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Evaluation of Physiological Parameters and Nitrogen
Partitioning and Remobilization in Beans (*Phaseolus*
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under stress and non-stress soil moisture conditions.
presented by

Mmasera Manthe

has been accepted towards fulfillment
of the requirements for
Doctoral degree in Crop Physiology


Major professor

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**EVALUATION OF PHYSIOLOGICAL PARAMETERS AND
NITROGEN PARTITIONING AND REMOBILIZATION IN
BEANS (Phaseolus vulgaris L.) AND COWPEAS
(Vigna unguiculata (walp) L.) UNDER STRESS
AND NON-STRESS SOIL MOISTURE CONDITIONS**

BY

MMASERA MANTHE

A DISSERTATION

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

DOCTOR OF PHILOSOPHY

Crop Physiology - Crop and Soil Science

1994

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ABSTRACT

Evaluation of Physiological Parameters and Nitrogen Partitioning and Remobilization in Beans (*Phaseolus vulgaris* L.) and Cowpeas (*Vigna unguiculata* (walp) L.) Under Stress and Non-stress Soil Moisture Conditions.

by

Mmasera Manthe

Soil moisture stress adversely affects crop growth and productivity. Crop canopy, the amount of light intercepted, assimilate production and nitrogen accumulation are also influenced by variations in water regimes in the soil. This study was conducted to examine the effect of terminal drought on yield and yield components, root growth and distribution, leaf water status, photosynthesis, stomatal conductance, transpiration ratio, carbon isotope discrimination, and nitrogen partitioning and remobilization in beans (*Phaseolus vulgaris* L.) and Cowpeas (*Vigna unguiculata* (walp) L.). The research was conducted in Michigan using either a rainshelter or black polyethylene plastic to impede water on a mixed mesic aericochraqualfs soil or a mixed mesic glossoboric hapludic soil, respectively. Moisture stress was imposed at the late vegetative stage (V₉) of plant growth. Four categories of beans and cowpeas were used in these studies: 1) drought resistant and high yielding; 2) drought resistant and low yielding; 3) drought susceptible and high yielding, and 4) drought susceptible and low yielding.

Moisture stress reduced bean yield by up to 50% and pods per plant by 36%. Leaf water retention capacity and leaf water content were significantly reduced by

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moisture stress in both beans and cowpeas. Relative water content was not influenced by moisture stress but varied among genotypes. Drought stress decreased root growth rate. resistant bean genotypes had a lower reduction in root growth rate than the susceptible genotypes.

Photosynthetic rate was reduced by moisture stress in beans and cowpeas but there were no genotypic differences. Stomatal conductance was not affected by moisture stress in beans but was decreased by stress in cowpeas. Soil moisture stress did not affect carbon isotope discrimination (CID) in either beans or cowpeas, but drought resistant bean genotypes had lower CID values.

Soil moisture stress decreased the proportion of ^{15}N in the roots, stem and leaves in beans and cowpeas. Drought resistant bean genotypes maintained their N remobilization levels under stress. Nitrogen concentration and dry weight were decreased by moisture stress.

—

Dedicated to my grandmother
MORWADI EMILY MANTHE

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INTRODUCTION

Beans (Phaseolus vulgaris L.) and cowpeas (Vigna unguiculata (walp) L.) are important grain legume crops in many countries around the world. They are used mainly in the grain form, however, green immature pods and leaves are also consumed as a vegetable. They are a source of essential proteins (22-24%), vitamins and minerals (Bressani, 1985). While these crops play a significant role in the diets of many developing countries, their importance is limited by their high cost relative to cereals due to low yield production. Global estimates indicate that unpredictable periods of drought occurring within the normal rainy season may account for an average production loss of 15% in tropical areas (Fischer et al., 1983). Christiansen (1982) estimated that production on 26% of the world's 14 billion hectares of arable land is limited by drought stress and that 85% of global cropland is rainfed.

Drought stress, as defined here, is when the amount of water available to the plant is insufficient to sustain growth and development. Drought stress may be terminal in which there is a gradual decrease of water through plant maturation, or it may be intermittent. Intermittent drought may be of short duration up to 1 week or of long duration, 3-4 weeks, and occurs at one or more times throughout the season. Drought resistance is defined as the ability of a genotype to survive drought stress with minimal yield loss. Drought resistant mechanisms have been discussed at great length by Levitt (1956, 1972, 1980). As soil moisture stress increases, growth will be retarded relative to the degree of "tolerance" of the tissues or the "avoidance" of the whole plant system.

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At a critical level of stress, growth will drop to zero.

Levitt suggested that the mechanisms for drought adaptation be defined as drought escape, avoidance and tolerance. Drought escape tends to minimize the interaction of drought with crop growth and yield. Tolerance gives the ability to produce despite loss of plant water status. Avoidance increases the ability to maintain relatively high plant water status despite a shortage of moisture in the environment (Fischer and Turner, 1978; Fischer and Sanchez, 1979; O'Toole and Chang, 1979).

DROUGHT ESCAPE

Early maturing varieties are known to escape the effects of late drought and this confers yield advantage (Levitt, 1972). Drought escape is often the most important and successful form of drought adaptation and is usually imparted through the combination of genotype maturity and planting date. Ludlow (1989) defined four main features with this strategy: 1) Short phenology which results in low yield potential, 2) developmental elasticity which is good for survival, 3) photoperiod insensitivity in native species so that they can flower and produce seed whenever rain falls, and 4) photoperiod sensitivity in crop plants so that the time of flowering coincides with the average date of the end of the rainy season. Due to the unpredictability of drought, drought adaptation through escape is generally not feasible. Drought adaptation through escape also fails to meet the farmer's needs for longer maturing varieties which will provide leaves for vegetable use. This need can be met through drought adaptation by avoidance or tolerance.

DROUGHT AVOIDANCE

Ludlow (1989) has explained the main features of dehydration avoidance as 1)

sensitivity of the plant tissues to dehydration, a mechanism which has no penalty for growth if water uptake is maximized; 2) maximization of water uptake by developing roots, a mechanism which has a short term but no long term cost for growth if water loss is reduced by elastic responses; 3) minimization of water loss by stomatal control, leaf movement, smaller leaves and the shedding of older leaves; and 4) low osmotic adjustment, little stomatal adjustment and photosynthetic adjustment.

Drought avoidance will result from increased resistance to water flux in the plant or from improved control over vapor transfer at the leaf surface. Resistance to water flux in the plant is greater in the root (Newman, 1974). Increased root resistance may be achieved through increased axial resistance or increased radial resistance. The ability of the root to adjust osmotically to increased soil moisture stress may also be an important component of drought avoidance (Hsaio and Acevedo, 1974; Newman, 1974).

Increasing soil water deficits near the soil surface seems to induce compensatory extension of the roots deeper into the unexploited soil layers. The deep rooting system characterizes plants that are drought avoiders because they are able to exploit soil moisture in the lower soil profiles (Newman, 1974). However, developing a deep root system may not necessarily be a beneficial strategy when soil moisture reserves are unavailable in the deeper levels because the plant then wastes assimilates. Increased root development comes at the expense of shoot growth so shoot growth is at a disadvantage when rain resumes. Drought avoidance promoted by a large, well branched, deep root system with efficiency of soil water extraction is desirable as long as there is moisture to be extracted from the volume of soil contacted by the roots. However, when the water

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supply is exhausted below the crop water requirement, the plant may rapidly suffer desiccation injury.

Reduction in leaf expansion is probably the first indicator of the plant's response to drought stress. A drought susceptible genotype will attain low leaf area which in turn will limit canopy photosynthesis leading to lower productivity (Hsaio, 1973). If drought becomes more severe, the stomata may close in order to minimize loss of water through transpiration. Stomata act as regulators for both carbon dioxide exchange and water loss in plants. So the closure of stomata may directly lead to greater resistance to carbon dioxide uptake and therefore affect photosynthesis and subsequent productivity.

DROUGHT TOLERANCE

The response and tolerance of any plant to reduction in leaf water potential is complex. It may involve any number of physiological and metabolic processes. It can be measured at the individual process level or at an integrated level. Growth as an integrated response can serve as a measure of plant tolerance under stress if and when maintenance of growth under stress is required (Berg and Turner, 1976; Blum, 1970).

When the tissue is not protected from dehydration by avoidance mechanisms, cells lose turgor and dehydrate. Several basic physiochemical events occur at the cellular level under the effect of dehydration such as reduction in the chemical activity of water, concentration of solutes and macromolecules, removal of water of hydration from macromolecules and alterations in the cellular membranes (Blum, 1988). Ludlow (1989) described dehydration tolerance as a measure of the plant's capacity to withstand severe dehydration defined in terms of leaf water potential (LWP), or relative water content

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(RWC) of the last surviving leaf on a plant subjected to a slow, continuous soil drying cycle (lethal value).

Osmotic adjustment results from the accumulation of solutes within cells, which lowers the osmotic potential and helps maintain turgor of both shoots and roots as plants experience water stress. This allows turgor driven processes such as stomatal opening and expansion growth to continue, although at reduced rates, to progressively lower water potentials. Ludlow (1989) contends that dehydration tolerance has moderate to high osmotic adjustment which is a good long term leaf and plant survival mechanism. On the other hand, Levitt (1980) noted that osmotic adjustment is an avoidance mechanism. Blum (1988) reported that when dehydration avoidance is expressed in terms of the maintenance of a higher water or turgor potential under conditions of water stress, osmotic adjustment as a means of retaining a higher turgor at a given tissue water potential is a component of dehydration avoidance. Ludlow and Muchow (1989) concluded that osmotic adjustment is positively correlated with dehydration avoidance and tolerance only if soil water is not exhausted and is negatively correlated with dehydration avoidance if soil water is exhausted.

At present the best and ultimate indicator of drought resistance used in breeding programs is grain yield measured under well-watered and water-stressed conditions. It would greatly aid the plant breeding process if a physiologically based drought resistance indicator could be found that breeders could use as a selection tool in large segregating populations or to screen potential parental lines. One approach to searching for such a physiological screening tool is to compare genotypes of the same species and of known

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but differing levels of drought resistance. This research study was conducted to evaluate physiological characteristics in beans and cowpeas and to determine the characteristics that can be used as screening tools in a breeding program designed to develop drought resistant lines. Most studies often look at the physiological parameters individually. This study was designed to simultaneously study physiological characteristics such as CO₂ assimilation rate, stomatal conductance, transpiration ratio, carbon isotope discrimination, radiation interception, leaf water, root growth, and nitrogen partitioning and remobilization.

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LITERATURE REVIEW

Effect of drought on yield and yield components

Drought stress which occurs during the growth of beans and cowpeas affects many physiological and morphological characteristics associated ultimately with seed yield. The duration and intensity of drought stress as well as the phenological stage of the crop at the time the stress occurs will determine the amount of damage done to the crop and therefore yield. The yield of beans and cowpeas may be considered as the product of their components: number of pods per plant, number of seeds per pod, number of plants and individual seed weight.

There is general agreement in the literature that the reproductive stage is the most sensitive to water stress in legumes, affecting seed yield by reducing pod set and single seed weight (Diputado and Rosario, 1985; Acosta-Gallegos and Shibata, 1989; Acosta-Gallegos and Adams, 1991; Gwathmey and Hall, 1992; Herbert and Baggerman, 1983). Shouse et al. (1981) reported yield reduction by moisture stress of 35 % at flowering and 69% at the pod fill stage in cowpeas. In beans, when drought stress was imposed at the beginning of the reproductive phase, it reduced seed yield 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. The number of pods per plant was the yield component most affected by water stress.

Summerfield et al. (1985) noted that in cowpeas under moderate water stress,

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determinate cultivars produced close to normal seed yield in spite of the stress imposed at flowering because the plants matured their fruits before the stress became severe. When more severe stress was imposed at different times of the reproductive period, stomatal closure and reductions in leaf area combined to limit dry matter production and led to substantial decreases in seed yield. Concurrent reduction in pod production and leaf area in cowpeas and beans due to drought stress has been reported by others also (Gwathmey and Hall, 1992; Acosta-Gallegos and Adams, 1991).

Effect of drought on leaf water relations

Plant water deficit is described in terms of water content or the energy status of the water in the cell. The water content is usually expressed as relative to that at full saturation. The relative water content and the energy status of the water is usually expressed as the total water potential (Turner, 1982). The ability of plants to retain water is important particularly under drought conditions. Leaf water content estimates the capacity of water retention by detached leaves at the time of detachment. Leaf water retention capacity measures percentage moisture lost after 24 or 48 hours of leaf detachment. The degree to which plants withstand desiccation, expressed as relative water content or water potential at which leaves die is called the critical or lethal value (Ludlow and Muchow, 1989). Low lethal water status influences the plant's survival by contributing to dehydration tolerance and leaf survival during intermittent drought stress and therefore to yield stability.

Walker (1983) observed that cowpea genotypes which previously had been found to have a high biomass production potential under drought conditions also had high leaf

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water retention capacity, suggesting that this trait can be used to improve seed yield of water stressed plants. Significant differences for leaf drying have also been detected between genotypes and for the interaction between genotype and time after detachment (Walker and Miller, 1986). Cowpeas exposed to drought stress maintained a fairly constant level of relative water content when drought was imposed at 20 to 50 days after emergence (Nagarajah and Schulze, 1983). When the stomates started to close, relative water content was as high under drought stress as in well watered controls. The maintenance of a high relative water content in the leaves characterized cowpea as a drought avoiding species (Bates and Hall, 1982).

In beans, leaf water content and leaf water retention capacity increased under drought stress (Acosta-Gallegos and Adams, 1991). Ramirez-Vallejo (1992) found a reduction in relative water content under stress and an increase in leaf water retention capacity in beans. There were also genotypic differences in leaf water content and relative water content. Genotypic differences in relative water content in wheat have also been observed (McCraig and Romagosa, 1991; Ritchie et al., 1990).

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 matter of higher plants is derived from CO₂ assimilated by photosynthesis (Zelith, 1982). Zelith contends 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 plants.

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It is now well established that the rate of CO₂ assimilation in the leaves is depressed at moderate leaf water deficits or even before leaf water status is changed in response to a drop in air humidity or in soil water potential. In such cases stomatal control of CO₂ diffusion plays the most important role in controlling photosynthesis. When drought period is lengthened, dehydration is more severe or other environmental stresses are superimposed. Changes may occur in metabolic functions and/or in whole plant behavior (Chaves, 1991).

CO₂ 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 CO₂ assimilation rate remained constant. Kuppers et al. (1988) concluded that the response of CO₂ assimilation and stomatal conductance during soil drying was fairly independent of the water status of the leaf. Similar observations by Bates and Hall (1981) indicated that stomatal closure due to soil water depletion was not associated with changes in leaf water status.

Studies on cotton (Gossypium hirsutum L.) have shown that an increase in stomatal resistance was associated with a substantial reduction in the photosynthetic rate as a result of moisture stress (Epithrath et al., 1990). Stomata limited the photosynthetic process in well-watered plants or in mildly stressed plants while mesophyll resistance was the main factor reducing it under more severe moisture stress. Early stress treatments had lower stomatal resistance and higher photosynthetic rates than the late stressed treatments.

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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 can be used to select genotypes for higher productivity. They observed that leaf photosynthesis, total biomass and grain production were significantly reduced by limited water supply. Leaf photosynthesis was positively correlated with total biomass and grain production. Similarly, Hamdani et al. (1991) showed genotypic reduction in water potential, stomatal conductance and CO₂ assimilation rate with decreasing available soil water. They concluded that stomatal conductance and photosynthesis have the potential to be used as screening tools for drought resistance of sorghum genotypes at the vegetative stage of growth.

Effect of drought on carbon isotope discrimination

Stable carbon isotopic composition is a potentially valuable characteristic for evaluating breeding lines for productivity and water use efficiency (WUE) on the basis of integrated plant responses (Johnson et al., 1990; Ehleringer et al., 1991). As water becomes limiting for a plant, the stomata eventually exhibit some degree of closure. If this closure restricts water loss from the leaf proportionately more than the decrease in photosynthetic rate (A) then intercellular CO₂ (c_i) is reduced (Cowan and Troughton, 1971). This response results in water savings to the plant and a subsequent increase in WUE. Because ribulose biphosphate carboxylase oxygenase (Rubisco) discriminates against ¹³CO₂, the proportion of ¹³CO₂ to ¹²CO₂ increases within the leaf. With this increased concentration of ¹³CO₂ in the interior of the leaf compared to ¹²CO₂, Rubisco has less opportunity to discriminate against ¹³CO₂. Consequently, ¹³CO₂ discrimination

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Although c_i and WUE can be reliably and accurately measured by gas exchange procedures, these are generally instantaneous measurements that do not provide information over an extended period of time. Because carbon is continually being fixed, carbon isotope discrimination can be used to provide a long term indication of c_i , and therefore measurements of CID reflect the combination of ^{13}C and ^{12}C over the development of the particular tissue being analysed. This combining ability suggests that measurements of CID may differentiate between genotypes better than most instantaneous physiological assays (Johnson et al., 1990).

Hall et al. (1992) in their review concluded that genotypic differences in CID were more consistent than differences in A/g , photosynthetic rate or stomatal conductance and so should be easier to select for in breeding. Ismail and Hall (1992) indicated significant correlations for WUE, CID, specific leaf weight, biomass, water use and leaf area per plant in cowpeas. Similar observations have also been made in beans (White et al., 1990). White et al. (1990) found a positive correlation between root length density and CID, concluding that leaf physiology (as measured by CID) was not independent of root activity and rooting density. Ehleringer et al. (1991) reported that CID is significantly correlated with transpiration efficiency estimates in beans.

