class 1 roots. Nutrient solution had no advantage over deionized water with regard to root length and morphology of the control and ABA experiments, however, the lack of nutrients decreased total root length and root length of root classes 1, 2, and 3 when plants were grown in -0.52 and -1.07 MPa PEG solutions.

When plants grown in 0.76 cm PVC tubes were subjected to a severe moisture stress, total root growth was fairly evenly distributed throughout the 5 equal sections of the PVC tube. When the stress was mild, root growth was concentrated in the top 30 cm. Severe moisture stress increased root length in classes 1 and 2 and total root length, and the increase was more pronounced at the 30 to 45 cm soil depth. Severe stress increased percentage of class 1 roots and decreased the percentage of class 2 roots in the top 15 cm of the soil depth. The ABA, -0.52, and -1.07 MPa PEG pouch experiments increased the root

length and percentage of class 1 roots (the finest roots), as did moisture stress in the PVC experiments. The ratio of secondary to primary roots appeared to be important in drought resistance and the -1.07 MPa experiment produced ratios that separated the resistant genotypes T3147-2 and BAT 477 from the susceptible genotype 8-42-M-2.

ABA increased both root and shoot dry weight so R/S ratio did not increase in comparison to the control. The -0.52 MPa experiment decreased R/S ratio and no change occurred with the -1.07 MPa PEG experiment. In contrast to the susceptible genotype 8-42-M-2, the resistant genotypes T3147-2 and BAT 477 maintained fairly consistent leaf, stem, and root dry weights and R/S ratios across the control, ABA, and both PEG experiments.

When root growth was distributed somewhat evenly across all soil depths during severe moisture stress, the control experiment, conducted in growth pouches, was a good predictor of total root length in the 15 to 30 cm soil depth and the -1.07 MPa PEG treatment predicted root length at the 30 to 45 cm depth. The ABA and -1.07 MPa PEG treatments, conducted in the growth pouches, were the best predictors of root growth at the 45 to 60 and the -1.07 MPa PEG at 60 to 75 cm soil depths. When roots were shallow as in the mild moisture stress of PVC experiment 2, the -1.07 MPa PEG experiment of the growth pouch study was the best predictor of root growth in the PVC tubes. A larger number of correlations occurred between plants in pouch and PVC experiments when plants in the growth pouches were grown in nutrient solution as opposed to deionized water. Clearly, a greater number of cultivars must be

studied before the growth pouch method can be accepted or rejected. The data is promising in that it supports further study rather than rejection of the concept.

The data suggest that seed weight may be an important factor in total root length until at least 40 DAP, that it may affect root length distribution among root classes, and that root length comparisons should only be made among genotypes that have a similar seed weight.

Recommendations

1. When assessing bean root growth via the growth pouch method, plants should be grown in half-strength Hoagland's nutrient solution.

2. Genotypes of similar seed weight should be used when attempting to assess drought resistance or susceptibility of bean genotypes via quantification of root length.

3. A minimum rooting depth of 1.0 meter is needed when attempting to assess rooting depth of drought resistant and drought susceptible bean genotypes.