In coffee (Coffea arabica L.), photosynthetic rates and stomatal conductance have had a positive correlation with CID (Meizner et al., 1990). Studies were made to evaluate CID on the leaves as well as the grain. In cowpea, leaf CID detected genotypic differences more readily than grain CID (Hall et al., 1990). This study also concluded

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that selection based upon CID in cowpeas should be equally effective under wet or dry conditions.

Effect of drought on root growth

Roots play an important role in the growth and survival of plants during periods of drought stress. Under drought, the root is characterized by a low root density in the dry surface layer and a higher root proliferation in the deeper, wetter soil layers. However, under non-stress conditions, roots proliferate in the soil zone with the lowest soil water retention (Garay and Wilhelm, 1983). In Peanuts (Arachis hypogaea L.) root growth from 20 to 50 days after planting was significantly reduced in the upper 40 cm of the soil profile by drought stress, but recovered upon rewatering (Meisner and Karnok, 1992).

Box et al. (1989) reported a 37% reduction in roots in the top 20 cm during an 18 day drought period and a 50% increase in root number at 60 to 150 cm depth in wheat (Triticum aestivum L.). The response to short term drought suggests that large quantities of photo-assimilated carbon may have been lost to the rhizosphere at the depth of shallow roots. Additionally, new allocations of plant carbon were required for the new growth of roots at greater soil depth.

It is generally agreed that there is more root growth at greater depths under drought stress (de Vries et al., 1989; Smucker et al., 1991; Stofella et al., 1979; Obisesan, 1986; O'Toole and Bland, 1987). In cowpeas under mild drought stress, Nagarajah and Schulze (1983) showed an increase in absolute root growth. In the early stages of soil drought, root weight in the stressed plants was greater than that of the

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Effect of drought on nitrogen partitioning and remobilization

Nitrogen metabolism is essential for crop growth and development. The assimilation and distribution of nitrogen in the vegetative and reproductive parts of edible grain legumes is an important process in determining seed yield (Westerman et al., 1985). Nitrogen assimilation and distribution during seed filling have a significant influence on the final seed nitrogen concentration and yield in beans. Evidence of differences in nitrogen accumulation, partitioning and remobilization among the limited number of species and cultivars studied to date supports the concept of studies to more strenuously evaluate differences among cultivars which vary in their resistance to drought (Chapman and Muchow, 1985; DeVries et al., 1989; Sinclair and Horie, 1989).

The literature indicates that a great proportion of the total nitrogen is translocated to the reproductive parts (pods and seeds) of grain legumes. Under water stress, cowpeas translocated a greater proportion of the total nitrogen to the pods than did well watered control plants (Wein et al., 1979). Similarly, Lynch and White (1992) reported that total nitrogen allocation to the seeds dominated the reproductive nitrogen budget in beans. They concluded that the relatively small nitrogen allocation to leaves as opposed to seeds suggested that carbon gain during reproductive growth may be limited by seed nitrogen demand.

Yield is positively associated with the seed filling duration and negatively associated with seed protein concentration. In general, high seed protein genotypes exhibit faster nitrogen partitioning and dry matter allocation into seeds, shorter seed

filling duration and lower yield (Navaro et al, 1985). On the other hand, Boon-Long et al.(1983) suggested that neither the maximum level of total nitrogen in the leaf nor the rate of redistribution seems to be closely related to the final seed yield.

The contribution of redistributed nitrogen to seed nitrogen varies among cultivars and is increased by nitrogen stress applied during the reproductive growth. Egli et al. (1983) reported that moisture stress did not consistently alter the contribution of redistributed nitrogen to the nitrogen in the seed. In soybeans (Glycine max L.), nitrogen accumulation in the roots and nodules was much less affected by irrigation treatment than was nitrogen accumulation in the shoots (Sinclair et al., 1987). In beans, the susceptible genotype utilized nitrogen less efficiently than the resistant genotype (Foster et al., 1991). The results also indicated that the shoot may be a greater determiner than the root with regard to nitrogen concentration and efficiency.

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CHAPTER 1

THE EFFECT OF SOIL MOISTURE STRESS ON DRY BEANS (Phaseolus vulgaris L.) AND COWPEAS (Vigna unguiculata L. (walp)). I. Yield and Yield Components, Leaf Water Status and Root Growth.

ABSTRACT

Soil moisture stress adversely affects the growth of different plant organs and hence crop productivity. This study was conducted to examine the effect of terminal drought on yield, pods per plant, seeds per pod, leaf water, and root growth and distribution of beans (Phaseolus vulgaris L.) and cowpeas (Vigna unguiculata L. (walp)) under field conditions. The research was conducted in Michigan using either a rainshelter or black polyethylene plastic to impede water on a mixed mesic aericochraqualfs soil or a mixed mesic glossoboric hapluidulfs soil, respectively. Moisture stress was imposed at the late vegetative stage (V₉), 37 and 55 DAP in 1990 and 1992 respectively.

Drought stress reduced seed yield by up to 50% in beans. Pods per plant were significantly reduced under stress by 36% in beans, but seeds per pod were not sensitive to a decrease in soil water content. Pods per plant and yield maintained a significant, consistent correlation in 1990 and 1992. Soil moisture had no effect on relative water content. Leaf water retention capacity and leaf water content were significantly reduced by moisture stress. Plants maintained high relative water content, leaf water retention

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capacity and leaf water content throughout each season. Drought stress decreased root growth rate in both beans and cowpeas. Resistant bean genotypes had a lower reduction in root growth rate than susceptible genotypes.

INTRODUCTION

Soil moisture stress occurring at flowering or pod filling stages has a detrimental effect on yield, but the effect is greatly influenced by the rate and duration of moisture stress. Akyeampong and Steponkus (1981) reported a 30% yield reduction when stress was imposed at flowering and an 80% yield reduction when stress was imposed at the pod filling stage in cowpeas (Vigna unguiculata L. (walp)). Yield reductions were largely due to a decrease in the number of pods per plant. Muchow (1985) showed similar results in soybeans (Glycine max L.), pigeon pea (Cajanus cajan L.), lablab bean, green gram, black gram and cowpeas.

The degree to which plant parts withstand desiccation is often expressed in terms of leaf water content at the time when the leaves die, thus the critical or lethal value. In excised wheat (Triticum aestivum L.) leaves, drought resistant genotypes lost water at a slower rate than the less resistant genotypes (Clarke and McCaig, 1982). A significant genotype x environment interaction has also been reported (Clarke, 1983).

Roots play an important role in the growth and survival of plants during periods of drought stress. Root characteristics are of primary importance in determining drought response of common beans (White and Castillo, 1989). Under conditions of water stress, root growth in the surface soil layers is relatively slow while the growth of new roots in

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The objective of this study was 1) to investigate the response of yield and yield components to drought stress, 2) to evaluate the potential use of leaf water status as a screening tool, and 3) to evaluate root growth and distribution in response to drought stress.

MATERIALS AND METHODS

A field study was conducted at the Agronomy Research Farm at Michigan State University in East Lansing during the summers of 1990 and 1992. In 1990 a rainshelter was used to impose moisture stress during the late stage of vegetative of growth (V_9) at 37 DAP. In 1992, black polyethylene plastic was used to impose moisture stress during the late stage of vegetative growth (V_9) at 55 DAP. The plastic was placed between rows and on non-rainy days it was rolled inside so that the soil surface was exposed for drying.

The soil type for the 1990 experiment was a fine loamy, mixed mesic aeris ochraqualfs with a slope of 0-3% (USDA Soil Conservation Service Classification). For the 1992 experiment, it was a fine loamy, mixed mesic glossoboric hapluidalfs with a slope of 2-6%. The rainfall and temperature data are presented in Fig 1 and Table 1 of Appendix A.

The experimental design was a modified split plot with four replications. The main plot was the moisture level and genotypes were the subplots. The moisture factor

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was confounded by site difference in that all stressed plots were grouped together and all non-stressed plots were grouped together. Each plot had four rows of 2 m length. The bean spacing was 50 x 10 cm and the cowpea spacing was 75 x 20 cm which resulted in a plant density of 20 plants per m² for beans and 10 plants per m² for cowpeas. In 1990 two bean genotypes (9-39-1 and 8-42-M-2) and two cowpea genotypes (TVX 3236 and B005-C) were used. In 1992 four bean genotypes (9-39-1, 8-42-M-2, N81017 and 8-25-2) and four cowpea genotypes (TVX 3236, Blackeye, ER₇, and IT83S-742-2) were used. The bean genotypes were chosen based upon their previous performance in the MSU bean breeding program and their subsequent designation as either drought resistant or susceptible. The cowpea genotypes were chosen based upon their performance from a preliminary growth chamber study conducted in 1989 and their performance in field studies at ITTA and in Botswana. Genotypic descriptions are presented in Table 2 of Appendix A.

Plots were hand planted using a hoe to open rows and 40 or 20 seeds were planted per row for beans and cowpeas respectively, along with abundant inoculant. The bean inoculum was Rhizobium phaseoli and the cowpea inoculum was Rhizobium Cowpea miscellany nitrogen EL.

Planting and Management Practices

1990

Both beans and cowpeas were planted on June 25 but because of poor germination the cowpeas were replanted on July 18. Fertilizer was applied as 19-19-19 at the rate of 40 Kg N/ha before planting. Three days after planting on June 28 all plots received 30

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mm of irrigation to facilitate germination. Total rainfall during the growing season (June 25-Oct 5) was 287.6 mm. On July 31, Sevin (Carbaryl insecticide) was applied at the rate of 4 teaspoons per gallon of water to control Mexican bean beetle and leafhopper.

1992

Planting occurred on June 12. The fertilizer 21-7-14 with 4 % Mn and 1 % Zn was applied at the rate of 40 Kg N/ha before planting. All plots received a total of 283.3 mm of irrigation in four applications before stress was imposed. The total rainfall during the growing season (June 12-Sept. 16) was 309.0 mm. A greater amount of irrigation was applied in 1992 in order to break the soil crust and enhance germination and plant stand establishment. Sevin was applied on July 29 to control leafhopper.

Soil moisture was monitored regularly in all plots at three depths in 1990 (0-30, 30-60, 60-90 cm) using a neutron probe. In 1992 readings were only recorded at the 0-30 and 30-60 cm depth because the field had a high water table. Undisturbed soil core samples were taken at the same depths to develop a soil moisture desorption curve which was used to convert the volumetric moisture content into matric potential. In 1992 leaf temperature, using the infrared thermometer and soil temperature were monitored. Leaf temperature was recorded on a single leaf per plant and on three plants per plot. Soil temperature was recorded from the center row of each plot.

Leaf Water Status

Relative water content (RWC) was determined in 1990 and RWC, leaf water content (LWC) and leaf water retention capacity (LWRC) were determined in 1992. Weather permitting, measurements were made every two weeks after stress was imposed.

Three plants per plot at the same growth stage were tagged and marked A, B and C. The center leaflet of the youngest fully developed leaf was placed in a plastic bag marked A₂, B₂ or C₂ depending on whether it was from plant A, B or C respectively. With the leaf face-up, the leaflet on the right was labelled A₃, B₃ or C₃ and the leaflet on the left was labelled A₁, B₁ or C₁. The RWC, LWC and LWRC measurements were made on samples marked number 1, 2 and 3 respectively. Immediately after leaf detachment, the samples were placed in ziplock bags and stored on ice in a cooler until their fresh weight was recorded.

RWC: Each sample was weighed and placed in a petri dish and covered with distilled water. After 4 hrs, turgid weight was recorded. The leaves were then oven dried at 70° C for 24 hrs to determine the dry weight. The RWC was computed as: $(Fw - Dw) / (Tw - Dw) * 100$.

LWC: The fresh weight was recorded. Then, leaves were oven dried as described above. The LWC was computed as: $(Fw - Dw) / Dw * 100$.

LWRC: After the fresh weight was recorded, samples were left uncovered in a dark environment at room temperature for 48 hrs. After 48 hrs, air dry weight (Dw₁) was recorded, leaves were oven dried at 70° C for 72 hrs, and the dry weight (Dw₂) was recorded. The LWRC was computed as: $(Fw - Dw_1) / (Fw - Dw_2) * 100$.

Root Growth

Root measurements were made using a minirhizotron camera. Only live roots were counted. This provided information on root distribution along the soil profile. Root growth rate was calculated from root counts of two successive recording dates as follows;

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(root count on date 1 - root count on date 2)/ number of days between date 1 and date 2, which was reported as number of roots/ cm²/ day. Each plot had one 6 foot x 2 inch inside diameter tube inserted at a 45° angle into the center row to a depth of 3 feet and measurements were taken, weather permitting, every 30 days.

At physiological maturity seed yield and yield components were recorded on the two center rows. The drought intensity index (DII) for the site and the drought susceptibility index (DSI) of each genotype was determined by the method of Fischer and Maurer (1978) (Appendix A). All measured parameters were analysed by MSTAT microcomputer statistical package for agricultural sciences or by the SAS package.

RESULTS AND DISCUSSION

Soil Moisture

The rainshelter used in 1990 provided moderate moisture stress. Soil water content decreased with increasing drought for the stress and non-stress treatments at all depths (Fig 1). The soil water content was lower for the stress than the non-stress treatment only at the 30 cm depth. At the 60 and 90 cm depths the stress treatment had higher moisture than the non-stress treatment. In 1992, the field had a high water table and rainfall was frequent and excessive during the season. Consequently the access tubes were usually full of water, making it impossible to take readings as scheduled. As a result only two readings were recorded. The stress treatment had higher moisture at the 60 cm depth (Fig 2). There was no difference at the 30 cm depth.

FIG 1. VOLUMETRIC SOIL MOISTURE CONTENT IN 1990

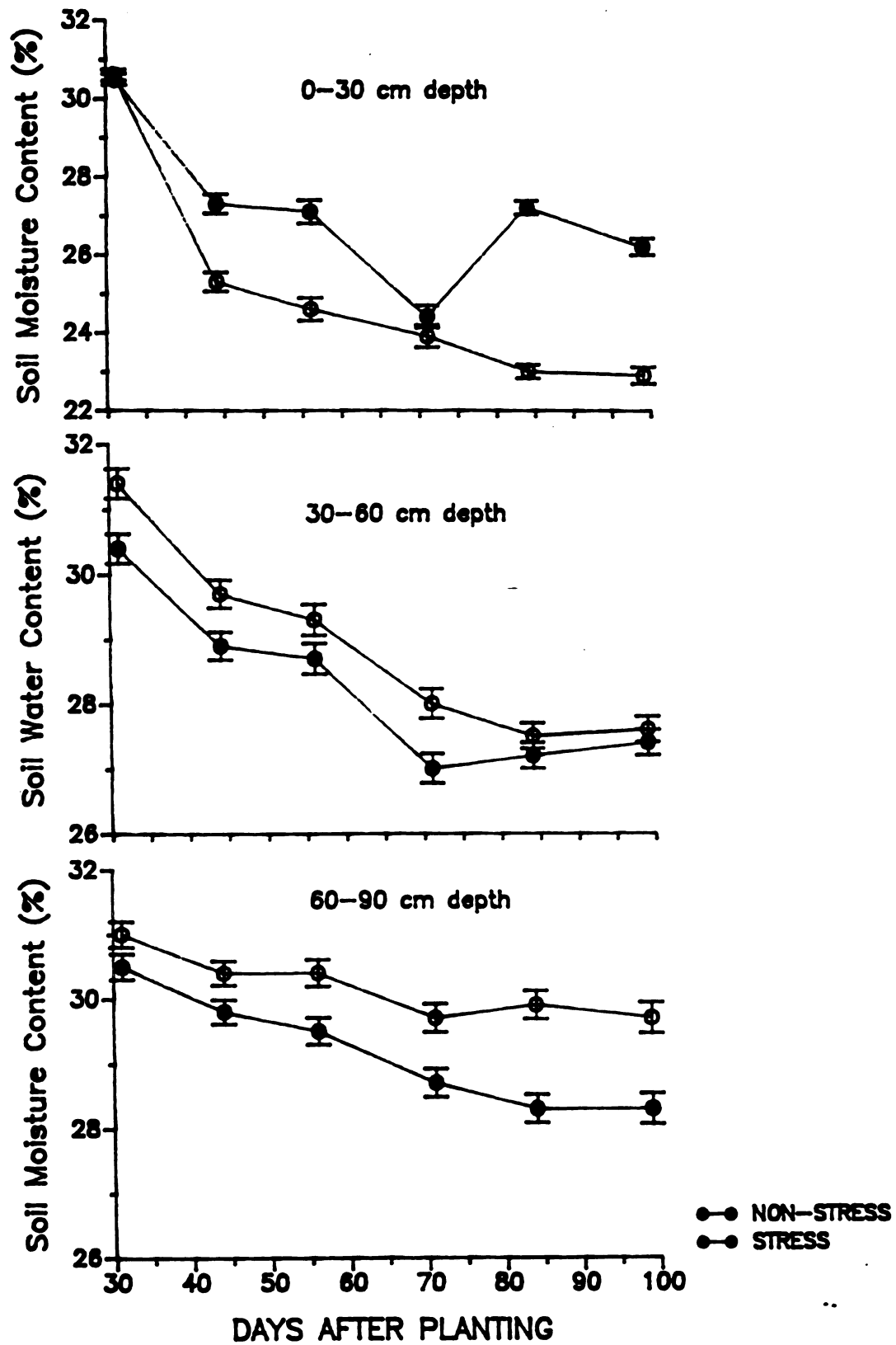
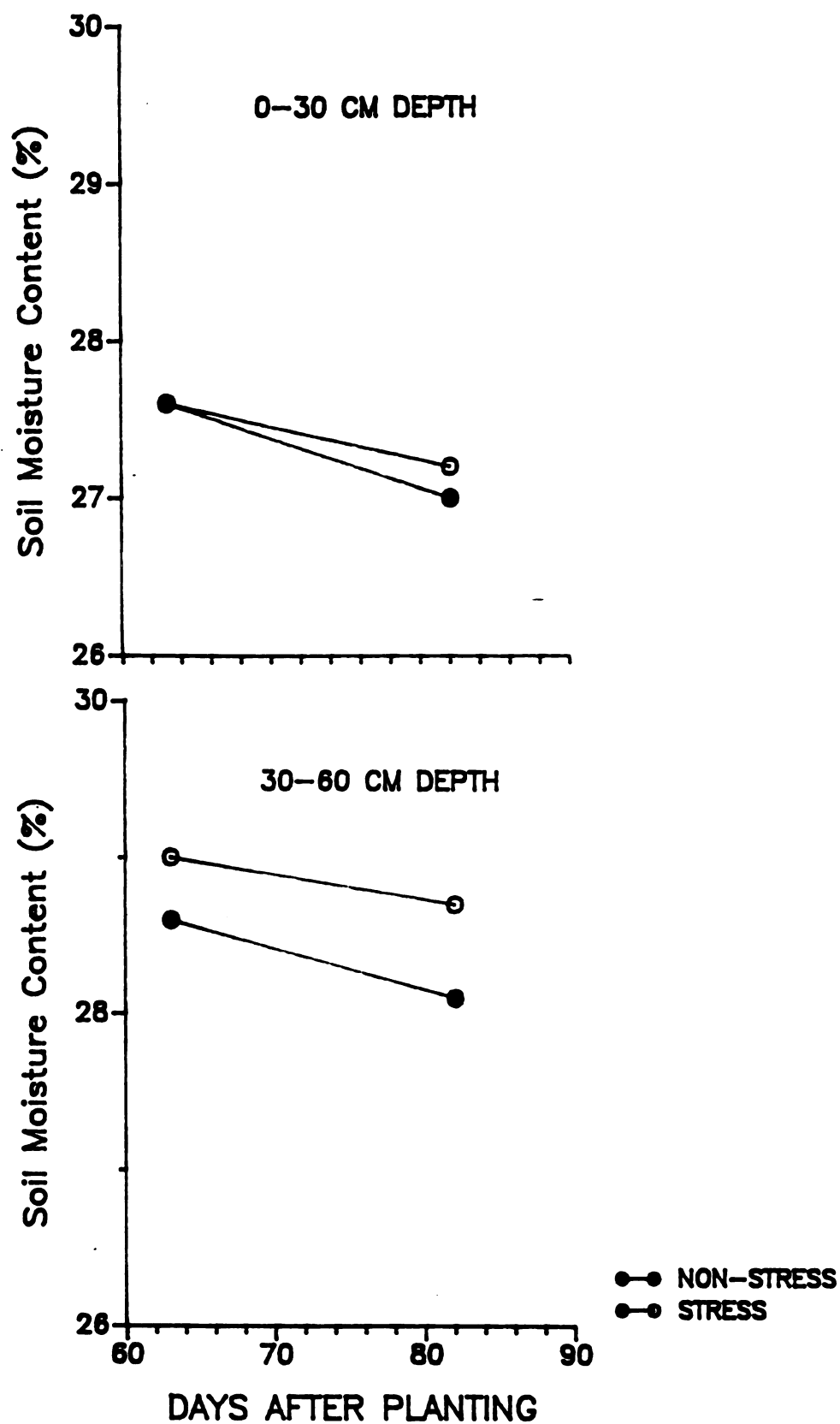


FIG 2. VOLUMETRIC SOIL MOISTURE CONTENT IN 1992



BEANS

Yield data

1990

Moisture stress significantly reduced yield of 8-42-M-2 by 51.4% but had no significant yield reduction on 9-39-1 (Table 1). The genotype 8-42-M-2 yielded significantly higher due to the greater yield of 8-42-M-2 under non-stress conditions. Pods per plant were significantly reduced by stress but seeds per pod did not differ between moisture treatments or genotypes.

1992

In the rainshelter, the genotypes N81017 and 8-25-2 did not show any differences between stress and non-stress. The drought intensity index was 0.07, indicating that there was essentially no stress. N81017 yielded significantly higher than 8-25-2 (Table 2). When plastic was used, the stress treatment had a significantly higher yield than the non-stress treatment (Table 3), due mainly to 9-39-1 which had a significantly reduced yield under the non-stress treatment. 1992 was an excessively wet year and the plastic did help to retard moisture penetration. Most of the time the soil was saturated. Often when soil moisture or minirhizotron readings were recorded, water had to be pumped out of the tubes prior to taking readings. The reduced yield of 9-39-1 under non-stress conditions may be due to excess moisture. The low yield of 9-39-1 under the non-stress treatment is considered reduced because the higher yield under stress is consistent with the yield that was obtained for 9-39-1 in 1990 and previous studies (unpublished results). Thus, 9-39-1 may be more susceptible to excess moisture than the other genotypes. The

TABLE 1. Yield and Yield Components of Bean Genotypes in a Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	SEEDS PER POD	PODS PER PLANT	YIELD (Kg/ha)	GEOMETRIC MEAN	% YIELD REDUCTION
8-42-M-2 (S) (NSD)	6 6	6 b 11 a	1395.1 b 2873.2 a	2002.1	51.4
9-39-1 (S) (NSD)	6 6 ns	8 b 10 a *	1288.5 b 1349.9 b *	1318.9	4.6
GENOTYPE					
8-42-M-2	6	9	2134.2 a		
9-39-1	6 ns	9 ns	1319.2 b **		
WATER					
Stress	6	7 b	1341.8 b		
Non-stress	6 ns	11 a **	2111.6 a **		

S = Stress NSD = Non-stress ns = not significant

**, * Different letters within a column indicate significant difference at p= 0.01 or 0.05 respectively according to Duncan Multiple Range Test

TABLE 2. Yield and Yield Components of Bean Genotypes in a Rainshelter
at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT	SEEDS PER POD	PODS PER PLANT	YIELD (Kg/Ha)	GEOMETRIC MEAN	% YIELD REDUCTION
N81017 (S)	5 b	15	1783.3		
(NSD)	5 b	13	1988.3	1883.0	10.3
8-25-2 (S)	5 b	11	1065.0		
(NSD)	6 a	10	1068.3	1066.6	0.31
	+	ns	ns		
GENOTYPE					
N81017	5	14 a	1885.8 a		
8-25-2	5	10 b	1066.7 b		
	ns	*	*		
WATER					
Stress	5 b	13	1424.2		
Non-stress	6 a	11	1528.3		
	*	ns	ns		

S = Stress NSD = Non-stress ns = not significant

*, + Different letters within a column indicate significant difference at $p = 0.05$ or 0.1 respectively according to Duncan Multiple Range Test.

TABLE 3. Yield and Yield Components of Bean Genotypes Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	SEEDS PER POD	PODS PER PLANT	YIELD (Kg/Ha)	GEOMETRIC MEAN	% YIELD REDUCTION
8-42-M-2 (S) (NSD)	5	9	2151.2 a		
	5	8	1885.1 ab	2013.8	12.4
9-39-1 (S) (NSD)	5	10	1236.9 bc		
	4	4	326.1 d	635.1	73.6
N81017 (S) (NSD)	6	13	1835.5 ab		
	5	11	1919.7 ab	1877.1	4.4
8-25-2 (S) (NSD)	5	8	937.7 cd		
	5	8	1438.8 abc	1161.5	34.8
	ns	ns	+		
GENOTYPE					
8-42-M-2	5	9 ab	2018.2 a		
9-39-1	5	7 b	781.5 c		
N81017	6	12 a	1877.6 ab		
8-25-2	5	8 b	1188.3 bc		
	ns	*	*		
WATER					
Stress	5	10 a	1540.4 a		
Non-stress	5	8 b	1392.4 b		
	ns	*	*		

S = Stress NSD = Non-stress ns = non-significant
*, + Different letters within a column indicate significant different at p = 0.05 or 0.1 respectively according to DMRT.

genotypes 8-42-M-2 and N81017 were high yielding and had a low yield reduction under stress. 9-39-1 had the highest yield reduction (Table 3), but it occurred in the non-stress treatment.

As reported by others, a significantly high correlation was observed between yield and pods per plant for both seasons (Table 4), (Acosta-Galegos and Shibata, 1989; Acosta-Gallegos and Adams, 1991; Neinhuis and Singh, 1986; Ramirez-Vallejo, 1992).

Drought Susceptibility Index

Originally, 8-42-M-2 was thought to be drought resistant and 9-39-1 drought susceptible. The 1990 and 1988 (unpublished) results indicated that 9-39-1 is actually resistant but low yielding and that 8-42-M-2 is high yielding, but susceptible (Table 5), based upon the Fischer drought susceptibility index (DSI). Since no stress occurred in the rainshelter in 1992, only results from the plastic were used to categorize the genotypes. N81017 was categorized as resistant and 8-25-2 was categorized as susceptible (Table 5). Based on the Fischer index, the geometric mean, the arithmetic mean and % yield reduction under stress a new classification was developed to define all genotypes as follows;

1. Resistant with high yield potential (RH)
2. Resistant with low yield potential (RL)
3. Susceptible with high yield potential (SH)
4. Susceptible with low yield potential (SL)

When the Fischer index was pooled for both seasons, N81017 ranked as a resistant genotype with a high yield potential and 9-39-1 as an average resistant genotype with low

TABLE 4. Yield and Yield Component Correlations

1990

	Yield	PPS	SPP
Yield	---	0.65**	-0.05
PPP		---	-0.23
SPP			---

1992

Plastic Expt.

Yield	---	0.68***	0.41
PPP		---	0.40
SPP			---

Shelter Expt.

Yield	---	0.69*	0.27
PPP		---	-0.12
SPP			---

PPP= Pods per plant SPP= Seeds per pod

* p= 0.05 ** p= 0.01 *** p= 0.001

**TABLE 5. Drought Susceptibility Index
and Drought Intensity Index**

GENOTYPE	RAIN SHELTER 1990	PLASTIC EXPT. 1992	RAIN SHELTER 1992
DII	0.36	0.17	0.07
DSI			
N81017	----	0.23	1.43
9-39-1	0.14	----	----
8-42-M-2	1.42	----	----
8-25-2	----	2.06	0.04

DSI: 0.0= Maximum Resistance
 1.0= Average Resistance
 > 1.0= Susceptible

DII: 0.0= No stress
 1.0= Maximum stress

**Pooled Drought Susceptibility
Index, 1990 and 1992**

N81017	0.8	Resistant
9-39-1	---	
8-42-M-2	2.3	Susceptible
8-25-2	2.2	Susceptible

yield potential. 8-42-M-2 ranked as a susceptible genotype with high yield potential and 8-25-2 as a susceptible genotype with low yield potential (Table 5). This classification of genotypes allows for easy evaluation of physiological parameters and determination of yield potential which is important in selecting for high yield.

Leaf Water Status

1990

RWC was the only leaf water measurement taken. The effect of soil moisture stress on RWC was measured at 19 days after stress was imposed, at flowering and pod development (R_1/R_2) stage (Table 6). Subsequent measurements were made at early pod fill stage (R_4) and at late pod fill stage (R_6), 34 and 47 days after stress was imposed respectively. There were no significant differences between stress and non-stress treatments or between genotypes. The RWC values were generally high, between 83 and 93%.

1992

There was a significant reduction in RWC under stress 13 days after stress was imposed (DAS) and also a genotypic difference at 27 DAS, R_6 (Table 8). At 27 DAS, N81017 (resistant and high yielding) had a lower RWC than 8-25-2 (susceptible and low yielding). The other two genotypes, 9-39-1 (resistant and low yielding) and 8-42-M-2 (susceptible and high yielding) were not significantly different from N81017 and 8-25-2. These results suggest that RWC as determined here with a 4 hour imbibition procedure may not distinguish between drought susceptible and resistant genotypes. Results are not conclusive with regard to moisture stress because there was only minimal stress in 1992.

TABLE 6. The Effect of Soil Water Changes on Relative Water Content in Beans in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>		
	19 ¹	34 ²	47 ³
	%		
8-42-M-2 (S)	86.5	86.6	89.1
9-39-1 "	88.3	87.9	88.8
8-42-M-2 (NSD)	85.0	83.4	90.3
9-39-1 "	90.3	86.8	95.2
	ns	ns	ns
	GENOTYPE		
8-42-M-2	85.6	85.0	89.7
9-39-1	89.3	87.4	92.0
	ns	ns	ns
	WATER		
Stress	87.4	87.3	89.0
Non-stress	87.6	85.1	92.8
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ Flowering and pod development stage (R₁/R₂)

² Early pod filling stage (R₄)

³ Late pod filling stage (R₆)

TABLE 7. The Effect of Soil Water Changes on Relative Water Content in Beans Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	2 ¹	13 ²	27 ³
	%		
N81017 (S)	89.1	80.2	85.8
9-39-1 "	85.8	85.3	89.1
8-42-M-2 "	86.7	81.9	86.4
8-25-2 "	89.6	87.7	88.4
N81017 (NSD)	91.5	83.9	88.9
9-39-1 "	92.2	85.9	94.7
8-42-M-2 "	89.6	86.4	93.2
8-25-2 "	88.7	88.4	97.9
	ns	ns	ns
GENOTYPE			
N81017	90.3	82.1	87.3 b
9-39-1	89.0	85.6	91.9 ab
8-42-M-2	88.2	84.1	89.9 ab
8-25-2	89.2	88.0	93.2 a
	ns	ns	**
WATER			
Stress	87.8	83.8	87.4
Non-stress	90.5	86.2	93.7
	ns	ns	***

S= Stress NSD= Non-stress ns= not significant

***, **, + Different letters within a column indicate significant difference at $p = 0.001$, 0.01 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Late vegetative stage (V_8)

² Flowering and pod development stage (R_1/R_2)

³ Pod filling stage (R_3/R_6)

There were also no differences between stress and non-stress treatments or between genotypes in LWRC and LWC (Tables 8 and 9). These parameters need to be assessed in plants grown under greater stress conditions and with an imbibition time that exceeds 4 hours.

Root Growth

Soil moisture stress did not significantly reduce root growth rate (Table 10) but there was a tendency for root growth rate to be reduced under stress in 1990 (14%). The genotype 9-39-1 maintained its root growth rate under stress while 8-42-M-2 had a 25% reduction. This may partially explain the low yield reduction (4.6%) observed for 9-39-1 compared to the 51% yield reduction for 8-42-M-2 in 1990. Genotypically, 9-39-1 had a lower root growth rate than other genotypes in 1990. It appears that the resistant genotype, 9-39-1 had a lower root growth rate than the susceptible genotype, 8-42-M-2.

Figures 3 and 4 show root distribution of 9-39-1 and 8-42-M-2 at 9 and 50 DAS, respectively, in 1990. There was a tendency for more roots under non-stress treatment at all soil depths for both genotypes. At 9 DAS root count was greater in the top 30 cm of the soil for both genotypes. At 50 DAS, moisture stress greatly reduced root count at 60-90 cm depth in both genotypes. In 1992 the minirhizotron tubes were placed only up to 60 cm depth because the rocky subsoil made it impossible to push the tubes down. Due to the high water table in this field and excessive rainfall later on, only one reading was taken during the season. At the 30 cm depth, all genotypes except N81017 had greater root count under the non-stress treatment. 9-39-1 and 8-42-M-2 had the same root

TABLE 8. The Effect of Soil Water Changes on Leaf Water Retention Capacity in Beans Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	2 ¹	13 ²	27 ³
	%		
N81017 (S)	95.3	96.6	96.8
9-39-1 "	94.6	97.6	97.1
8-42-M-2 "	94.6	94.7	97.6
8-25-2 "	95.1	97.1	98.1
N81017 (NSD)	94.1	97.7	97.5
9-39-1 "	94.6	97.2	98.2
8-42-M-2 "	95.8	97.8	97.8
8-25-2 "	95.6	97.6	97.2
	ns	ns	ns
GENOTYPE			
N81017	94.7	97.2	97.1
9-39-1	94.6	97.4	97.6
8-42-M-2	95.2	96.2	97.7
8-25-2	95.4	97.6	97.2
	ns	ns	ns
WATER			
Stress	94.9	96.5	97.4
Non-stress	95.0	97.6	97.7
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ Late vegetative stage (V₈)

² Flowering and pod development stage (R₁/R₂)

³ Pod filling stage (R₅/R₆)

TABLE 9. The Effect of Soil Water Changes on Leaf Water Content in Beans Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	2 ¹	13 ²	27 ³
	%		
N81017 (S)	79.4	82.1	82.8
9-39-1 "	78.3	81.2	81.7
8-42-M-2 "	80.9	82.0	82.5
8-25-2 "	79.7	81.3	81.2
N81017 (NSD)	79.6	81.0	82.7
9-39-1 "	78.8	83.3	83.6
8-42-M-2 "	79.3	81.6	82.8
8-25-2 "	76.9	81.5	82.4
	ns	ns	ns
GENOTYPE			
N81017	79.5	81.6	82.8
9-39-1	78.6	82.2	82.7
8-42-M-2	80.1	81.8	82.6
8-25-2	78.3	81.4	81.8
	ns	ns	ns
WATER			
Stress	79.6	81.7	82.1
Non-stress	78.7	81.9	82.9
	ns	ns	ns

S= Stress NSD= Non-stress ns= not significant

¹ Late vegetative stage (V₈)

² Flowering and pod development stage (R₁/R₂)

³ Pod filing stage (R₅/R₆)

**TABLE 10. Root Growth Rate of Bean Genotypes at the
MSU Agronomy Farm in East Lansing, MI. 1990.**

TREATMENT		8/23 - 9/20
# of roots/cm²/day		
8-42-M-2	(S)	1.28
9-39-1	"	0.94
8-42-M-2	(NSD)	1.72
9-39-1	"	0.86
		ns
GENOTYPE		
8-42-M-2		1.50
9-39-1		0.90
		ns
WATER		
Stress		1.11
Non-stress		1.29
		ns

S = Stress NSD = Non-stress ns = not significant

FIGURE 3. BEAN ROOT DISTRIBUTION AT 9 DAS IN 1990

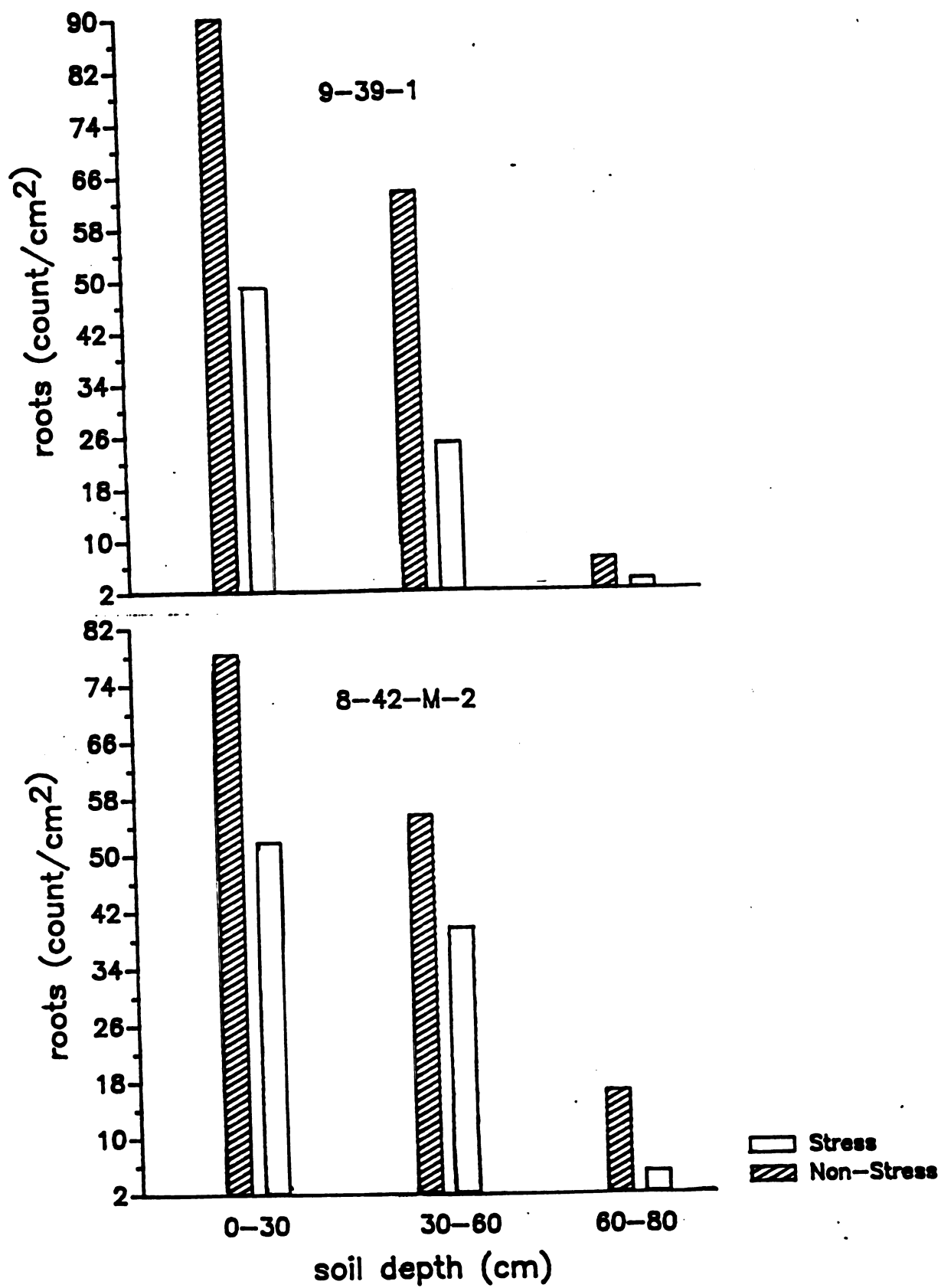
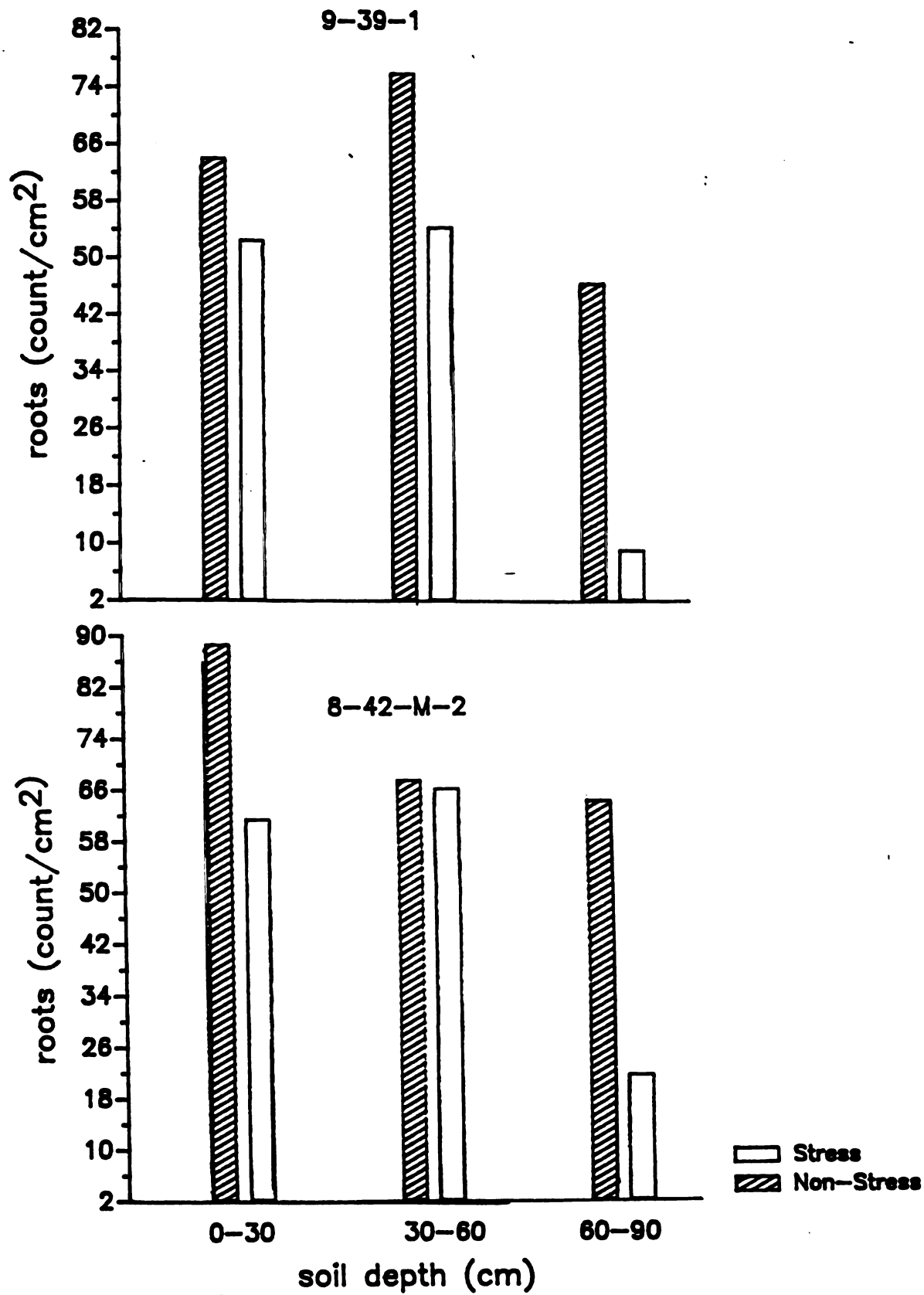


FIGURE 4. BEAN ROOT DISTRIBUTION AT 50 DAS IN 1990



count under the stress and non-stress treatment at the 60 cm depth. At 6 days before stress was imposed the treatment designated as stress had a reduced root count in N81017 and a slightly increased root count in 8-25-2 (Fig 5) at 60 cm. As the season progressed, excessive rainfall made it impossible for the plastic to impede moisture so stress could not be maintained and a high water table prevented additional root measurements. None of the root count measurements were significantly different mainly due to the high coefficient of variation that was found. In order to eliminate this problem, more than one tube has to be used per treatment. This was not possible to do in this study because of the small plot size that was used.

COWPEAS

Yield data

In 1990, planting occurred late on June 25, in order to obtain a warmer soil temperature. However, cowpea germination was still very poor so they were replanted on July 18. Consequently, their growth period was shortened so they did not reach maturity because frost occurred when the plants had just flowered. Similarly, the 1992 growing season was generally cool and plant growth was slow. Again, frost occurred when the plants were flowering. As a result, there was no yield data for cowpeas in 1990 and 1992. The genotype B005-C was not planted in 1992 because of its long maturity. It was a late maturing variety which could not mature during the Michigan growing season.

FIGURE 5. BEAN ROOT DISTRIBUTION AT -6 DAS IN 1992

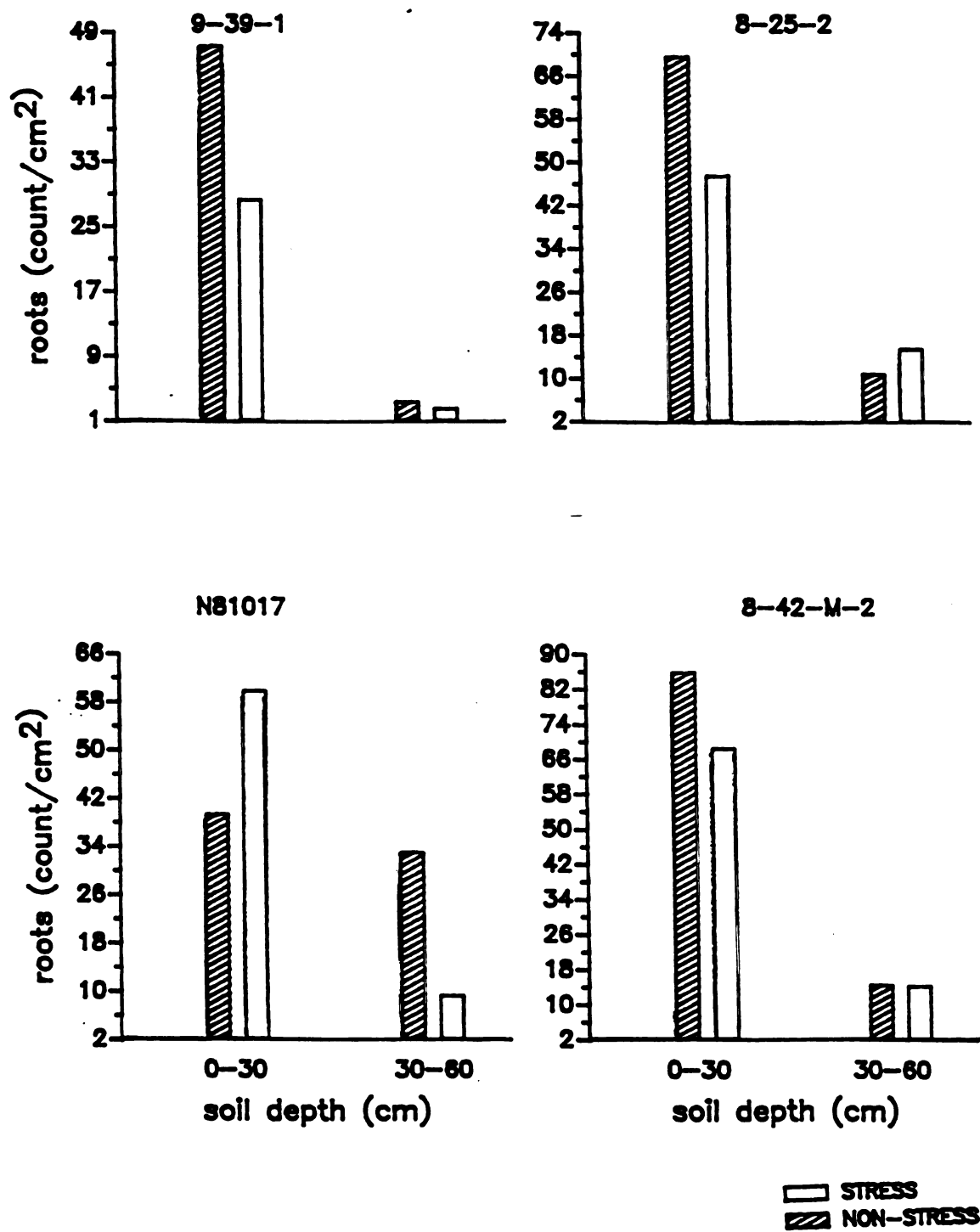
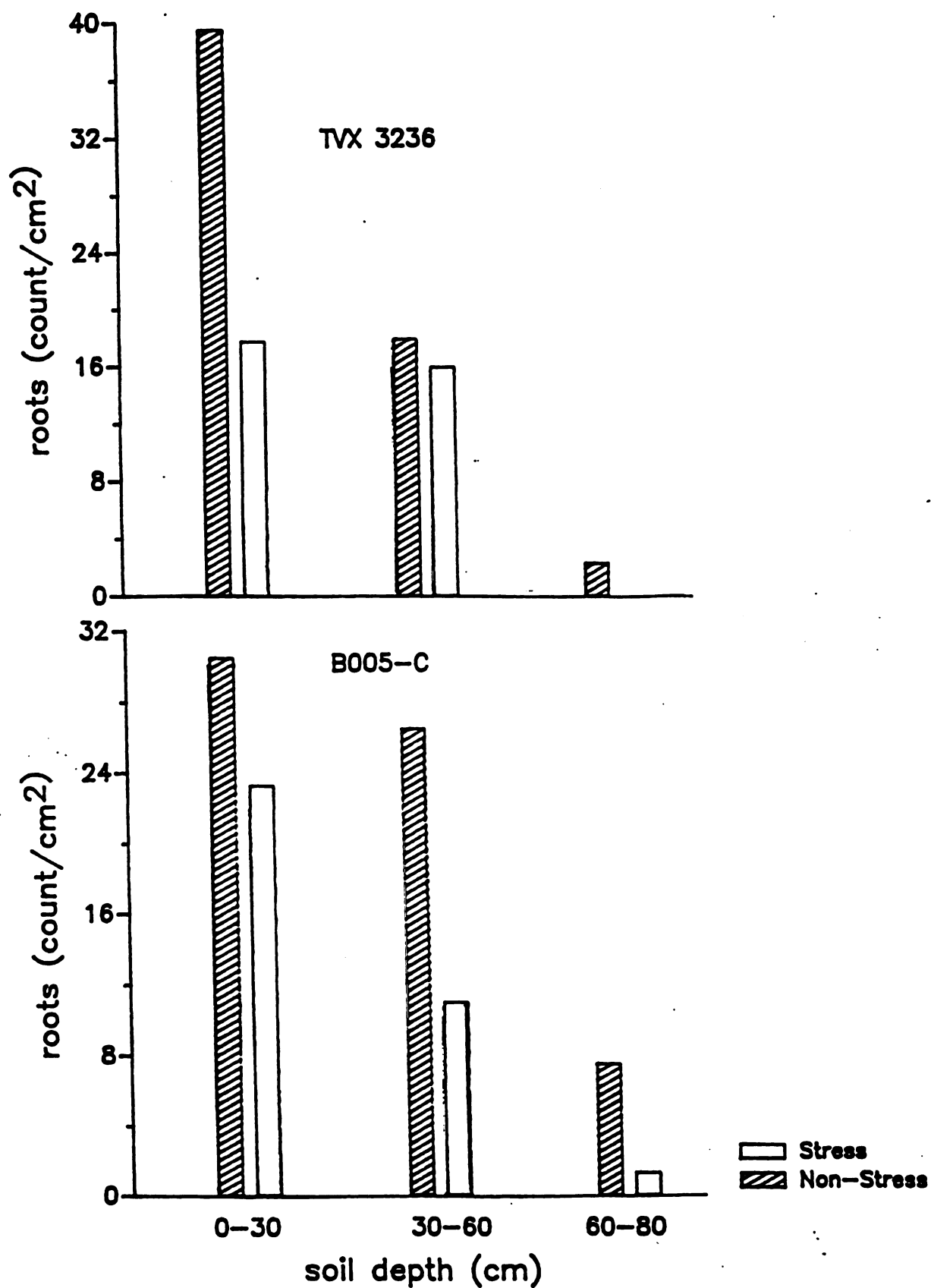


FIG 6. COWPEA ROOT DISTRIBUTION AT -1 DAS IN 1990



Leaf Water Status

In 1990 RWC was measured at three growth stages; early vegetative (V_4), late vegetative (V_9) and flowering (R_1) stages under stress and non-stress soil moisture conditions. No differences were observed with the water treatments or the water x genotype interaction (Table 11). TVX 3236 had a significantly higher RWC than B005-C 4 days before stress was imposed. In 1992 stress significantly reduced RWC only at the pod filling stage, 27 DAS (Table 12). There were genotypic differences at all sampling dates. Blackeye consistently had lower RWC than the other genotypes. Similarly, stress significantly reduced LWC only at 27 DAS. There were genotypic differences at all sampling dates (Table 13). Soil moisture stress decreased LWRC at 13 DAS (R_1/R_2) and at 27 (R_3/R_4) days after stress was imposed (Table 14). There were no genotypic differences. There was no pattern in the response of the genotypes in RWC or LWC. TVX 3236 had a significantly higher RWC and LWC than Blackeye at all sampling dates.

Root Growth

In 1990, B005-C had a significantly higher root growth rate than TVX 3236 (Table 15). Figures 6 and 7 show root distribution a day before stress was imposed and at 27 DAS respectively, in 1990. Both genotypes had more roots under the non-stress treatment at all depths except B005-C at the 80 cm depth at 27 DAS (Fig 7). None of the differences was statistically significant. In 1992, 6 days before stress was imposed there were more roots under the treatment designated as stress at 60 cm for all genotypes (Fig 8). The soil was highly saturated. it was not possible to take soil moisture or

TABLE 11. The Effect of Soil Water Changes on Relative Water Content in Cowpeas in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	-4 ¹	11 ²	24 ³
	%		
B005-C (S)	89.7	91.7	93.7
TVX 3236 "	95.2	93.9	95.9
B005-C (NSD)	92.7	91.9	90.9
TVX 3236 "	95.8	94.7	95.1
	ns	ns	ns
GENOTYPE			
B005-C	91.2	91.8	92.3
TVX 3236	95.5	94.3	95.5
	**	ns	ns
WATER			
Stress	92.4	92.8	94.8
Non-stress	94.2	93.3	93.0
	ns	ns	ns

S= Stress NSD= Non-stress ns= not significant

** p(0.01)

¹ Early vegetative stage (V₄)

² Late vegetative stage (V₈)

³ Flowering and pod development (R₁/R₂)

TAI

—
TRE

TVX
BLA
ER,
IT83

TVX
BLA
ER,
IT83

TVX
BLA
ER,
IT83

Stres.
Non-

—
S= S

***,
0.001

¹ Late
² Flo
³ Pod

TABLE 12. The effect of Soil Water Changes on Relative Water Content in Cowpeas Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	2 ¹	13 ²	27 ³
	%		
TVX 3236 (S)	87.0	89.4	90.3 ab
BLACKEYE "	80.9	83.1	82.1 c
ER ₇ "	81.4	84.4	87.1 bc
IT83S-742-2 "	81.9	86.5	84.4 c
TVX 3236 (NSD)	88.5	87.7	92.2 ab
BLACKEYE "	80.9	79.9	94.1 a
ER ₇ "	82.8	84.2	95.4 a
IT83S-742-2 "	88.9	87.0	91.8 ab
	ns	ns	+
GENOTYPE			
TVX 3236	87.8 a	88.5 a	91.2 a
BLACKEYE	80.9 b	81.5 c	88.1 b
ER ₇	82.1 ab	84.3 bc	91.2 a
IT83S-742-2	85.4 ab	86.8 ab	88.1 b
	*	***	**
WATER			
Stress	82.8	85.9	86.0
Non-stress	85.3	84.7	93.4
	ns	ns	***

S = Stress NSD = Non-stress ns = not significant

***, **, *, + Different letters within a column indicate significant difference at p = 0.001, 0.01, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Late vegetative stage (V₈)

² Flowering and pod development stage (R₁/R₂)

³ Pod filling stage (R₅/R₆)

TAB

TRE

TVX
BLAC
ER,
IT83S

TVX
BLAC
ER,
IT83S

TVX
BLAC
ER,
IT83S

Stress
Non-s

S= St

** , *

¹ Late
² Flow
³ Pod

TABLE 13. The Effect of Soil Water Changes on Leaf Water Content in Cowpeas Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	2 ¹	13 ²	27 ³
	%		
TVX 3236 (S)	85.4	86.1	85.1
BLACKEYE "	81.6	84.3	83.9
ER ₇ "	81.8	84.1	84.4
IT83S-742-2 "	82.1	83.5	84.4
TVX 3236 (NSD)	85.3	85.9	85.8
BLACKEYE "	80.1	84.0	84.6
ER ₇ "	81.8	84.7	85.5
IT83S-742-2 "	82.8	84.6	85.9
	ns	ns	ns
GENOTYPE			
TVX 3236	85.3 a	86.0 a	85.4 a
BLACKEYE	80.9 b	84.1 b	84.3 b
ER ₇	81.8 b	84.4 b	84.9 ab
IT83S-742-2	82.4 ab	84.0 b	85.1 a
	*	*	+
WATER			
Stress	82.7	84.5	84.4
Non-stress	82.5	84.8	85.4
	ns	ns	**

S= Stress NSD- Non-stress ns= not significant

** , * , + Different letters within a column indicate significant difference at $p = 0.01$, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Late vegetative stage (V₈)

² Flowering and pod development stage (R₁/R₂)

³ Pod filling stage (R₅/R₆)

TABLE 14. The Effect of Soil Water Changes on Leaf Water Retention Capacity in Cowpeas at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	2 ¹	13 ²	27 ³
	%		
TVX 3236 (S)	96.7	96.0	97.4
BLACKEYE "	96.7	97.7	96.0
ER, "	96.6	95.4	97.5
IT83S-742-2 "	97.7	96.8	96.4
TVX 3236 (NSD)	97.4	98.2	97.6
BLACKEYE "	96.3	98.2	97.8
ER, "	96.8	97.9	98.3
IT83S-742-2 "	97.2	98.7	98.3
	ns	ns	ns
	GENOTYPE		
TVX 3236	97.0	97.1	97.5
BLACKEYE	96.5	98.0	96.9
ER,	96.7	96.6	97.9
IT83S-742-2	97.5	97.8	97.4
	ns	ns	ns
	WATER		
Stress	96.9	96.5	96.8
Non-stress	96.9	98.3	98.0
	ns	***	***

S = Stress NSD = Non-stress ns = not significant

*** p(0.001)

¹ Late vegetative stage (V₃)

² Flowering and pod development stage (R₁/R₂)

³ Pod filling stage (R₃/R₆)

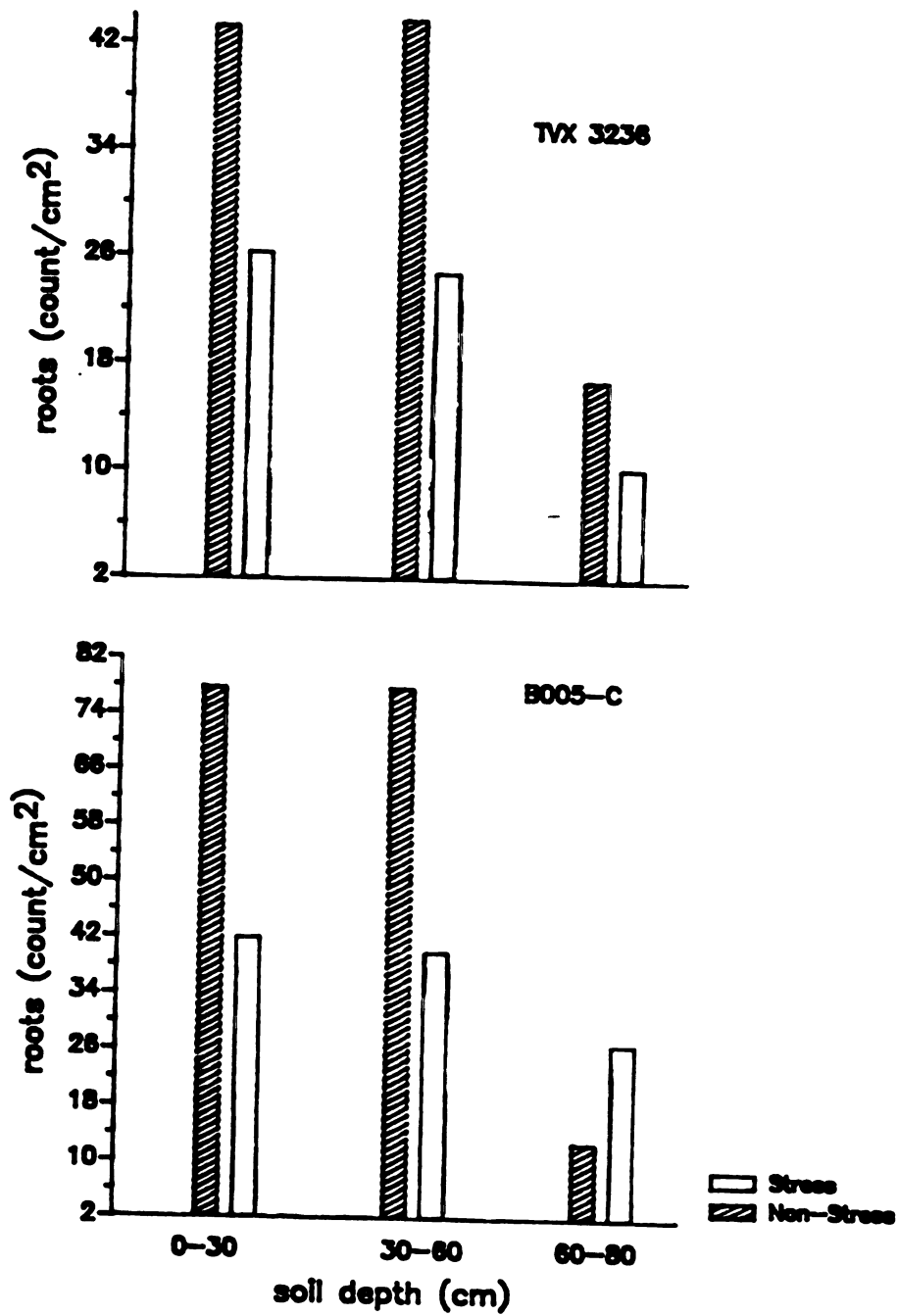
**TABLE 15. Root Growth Rate of Cowpea Genotypes at the
MSU Agronomy Farm in East Lansing. MI. 1990.**

TREATMENT		8/23 - 9/20
B005-C	(S)	2.77
TVX 3236	"	0.98
B005-C	(NSD)	3.71
TVX 3236	"	1.57
		ns
GENOTYPE		
B005-C		3.24
TVX 3236		1.28
		*
WATER		
Stress		1.88 -
Non-stress		2.64
		ns

S= Stress NSD= Non-stress ns= not significant

*** p= 0.05**

FIG 7. COWPEA ROOT DISTRIBUTION AT 27 DAS IN 1990



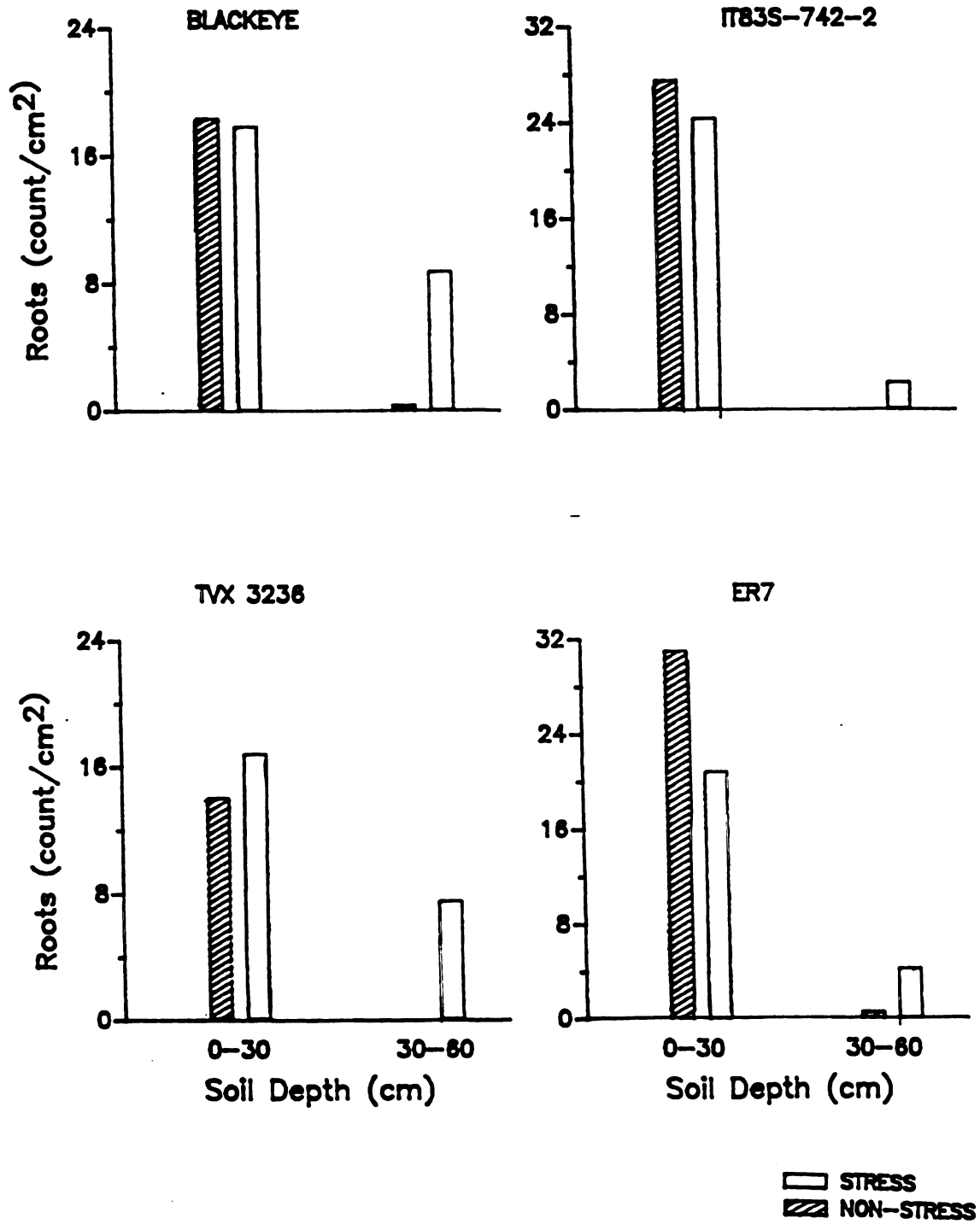
Roots (count/cm²)

24
18
8
0

Roots (count/cm²)

24
18
8
0

FIG 8. COWPEA ROOT DISTRIBUTION AT -6 DAP IN 1992



minirhizotron readings without first pumping out the water.

Soil and Leaf Temperature

At 13 and 41 DAS (68 and 86 DAP respectively) the non-stress treatment had a lower leaf temperature than the stress treatment and had a lower soil temperature 2 days before stress was imposed and at 25 DAS. Both probably contributed to the slow plant growth rate that was observed in 1992 (Fig 9). The arrows in the graphs indicate when moisture stress was imposed (55 DAP).

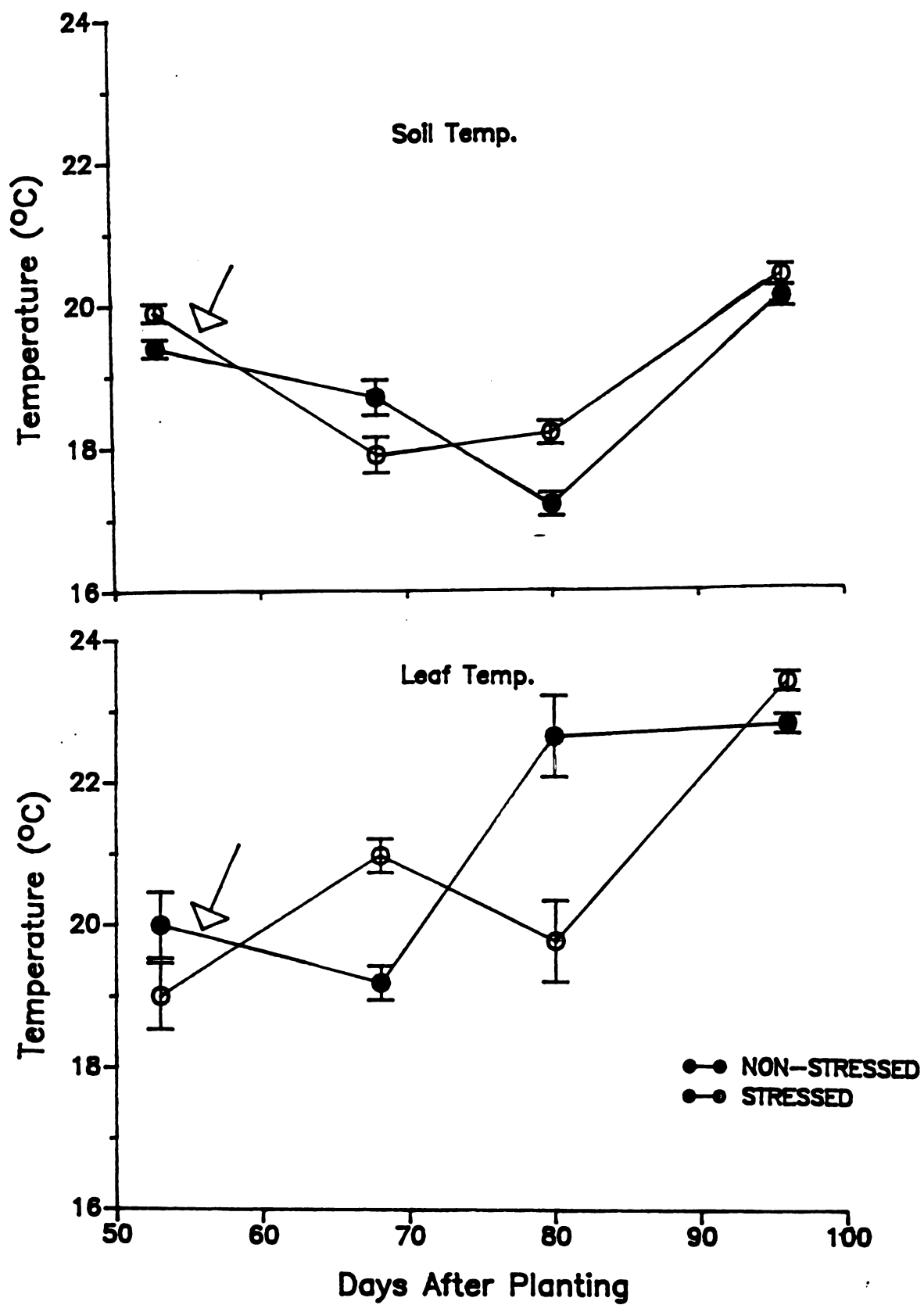
SUMMARY

RESPONSE UNDER MOISTURE STRESS		
<u>PARAMETER</u>	<u>BEANS</u>	<u>- COWPEAS</u>
Yield components		
PPP ¹	*	
SPP ²	ns	
Leaf water		
(RWC, LWRC, LWC)	*	*
Root growth	ns	ns

¹ PPP = Pods per plant

² SPP = Seeds per pod

FIG 9. COWPEA SOIL AND LEAF TEMPERATURE IN 1992



CONCLUSIONS

Soil moisture stress decreased seed yield, especially through decreased number of pods per plant in beans. The number of seeds per pod was insensitive to water stress. It seems that bean yield can best be improved by maximizing the number of pods per plant.

The cowpea genotype, Blackeye consistently had a lower RWC in 1992. The high yielding resistant genotype (N81017) had the lower RWC in beans on the last sampling date of 1992. Leaf water content provided genotypic and stress treatment differences in bean and cowpea in 1992. Results are inconclusive with regard to the use of these measurements as screening tools for drought resistance due to minimal moisture stress in 1992. The tests need to be repeated in an environment which can guarantee moisture stress.

Soil moisture stress in 1990 reduced root growth rate in both bean and cowpeas. Resistant bean genotypes had a lower reduction in root growth rate than susceptible genotypes. In general, root count decreased with increasing soil depth and stress. In beans, resistant genotypes had more roots than susceptible genotypes. There was no pattern between root growth and yield potential of the genotypes. There was no genotypic pattern of root growth in cowpeas. Root growth analysis can be a useful tool when used to explain the response of a genotype in beans; however, the minirhizotron technique does not make it feasible to be used on a large number of cultivars because of the amount of work and time involved with the minirhizotron installation and data collection. The minirhizotron technique also requires that a large number of tubes be installed for each

plot in order to reduce the coefficient of variation. This is not practical for examining large numbers of lines.

The resistant genotypes performed better than the susceptible genotypes in terms of yield and root growth. This shows the need to categorize genotypes according to their resistance and yield potential in order to successfully evaluate parameters that can be used as screening tools.

Others have used plastic to impose moisture stress successfully. However, in this study the use of plastic to impose moisture stress was not effective. The plastic conserved moisture and therefore did not impose moisture stress. Thus, when the plastic was pulled back, there was moisture on the soil surface. Water also went in between the plants since that space was not covered with plastic. The plastic only covered between the rows and not between plants within a row.

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CHAPTER 2

THE EFFECT OF SOIL MOISTURE STRESS ON DRY BEANS

(Phaseolus vulgaris L.) AND COWPEAS (Vigna unguiculata L. (walp)). II. Photosynthesis, Light Interception, Stomatal Conductance, Transpiration Ratio and Carbon Isotope Discrimination.

ABSTRACT

Soil water changes affect crop canopy and hence the amount of light intercepted by a crop and assimilate production. The objective of this study was to investigate the effect of soil water deficit on changes in light interception, photosynthesis, stomatal conductance, transpiration ratio and carbon isotope discrimination. The study was carried out in the field using either a rainshelter or black polyethylene plastic to impose terminal drought stress at the late vegetative growth stage (V_9).

Photosynthetic rate was reduced by severe water stress in both beans (Phaseolus vulgaris L.) and cowpeas (Vigna unguiculata L. (walp)). Stomatal conductance was not affected by moisture stress in beans but was reduced by 33 % in cowpeas. There were no genotypic differences for photosynthetic rate in beans or cowpeas but there were genotypic differences for stomatal conductance. Moisture stress decreased transpiration ratio in beans but increased it in cowpeas. Soil moisture stress did not affect carbon isotope discrimination in either species but there were genotypic differences in beans. Drought resistant bean genotypes had lower CID values than drought susceptible bean

genotypes and CID was positively correlated to yield in beans.

INTRODUCTION

Photosynthesis plays an important role in dry matter production and subsequently yield. Genotypic variability in photosynthesis per unit leaf area may be useful in increasing gross productivity of crop plants and as a screening tool if it can be demonstrated to be measurable and related to growth in field studies and if it is physiologically linked to compensating differences in leaf area production (Mahon, 1990).

Although severe drought affects plant growth in many ways, the response of photosynthesis to water deficits has gained special attention. The main reason is that the stomates respond very early to changes in humidity or water stress and thereby often decrease the rate of photosynthesis long before the leaf water status has changed (Kaiser, 1987). Stomatal movements provide the leaf with opportunity to change both the partial pressure of CO₂ at the sites of carboxylation and the rate of transpiration. In turn, changes in transpiration rate can cause changes in the temperature and water potential of the leaf (Farquhar and Sharkey, 1982). Studies have shown that leaf conductance decreased with decreasing soil water content in wheat (Triticum aestivum L.) and sunflower (Helianthus annuus L.) (Gollan et al, 1986). Blackman and Davis (1985) reported similar observations in maize (Zea mays L.).

The objective of this study was to investigate the effect of soil water changes on photosynthesis, stomatal conductance, transpiration ratio, light interception, and carbon

isotope discrimination in beans and cowpea.

MATERIALS AND METHODS

A field study was conducted at the Agronomy Research Farm at Michigan State University in East Lansing during the summers of 1990 and 1992. In 1990 a rainshelter was used to impose moisture stress at 37 DAP. In 1992, black polyethylene plastic was placed between the rows to impose moisture stress at 58 DAP. Moisture stress was initiated at the late vegetative growth stage (V_9) for both years but this stage occurred at different DAP due to the different environmental conditions each year.

The soil type for the 1990 experiment was a fine loamy, mixed mesic aerice ochroqualfs with a slope of 0-3% (USDA Soil Conservation Service Classification). For the 1992 experiment, it was a fine loamy, mixed mesic glossoboric hapluidalfs with a slope of 2-6%. The rainfall and temperature data are presented in Fig 1 and Table 1 of Appendix A.

The experimental design was a modified split plot with four replications. Moisture stress was the main plot and genotypes were the subplot. The moisture factor was confounded by site difference in that all stressed plots were grouped together and all non-stressed plots were grouped together. Each plot had four rows of 2 m length. The bean spacing was 50 x 10 cm and the cowpea spacing was 75 x 20 cm which resulted in a plant density of 20 plants per m^2 for beans and 10 plants per m^2 for cowpeas. In 1990, two bean genotypes (9-39-1 and 8-42-M-2) and two cowpea genotypes (TVX 3236 and B005-C) were used. In 1992 four bean genotypes (9-39-1, 8-42-M-2, N81017 and 8-25-

2) and four cowpea genotypes (TVX 3236, Blackeye, ER₇, IT83S-742-2) were used. The bean genotypes were chosen based upon their performance in the MSU bean breeding program as either being drought resistant or susceptible. The cowpea genotypes were chosen based upon their performance from a preliminary growth chamber study conducted in 1989 and based upon their performance at IITA and in Botswana. Genotypic description are presented in Table 2 of Appendix A.

All plots were hand planted using a hoe to open rows. Forty or 20 seeds per row were planted for beans and cowpeas respectively, with abundant inoculant. The bean inoculum was Rhizobium phaseoli and the cowpea inoculum was Rhizobium cowpea miscellany nitrogen EL.

Planting and Management Practices

1990

Both beans and cowpeas were planted on June 25 but because of poor germination, cowpeas were replanted on July 18. Fertilizer was applied as 19-19-19 at the rate of 40 Kg N/ha before planting. Three days after planting, on June 28 all plots received 30 mm of irrigation to facilitate germination. The total rainfall during the growing season (June 25-Oct 5) was 287.6 mm. On July 31, Sevin (Carbaryl insecticide) was applied at the rate of 4 teaspoons per gallon of water to control Mexican bean beetle and leafhopper.

1992

Planting occurred on June 12. The fertilizer (21-7-14) with 4% Mn and 1% Zn was applied at the rate 42 pounds N per acre before planting. All plots received a total

of 283.3 mm of irrigation in four applications before stress was imposed. The total rainfall during the growing season (June 12-Sept. 16) was 309.0 mm. A greater amount of irrigation was applied in 1992 in order to break the soil crust, enhance germination and facilitate stand establishment. Sevin was applied on July 29 to control leafhopper.

Soil moisture was monitored regularly in all plots at three depths in 1990 (0-30, 30-60, 60-90) using a neutron probe. In 1992 readings were only recorded at the 0-30 and 30-60 cm depths because the field had a high water table. Undisturbed soil core samples were taken at the same depths to develop a soil moisture desorption curve which was used to convert the volumetric moisture content into matric potential.

Photosynthesis

Three plants per plot were tagged and measurements were taken from these plants on the uppermost fully expanded leaf. The ADC-LCA 2 photosynthesis system (The Analytical Development Co. Ltd., Hoddesdon. UK) was used under the following conditions (flow rate = 400 ml m^{-1} , leaf temperature = $30 \pm 2 \text{ }^{\circ}\text{C}$, vapor pressure deficit (VPD) = 3 kPa , ambient $\text{CO}_2 \pm 10 \text{ ml l}^{-1}$, and photosynthetically active radiation (PAR) $\geq 1000 \mu\text{mol m}^{-2} \text{ s}^{-1}$). The leaf was enclosed in a leaf chamber and exposed to incoming solar radiation. All readings were recorded at approximately the same photosynthetically active radiation (PAR). Each reading took approximately 30 seconds before a stable value was recorded. Measurements were taken between 10 am and 2 pm EDT on a cloudless day. Photosynthesis, stomatal conductance and transpiration ratio were calculated from a program developed by Moon and Flore (1986), (Appendix B1).

Light

Device

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2 pm

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Light Interception

Light interception was measured in 1992 using the Sunfleck Ceptometer (Decagon Devices, Inc. Pullman. Wa). The amount of incident radiation transmitted to and reflected by the crop canopy were measured by placing the ceptometer horizontally below or above the crop canopy and calculations were made to determine the fractional light intercepted by the canopy (Appendix B2). Measurements were taken between 10 am and 2 pm EDT on a cloudless day at flowering (R_1) and early pod development (R_2) growth stages.

Carbon Isotope Discrimination

Samples for carbon isotope discrimination were taken during the pod filling growth stage (R_3) on five plants per plot only in 1992. Five leaves were sampled from each plant so 25 leaves were sampled from each plot. The uppermost fully expanded leaves were detached and samples were bulked for each plot. The samples were oven dried at 60°C for five days before grinding. The samples were sent to Isotope Services, Inc in Los Alamos, NM, USA for analysis via mass spectrometry.

RESULTS AND DISCUSSION

BEANS

Photosynthesis

In 1990, moisture stress did not affect photosynthetic rate until later in the season when the stress period had been in effect for 41 days (Table 1). Drought stress reduced

photosynthesis by 38%. Cornic et al. (1987) demonstrated that when bean plants were exposed to a rapid or slow drought cycle, photosynthetic rate declined and upon rewatering it increased. Similarly a 40% decrease in net photosynthetic rate with decreasing soil water potential has been reported in cotton (*Gossypium hirsutum* L.) (Plaut and Federman, 1990). There were no genotypic differences in the rate of photosynthesis (Table 1). There were no differences between the stress and non-stress treatments or between genotypes in 1992 (Table 2). The drought intensity index (Fischer Index) in 1992 was 0.17, indicating that there was mild drought stress. Light interception was significantly higher under the plastic covered stress treatment at 11 DAS (Table 3). Nunez-Barrios (1991) observed a reduction in light interception during drought in beans. The observed increase in light interception under-stress is probably related to the fact that there was minimal moisture stress in 1992 and because the plastic covered stress plots had an added advantage of warmer soil temperature (Fig 1) during the latter part of the season (25 DAS), helping facilitate growth. Arrows in Figure 1 indicate the time when stress was imposed (55 DAP). The stress treatment also had a slightly higher leaf temperature at 47 DAS. The genotype 8-42-M-2 intercepted more light than the other genotypes.

Transpiration Ratio

In 1990, at 41 DAS (Table 4), the stress treatment had a significantly lower transpiration ratio than the non-stress treatment. This corresponds with the lower photosynthetic rate in the stress treatment at 41 DAS (Table 1). In 1992 there were no significant differences between stress and non-stress treatments except at 1 DAS where

TABLE 1. The Effect of Soil Water Changes on CO₂ Assimilation Rate in Beans in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	6 ¹	27 ²	41 ³
	$\mu\text{mols m}^{-2} \text{ s}^{-1}$		
8-42-M-2 (S)	10.8	8.1	6.0
9-39-1 "	11.0	7.9	4.6
8-42-M-2 (NSD)	13.5	6.9	8.4
9-39-1 "	10.5	7.2	8.9
	ns	ns	ns
GENOTYPE			
8-42-M-2	12.1	7.5	7.2
9-39-1	10.8	7.5	6.8
	ns	ns	ns
WATER			
Stress	10.9	8.0	5.3
Non-stress	11.9	7.0	8.6
	ns	ns	*

S = Stress NSD = Non-stress ns = not significant

* p = 0.05

¹ Late vegetative stage (V₉)

² Flowering and pod development stage (R₁/R₂)

³ Pod filling stage (R₅)

1

-

1

8

9

M

8

8

9

M

8

8

9

M

8

S

M

-

S

1

2

TABLE 2. The Effect of Soil Water Changes on CO₂ Assimilation Rate in Beans Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED	
	1 ¹	15 ²
$\mu\text{mols m}^{-2} \text{ s}^{-1}$		
8-42-M-2 (S)	12.4	7.9
9-39-1 "	13.9	9.1
N81017 "	13.3	6.5
8-25-2 "	14.3	8.8
8-42-M-2 (NSD)	12.0	8.3
9-39-1 "	11.4	6.9
N81017 "	11.1	9.3
8-25-2 "	14.9	9.7
	ns	ns
GENOTYPE		
8-42-M-2	12.2	8.1
9-39-1	12.6	8.0
N81017	12.2	7.9
8-25-2	14.6	9.2
	ns	ns
WATER		
Stress	13.5	8.1
Non-stress	12.3	8.5
	ns	ns

S= Stress NSD= Non-stress ns= not significant

¹ Late vegetative stage (V₉)

² Flowering and pod development (R₁/R₂)

TRE

N810
9-39
8-42
8-25

N810
9-39
8-42
8-25

N810
9-39
8-42
8-25

Stres
Non-

S = S

*, +

¹R₁

²R₂

TABLE 3. The Effect of Soil Water Changes on Light Intercepted by Beans at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>	
	4 ¹	11 ²
	%	
N81017 (S)	67.4	83.3
9-39-1 "	74.3	81.4
8-42-M-2 "	82.3	89.7
8-25-2 "	70.8	80.8
N81017 (NSD)	77.9	76.8
9-39-1 "	66.5	74.4
8-42-M-2 "	81.1	87.0
8-25-2 "	74.9	79.0
	ns	ns
GENOTYPE		
N81017	72.6	80.1 b
9-39-1	70.4	77.9 b
8-42-M-2	81.7	88.4 a
8-25-2	72.8	79.9 b
	ns	*
WATER		
Stress	73.7	83.8 a
Non-stress	75.1	79.3 b
	ns	+

S= Stress NSD= Non-stress ns= not significant

*, + Different letters within a column indicate significant difference at $p = 0.05$ or 0.1 respectively according to Duncan Multiple Range Test.

¹ R₁

² R₂

24

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FIGURE 1. BEAN SOIL AND LEAF TEMPERATURE IN 1992

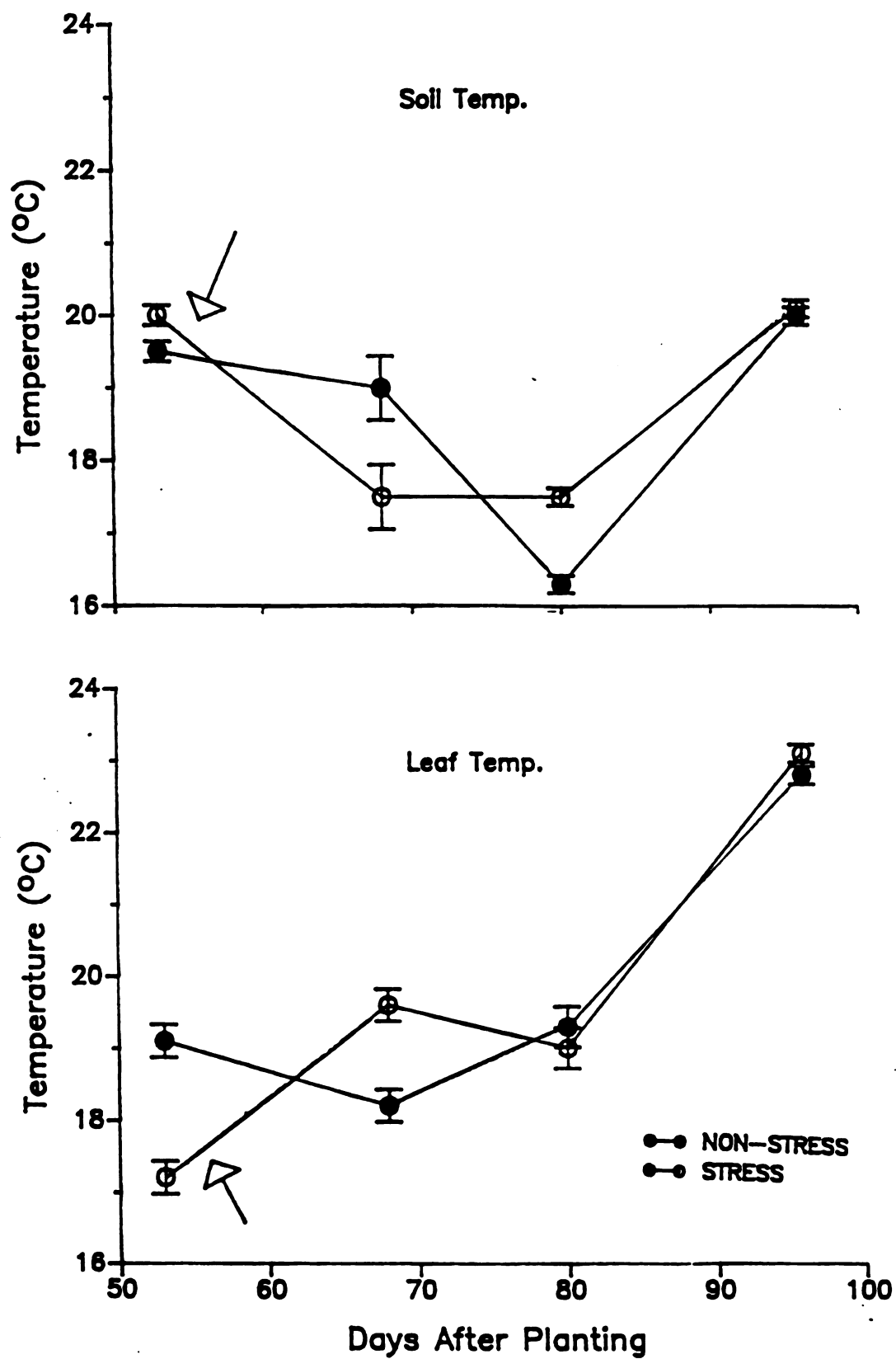


TABLE 4. The Effect of Soil Water Changes on Transpiration Ratio in Beans in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	6 ¹	27 ²	41 ³
	mol H ₂ O/ mol CO ₂		
8-42-M-2 (S)	417.6	644.4	268.8
9-39-1 "	481.3	531.3	227.0
8-42-M-2 (NSD)	403.2	482.2	384.0
9-39-1 "	469.0	527.2	445.2
	ns	ns	ns
GENOTYPE			
8-42-M-2	410.4	563.3	324.9
9-39-1	475.1	529.2	336.1
	ns	-ns	ns
WATER			
Stress	449.5	587.8	247.9
Non-stress	436.1	504.7	414.6
	ns	ns	*

* P = 0.05

S = Stress NSD = Non-stress ns = not significant

¹ Late vegetative stage (V₉)

² Flowering and pod development (R₁/R₂)

³ Pod filling stage (R₃)

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stress increased the transpiration ratio (Table 5).

Stomatal Closure

In 1990 soil moisture stress had no effect on stomatal conductance and there were no genotypic differences. A water x genotype interaction was significant at 6 DAS (Table 6). The resistant genotype, 9-39-1 maintained stomatal conductance under stress while the susceptible genotype, 8-42-M-2, significantly decreased its stomatal conductance under stress. This may have contributed to the high yield reduction for 8-42-M-2, suggesting that stomatal conductance was limiting under moisture stress early in the season. Trejo and Davis (1991) showed an early reduction in stomatal conductance in response to soil drying in beans. In young bean seedlings stomata started to close before any leaf water deficit was detected. In 1992 there were no differences between stress and non-stress treatments or between genotypes (Table 7).

Carbon Isotope Discrimination

Carbon isotope discrimination was not affected by water stress but genotypic differences were observed (Table 8). Genotypic variability in CID has been reported in soybeans (Glycine max L.) (Ashley, 1991) and peanuts (Arachis hypogaea L.) (Brown and Bryd, 1991). In 1992, 9-39-1 had a lower CID value than N81017 and 8-25-2. The use of CID as a determining factor would have selected 9-39-1, a low yielding genotype, as desirable whereas N81017 is the more desirable genotype. These results, seem to indicate that CID can not separate low yielding genotypes from higher yielding ones. Carbon isotope discrimination was positively and significantly correlated to yield.

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TABLE 5. The Effect of Soil Water Changes on Transpiration Ratio in Beans Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED	
	1 ¹	15 ²
	mol H ₂ O/ mol CO ₂	
8-42-M-2 (S)	349.5	488.7
9-39-1 "	275.9	325.7
N81017 "	370.9	867.3
8-25-2 "	317.7	375.4
8-42-M-2 (NSD)	294.7	347.7
9-39-1 "	297.6	351.4
N81017 "	310.9	296.3
8-25-2 "	261.4	284.6
	ns	ns
GENOTYPE	-	
8-42-M-2	322.1	418.2
9-39-1	286.8	338.6
N81017	340.9	581.8
8-25-2	289.5	330.0
	ns	ns
WATER		
Stress	328.5	514.3
Non-stress	291.2	320.0
	+	ns

S= Stress NSD= Non-stress ns= not significant

+ p= 0.1

¹ Late vegetative stage (V₉)

² Flowering and pod development (R₁/R₂)

TABLE 6

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¹ Late veg

² Flowering

³ Pod filling

TABLE 6. The Effect of Soil Water Changes on Stomatal Conductance in Beans in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	6 ¹	27 ²	41 ³
mmols m ⁻² s ⁻¹			
8-42-M-2 (S)	169.9 b	79.9	66.9
9-39-1 "	209.9 ab	64.8	45.0
8-42-M-2 (NSD)	250.5 a	46.8	87.7
9-39-1 "	170.1 b	61.8	72.9
	*	ns	ns
GENOTYPE			
8-42-M-2	210.2	63.4	77.3
9-39-1	190.0	63.3	59.0
	ns	-ns	ns
WATER			
Stress	190.0	72.3	56.0
Non-stress	210.3	54.3	80.3
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

* Different letters within a column indicate significant difference at $p = 0.05$ according to Duncan Multiple Range Test

¹ Late vegetative stage (V₉)

² Flowering and pod development (R₁/R₂)

³ Pod filling stage (R₃)

TABLE

TREATM

8-42-M-1
9-39-1
N81017
8-25-2

8-42-M-1
9-39-1
N81017
8-25-2

8-42-M-1
9-39-1
N81017
8-25-2

Stress
Non-stress

S = Stress

¹ Late vegetative
² Flowering

TABLE 7. The Effect of Soil Water Changes on Stomatal Conductance in Beans Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>	
	1¹	15²
	mmols m⁻² s⁻¹	
8-42-M-2 (S)	133.1	85.6
9-39-1 "	132.1	69.5
N81017 "	151.0	73.4
8-25-2 "	140.4	78.5
8-42-M-2 (NSD)	128.5	83.9
9-39-1 "	115.8	71.1
N81017 "	120.0	81.6
8-25-2 "	144.9	80.3
	ns	ns
GENOTYPE		
8-42-M-2	130.8	84.7
9-39-1	123.9	70.3
N81017	135.5	77.5
8-25-2	142.7	79.4
	ns	ns
WATER		
Stress	139.1	76.7
Non-stress	127.1	79.2
	ns	ns

S= Stress NSD= Non-stress ns= no significant

¹ Late vegetative stage (V₉)

² Flowering and pod development (R₁/R₂)

TABLE 8. The Effect of Soil Water Changes on Carbon Isotope Discrimination in Beans Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT		
		Delta
N81017	(S)	20.5
9-39-1	"	20.0
8-42-M-2	"	20.4
8-25-2	"	20.5
N81017	(NSD)	21.4
9-39-1	"	19.1
8-42-M-2	"	20.1
8-25-2	"	21.1
		ns
	GENOTYPE	
N81017		21.0 a -
9-39-1		19.6 b
8-42-M-2		20.2 ab
8-25-2		20.8 a
		*
	WATER	
Stress		20.4
Non-stress		20.4
		ns

S= Stress NSD= Non-stress ns= not significant

* Different letters within a column indicate significant difference at $p = 0.05$ according to Duncan Multiple Range Test

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Photosynthesis

In 1990, moisture stress significantly reduced photosynthetic rate at 4 and 18 DAS (Table 9). TVX 3236 had significantly higher photosynthetic rate than BOO5-C at 4 DAS. The genotype x water level interaction was significant only at 18 DAS (Table 9). The genotype TVX 3236 was more sensitive to moisture stress with a 46% reduction in photosynthetic rate while BOO5-C had a 23% reduction. Littleton et al. (1981) found reduced photosynthetic rate in cowpeas under water shortage. A 59% reduction in photosynthetic rate by cowpeas due to moisture stress has also been reported by Hall et al. (1992). In 1992, there were no differences between stress and non-stress treatments but genotypic differences were observed at 15 DAS (Table 10). Blackeye had the lowest photosynthetic rate.

Light Interception

There were no differences between the stress and non-stress treatments in 1992 in the amount of light intercepted, but Blackeye intercepted more light than the other genotypes at 11 DAS (Table 11). At 4 DAS under the non-stress treatment, TVX 3236 and IT83S-742-2 had negative light interception. This is because they performed poorly in terms of canopy development. They were upright with very little canopy cover so when the readings were recorded for the amount of light reflected above and below the canopy, there was very little difference between the two readings. This translated as high light transmission through the canopy and low light interception. Therefore when light interception was calculated (Appendix B2) it was negative. Blackeye had a low

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TABLE 9. The Effect of Soil Water Changes on CO₂ Assimilation Rate in Cowpeas in the Rainshelter at the MSU Agronomy Farm in East Lansing. MI. 1990

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	-17 ¹	4 ²	18 ³
	$\mu\text{mols m}^{-2} \text{ s}^{-1}$		
BOO5-C (S)	12.0	11.7	10.1 c
TVX 3236 "	12.5	17.2	8.9 c
BOO5-C (NSD)	13.2	17.5	13.1 b
TVX 3236 "	13.1	19.8	16.6 a
	ns	ns	+
GENOTYPE			
BOO5-C	12.6	14.6 b	11.6
TVX 3236	12.8	18.5 a	12.7
	ns	*	ns
WATER			
Stress	12.2	14.4 b	9.5 b
Non-stress	13.1	18.6 a	14.9 a
	ns	*	*

S= Stress NSD= Non-stress ns= not significant

*, + Different letters within a column indicate significant difference at $p = 0.05$ or 0.1 respectively according to Duncan Multiple Range Test

¹ Early vegetative stage (V₃)

² Late vegetative stage (V₇)

³ Flowering stage (R₁)

TABLE 10. The Effect of Soil Water Changes on CO₂ Assimilation Rate in Cowpeas Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>	
	1 ¹	15 ²
$\mu\text{mols m}^{-2} \text{ s}^{-1}$		
TVX 3236 (S)	14.7	14.6
BLACKEYE "	11.9	4.5
ER ₇ "	12.8	9.7
IT83S-742-2 "	13.9	10.6
TVX 3236 (NSD)	14.2	12.0
BLACKEYE "	12.6	6.0
ER ₇ "	13.2	8.6
IT83S-742-2 "	11.6	10.2
	ns	ns
GENOTYPE		
TVX 3236	14.4	13.3 a
BLACKEYE	12.2	5.3 c
ER ₇	13.0	9.2 b
IT83S-742-2	12.7	10.4 ab
	ns	***
WATER		
Stress	12.9	9.2
Non-stress	13.3	9.8
	ns	ns

S = Stress NSD = Non-stress ns = not significant

*** Different letters within a column indicate significant difference at $p = 0.001$ according to Duncan Multiple Range Test.

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TABLE 11. The Effect of Soil Water Changes on Light Intercepted by Cowpeas at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>	
	4 ¹	11 ²
	%	
TVX 3236 (S)	21.0 a	1.6 c
BLACKEYE "	8.7 a	18.7 ab
ER ₇ "	5.7 a	11.3 bc
IT83S-742-2 "	5.7 a	18.7 ab
TVX 3236 (NSD)	-42.0 b	5.1 c
BLACKEYE "	7.2 a	30.7 a
ER ₇ "	15.3 a	-1.7 c
IT83S-742-2 "	-3.3 a	6.8 bc
	+	+
GENOTYPE		
TVX 3236	-10.5	3.3 b
BLACKEYE	8.0	24.7 a
ER ₇	10.5	4.8 b
IT83S-742-2	1.2	12.8 ab
	ns	**
WATER		
Stress	10.3	12.6
Non-stress	-5.7	10.2
	ns	ns

S= Stress NSD= Non-stress ns= not significant

**, + Different letters within a column indicate significant difference at p= 0.01 or 0.1 respectively according to Duncan Multiple Range Test.

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photosynthetic rate, but intercepted the highest amount of radiation while TVX 3236 had a higher photosynthetic rate and low interception. Blackeye was the most prostrate genotype. There appeared to be a negative relationship between photosynthesis and the amount of light intercepted suggesting that light was not being efficiently utilized.

Transpiration Ratio

Moisture stress significantly increased transpiration ratio at 4 days after stress was imposed in 1990. At 18 DAS, B005-C had a significantly higher transpiration ratio than TVX 3236 (Table 12). In 1992 there were no differences between stress and non-stress treatments. TVX 3236 had lower transpiration ratio than Blackeye at 15 DAS in 1992 (Table 13).

Stomatal Conductance

Moisture stress reduced stomatal conductance by 33% at 18 DAS in 1990 (Table 14), consistent with other reports of reductions up to 71% in cowpeas (Hall et al., 1992). The genotype B005-C had a significantly lower stomatal conductance than TVX 3236 at 4 DAS which correlates with its lower photosynthetic rate (Table 9). There were no differences between stress and non-stress treatments in 1992 (Table 15), but Blackeye had lower stomatal conductance than TVX 3236 and IT83S-742-2 at 15 DAS.

Carbon Isotope Discrimination

There was no difference between the stress and non-stress treatments or between genotypes in carbon isotope discrimination in 1992 (Table 16). However, Blackeye tended to have low CID under stress.

TABLE 12. The Effect of Soil Water Changes on Transpiration Ratio in Cowpeas in the Rainshelter at the MSU Agronomy Farm in East Lansing. MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	-17 ¹	4 ²	18 ³
	mol H ₂ O/ mol CO ₂		
BO05-C (S)	431.3	535.5	291.6
TVX 3236 "	400.4	556.8	251.6
BO05-C (NSD)	393.9	399.5	346.1
TVX 3236 "	352.4	370.3	252.1
	ns	ns	ns
GENOTYPE			
BO05-C	412.6	467.5	318.8
TVX 3236	376.4	463.6	251.8
	ns	ns -	+
WATER			
Stress	415.8	546.1	271.6
Non-stress	373.2	384.9	299.1
	ns	*	ns

* p= 0.05 + p= 0.1

S= Stress NSD= Non-stress ns= not significant

¹ Early vegetative stage (V₃)

² Late vegetative stage (V₇)

³ Flowering stage (R₁)

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TABLE 13. The Effect of Soil Water Changes on Transpiration Ratio in Cowpeas Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>	
	1 ¹	15 ²
	mol H ₂ O/ mol CO ₂	
TVX 3236 (S)	252.6	311.7
BLACKEYE "	270.7	601.9
ER ₇ "	271.0	380.9
IT83S-742-2 "	267.3	365.8
TVX 3236 (NSD)	211.3	299.3
BLACKEYE "	272.3	433.7
ER ₇ "	243.5	381.3
IT83S-742-2 "	306.1	411.9
	ns	ns
GENOTYPE		
TVX 3236	231.9	305.5 b
BLACKEYE	271.5	517.8 a
ER ₇	257.3	381.1 ab
IT83S-742-2	286.7	388.8 ab
	ns	***
WATER		
Stress	265.4	415.1
Non-stress	258.3	381.5
	ns	ns

S= Stress NSD= Non-stress ns= not significant

*** Different letters within a column indicate significant difference at p= 0.001 according to Duncan Multiple Range Test.

¹ Late vegetative stage V₈

² Flowering and pod development (R₁/R₂)

TABLE 14. The Effect of Soil Water Changes on Stomatal Conductance in Cowpeas in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	-17 ¹	4 ¹	18 ³
	mmols m ⁻² s ⁻¹		
BOO5-C (S)	205.9	101.1 c	75.4
TVX 3236 "	172.9	184.9 a	65.7
BOO5-C (NSD)	162.2	135.1 b	109.4
TVX 3236 "	144.6	143.6 b	103.7
	ns	*	ns
GENOTYPE			
BOO5-C	184.0	118.1 b	92.4
TVX 3236	158.8	164.2 a	84.7
	ns	*	ns
WATER			
Stress	189.4	143.0	70.6 b
Non-stress	153.4	139.4	106.6 a
	ns	ns	*

S = Stress NSD = Non-stress ns = non-significant

* Different letters within a column indicate significant difference at $p = 0.05$ according to Duncan Multiple Range Test

¹ Early vegetative stage (V₃)

² Late vegetative stage (V₇)

³ Flowering (R₁)

TABLE 15. The Effect of Soil Water Changes on Stomatal Conductance in Cowpeas Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED	
	1 ¹	15 ²
	mmols m ⁻² s ⁻¹	
TVX 3236 (S)	117.3	122.5
BLACKEYE "	96.3	61.5
ER ₇ "	108.5	85.1
IT83S-742-2 "	122.0	100.8
TVX 3236 (NSD)	100.3	113.9
BLACKEYE "	115.7	71.2
ER ₇ "	121.9	92.5
IT83S-742-2 "	116.4	127.6
	ns	ns
GENOTYPE		
TVX 3236	108.8	118.2 a
BLACKEYE	106.0	66.3 c
ER ₇	115.2	88.8 bc
IT83S-742-2	119.2	114.2 ab
	ns	***
WATER		
Stress	111.0	92.5
Non-stress	113.6	101.3
	ns	ns

S = Stress NSD = Non-stress ns = not significant

*** Different letters within a column indicate significant difference at $p = 0.001$ according to Duncan Multiple Range Test.

¹ Late vegetative stage (V₈)

² Flowering and pod development (R₁/R₂)

TABLE 16. The Effect of Soil Water Changes on Carbon Isotope Discrimination in Cowpeas Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT		
		Delta
TVX 3236	(S)	20.6
BLACKEYE	"	19.9
ER ₇	"	20.6
IT83S-742-2	"	20.4
TVX 3236	(NSD)	21.3
BLACKEYE	"	20.1
ER ₇	"	20.2
IT83S-742-2	"	20.3
		ns
	GENOTYPE	
TVX 3236		20.9 -
BLACKEYE		20.0
ER ₇		20.4
IT83S-742-2		20.3
		ns
	WATER	
Stress		20.5
Non-stress		20.4
		ns

S = Stress NSD = Non-stress ns = not significant

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SUMMARY

RESPONSE UNDER MOISTURE STRESS IN 1990		
	BEANS	COWPEAS
Photosynthesis	* at R ₅ - 41 DAS	* at V ₇ - 4 DAS * at R ₁ - 18 DAS
Transpiration	* at R ₅ - 41 DAS	* at V ₇ - 4 DAS
Ratio		
Stomatal Conductance	ns	ns
CID	ns	ns

* significant at p=0.05 ns = not significant

DAS = Days after stress was imposed

CONCLUSIONS

Water stress decreased photosynthesis late in the season when the stress was severe while stomatal conductance was affected earlier in the season in both beans and cowpeas. Genotypic differences were found only for stomatal conductance but not for photosynthesis. The resistant bean genotype, 9-39-1 maintained its stomatal conductance under stress while the susceptible genotype significantly decreased stomatal conductance under stress. This suggests that stomatal conductance may have potential to be used as a screening tool in a bean or cowpea improvement program. More work is needed on a

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wide range of genotypes.

Carbon isotope discrimination was not affected by stress, contrary to reports that have been made that CID decreased with increasing stress. Genotypic differences were observed in beans only. CID values were not effective in separating resistant genotypes from susceptible ones in either beans or cowpeas. The high cost of CID analysis limits the potential use of CID in breeding programs.

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CHAPTER 3

THE EFFECT OF SOIL MOISTURE STRESS ON DRY BEANS (Phaseolus vulgaris L.) AND COWPEAS (Vigna unguiculata (walp) L.). III. Nitrogen Partitioning and Remobilization.

ABSTRACT

Nitrogen accumulation and partitioning in grain legumes is important in terms of both the physiology of pod filling and the nutritive value of the grain. Soil water deficits affect nitrogen accumulation. The objective of this study was to determine the effects of soil water changes on nitrogen accumulation, partitioning and remobilization in bean (Phaseolus vulgaris L.) and cowpea (Vigna unguiculata (walp) L.). This study was carried out in the field using a rainshelter or black polyethylene plastic to impose terminal drought stress at the late vegetative stage (V_9).

A moderate moisture stress with a drought intensity index of 0.36 decreased the proportion of ^{15}N in the roots, stem and leaves in beans and cowpeas. Resistant genotypes remobilized more N to the seeds and other plant parts than susceptible genotypes suggesting that N remobilization may contribute to yield stability. N concentration and dry weight were reduced by moisture stress.

INTRODUCTION

Nitrogen management is one of the greatest challenges in crop production. To realize higher yield of grain legumes with high protein requires higher rates of nitrogen fixation by legumes and increased partitioning of nitrogen into the seeds. A thorough understanding of nitrogen partitioning during growth and development may facilitate efforts to achieve higher yield, especially in moisture limiting environments.

In soybean (Glycine max L.), leaf nitrogen contributed 45-64% of the total N that was remobilized to seeds and the stem N contributed 19-27% (Zeihner et al., 1982). Severe moisture stress decreased N concentration in soybean leaves and the proportion of seed nitrogen coming from remobilization was not related to yield since moisture stress did not consistently alter the contribution that remobilized N made to seed N (Egli et al., 1983). Navarro et al (1985) in soybean studies concluded that high seed protein genotypes exhibited faster nitrogen partitioning and dry matter allocation into seeds. When three bean lines were labelled with ^{15}N at the early pod fill stage, they displayed an increase in nitrogen content in flowers and fruits (Dubois and Burris, 1986).

In cowpeas, nitrogen fixed after flowering contributed 40% of the fruit's intake of nitrogen. The mobilization of nitrogen fixed before flowering contributed 60% (Peoples et al., 1983). Muchow et al. (1993) reported no differences in N partitioning to leaves in soybean, mungbean and cowpea grown under wet and dry water regimes. Biomass accumulation was positively correlated to nitrogen accumulation.

The objective of this study was to determine the effect of water stress on nitrogen partitioning and remobilization in beans and cowpeas.

MATERIALS AND METHODS

A field study was conducted at the Agronomy Research Farm at Michigan State University in East Lansing during the summers of 1990 and 1992. In 1990 a rainshelter was used to impose moisture stress at 37 DAP. In 1992 a black polyethylene plastic was placed between the rows at 55 DAP, to impose moisture stress. Moisture stress was imposed at the late vegetative stage (V_9) each year, but different environmental conditions led to different growth rates for each year, hence the late vegetative stage did not occur at the same number of DAP.

The soil type for the 1990 experiment was a fine loamy, mixed mesic aericochraqualfs with a slope of 0-3% (USDA Soil Conservation Service Classification). For the 1992 experiment it was a fine loamy, mixed mesic glossoboric hapludalfs with a slope of 2-6%. The rainfall distribution and temperature data are presented in Fig 1 and Table 1 of Appendix A.

The experimental design was a modified split plot with four replications. Moisture level was the main plot and genotypes were the subplot. The moisture factor was confounded by site difference in that all stressed plots were grouped together and all non-stressed plots were grouped together. Each plot had four rows of 2 m length. The bean spacing was 50 x 10 cm and the cowpea spacing was 75 x 20 cm which resulted in a plant density of 20 plants per m^2 for beans and 10 plants per m^2 for cowpeas. In 1990 two bean genotypes, 9-39-1 and 8-42-M-2, and two cowpea genotypes, TVX 3236 and B005-C, were grown. In 1992 four bean genotypes, 9-39-1, 8-42-M-2, N81017 and 8-25-2, and four cowpea genotypes, TVX 3236, Blackeye, ER, and IT83S-742-2, were grown.

The bean genotypes were chosen based upon their previous performance in the MSU bean breeding program and their subsequent designation as either drought resistance or susceptible. The cowpea genotypes were chosen based upon their performance from a preliminary growth chamber study conducted in 1989 and their performance in field studies at IITA and in Botswana. Genotypic descriptions are presented in Table 2 of Appendix A.

All plots were hand planted using a hoe to open rows. Forty or 20 seed were planted for beans and cowpeas respectively, with abundant inoculant. The bean inoculum was Rhizobium phaseoli and the cowpea inoculum was Rhizobium cowpea miscellany nitrogen EL.

Planting and Management Practices

1990

Both beans and cowpeas were planted on June 25 but because of poor germination the cowpeas were replanted on July 18. Fertilizer was applied as 19-19-19 at the rate of 40 Kg N/ha before planting. Three days after planting on June 28, all plots received 30 mm of irrigation water to facilitate germination. The total rainfall during the growing season (June 25-Oct 5) was 287.6 mm. On July 31, Sevin (Carbaryl insecticide) was applied at the rate of 4 teaspoons per gallon of water to control Mexican beetle and leafhopper.

1992

Planting occurred on June 12. The fertilizer 21-7-14 with 4 % Mn and 1 % Zn was applied at the rate of 40 Kg N/ha before planting. All plots received a total of 283.3 mm

of irrigation in four applications before stress was imposed. The total rainfall during the growing season (June 12-Sept. 16) was 309.0 mm. A greater amount of water was applied by irrigation in 1992 in order to break the crust and enhance germination and stand establishment. Sevin was applied on July 29 to control leafhopper.

Soil moisture was monitored regularly in all plots at three depths in 1990 (0-30, 30-60, 60-90) using a neutron probe. In 1992 readings were only recorded at the 0-30 and 30-60 cm depths because the field had a high water table. Undisturbed soil core samples were taken at each depth to develop a soil moisture desorption curve which was used to convert the volumetric moisture content into matric potential.

¹⁵N Measurement

In 1990 ten plants per plot from the border rows were labelled with ¹⁵N on August 10. Five plants of approximately the same growth stage were tagged from each border row then designated as 1 to 10 in alternating rows so that the odd numbered plants were in one row and the even numbered plants were in another row. In 1992 eight plants per plot were labelled with ¹⁵N on August 11. Each year plants were labelled at the late vegetative stage (V₉).

Treating Plants with ¹⁵N

¹⁵N-urea was used to label the plants. Plants were labelled in the morning between 8 am and 12 noon. Upon labelling, each plant was covered with plastic so that the entire trifoliolate was separated from the rest of the plant. The trifoliolate was dipped into the solution of 0.35 % N and 0.001 % ortho L-77 surfactant for a few seconds then removed. The plastic around the plant prevented the solution from dripping onto the plant or the

soil. Control plants were treated with surfactant only. As soon as the leaf was dry, the plastic was removed, rinsed with water, and dried in the sun. The petiole of the labelled leaf was tagged and a flag was placed in front of the plant for easy identification. After a minimum of two hours, the labelled plant was recovered with plastic as before and the leaf was dipped in water to remove all urea from the outside of the leaf.

Sampling Plants

A screw driver was used to loosen the soil around the labelled plant and the plant was pulled from the soil with as much root as possible. The plant was cut at the soil line to separate the roots. The labelled leaf and its petiole were separated from the rest of the plant, washed with water to remove all soil, and placed in a bag for drying. A separate container was used to wash soil from the remainder of the plant. A tape measurer was used to determine the height of each plant and to determine the middle of the plant for separation into upper and lower leaves, upper and lower stems, and upper and lower reproductive parts (flowers and/or pods). Each plant part was bagged separately for drying.

Two labelled plants were sampled the day after treatment in order to determine how much ^{15}N -urea entered the plant. In 1990 two labelled plants were subsequently sampled at flowering and pod development (R_1/R_2), pod filling (R_3) and physiological maturity (R_7). In 1992 labelled plants were subsequently sampled only at pod filling and physiological maturity.

Sample Analysis

The samples were oven dried for 48 hrs at 72°C before grinding in a Udy mill

grinder. The dry weight was also recorded. Extreme care was taken not to contaminate plant parts. Whirlpak bags were used to collect samples from the grinder. After each sample was ground, the entire grinder, working surface, and the instruments were carefully cleaned. Compressed air was used to clean the grinder.

Samples were analyzed for N and ^{15}N using a gas chromatography mass spectrometer (ANCA-MS, Europa Scientific, Crewe. U.K) after conversion of sample N to N_2 by Dumas combustion in a roboprep CN analyzer. Ammonium sulfate (0.3663 atom % ^{15}N) Whatman number 1 filter paper was used as a reference standard.

RESULTS AND DISCUSSION

BEANS

^{15}N Content

1990

Moisture stress did not significantly reduce ^{15}N content in the portion of the root that was retrieved but there was a tendency for lower ^{15}N content under stress. There were no genotypic differences (Table 1). There was a tendency for a higher ^{15}N content under the non-stress treatment in the lower stem and a tendency for a lower ^{15}N content under the non-stress treatment in the upper stem at pod filling and physiological maturity (Table 2). At 65 DAS (R_2), 9-39-1 contained a significantly greater proportion of total ^{15}N than 8-42-M-2 in the lower stems, possibly indicating less N remobilization to seeds or other plant parts. Moisture stress significantly decreased ^{15}N content in the lower leaves at 29 DAS (Table 3). 8-42-M-2 contained significantly more ^{15}N than 9-39-1 in

TABLE 1. The Effect of Soil Water Changes on ^{15}N Content in Bean Roots in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	21 ¹	29 ²	65 ³
	%		
8-42-M-2 (S)	0.71	0.79	0.53
9-39-1 "	0.34	0.55	0.75
8-42-M-2 (NSD)	1.57	1.26	0.55
9-39-1 "	1.06	1.10	0.71
	ns	ns	ns
GENOTYPE			
8-42-M-2	1.14	1.03	0.54
9-39-1	0.70	0.83	0.73
	ns	ns	ns
WATER			
Stress	0.52	0.67	0.64
Non-stress	1.31	1.18	0.63
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₂/R₃ Flowering and early pod development

² = R₅ Pod filling

³ = R₇ Physiological maturity

TABLE 2. The Effect of Soil Water Changes on ^{15}N Content in Bean Stems in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	21 ¹	29 ²	65 ³
<u>Lower stem</u>		%	
8-42-M-2 (S)	10.29 a	6.85	1.74
9-39-1 "	5.11 b	6.19	3.70
8-42-M-2 (NSD)	9.12 a	12.58	2.34
9-39-1 "	10.56 a	11.06	6.95
	+	ns	ns
GENOTYPE			
8-42-M-2	9.79	9.31	2.00
9-39-1	7.83	8.62	5.33
	ns	ns	*
WATER			
Stress	7.70	6.52	2.72
Non-stress	9.94	11.71	4.97
	ns	**	ns
<u>Upper stem</u>			
8-42-M-2 (S)	5.82	4.09	2.21
9-39-1 "	2.25	4.97	2.07
8-42-M-2 (NSD)	4.34	3.50	0.98
9-39-1 "	5.05	3.73	2.02
	ns	ns	ns
GENOTYPE			
8-42-M-2	5.08	3.84	1.59
9-39-1	3.65	4.35	2.04
	ns	ns	ns
WATER			
Stress	4.04	4.52	2.15
Non-stress	4.70	3.63	1.50
	ns	ns	ns

S= Stress NSD= Non-stress ns= not significant

**, * + Different letters within a column indicate significant difference at $p = 0.01, 0.05$ or 0.1 respectively according to DMRT.

$$^1 = R_2/R_3 \quad ^2 = R_5 \quad ^3 = R_7$$

TABLE 3. The Effect of Soil Water Changes on ^{15}N
Content in Bean Leaves in the Rainshelter at
the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	21 ¹	29 ²	65 ³
<u>Lower leaves</u>		%	
8-42-M-2 (S)	9.06	5.71	0.81
9-39-1 "	11.37	1.09	3.40
8-42-M-2 (NSD)	9.13	23.07	1.32
9-39-1 "	22.24	9.94	2.37
	ns	ns	ns
GENOTYPE			
8-42-M-2	9.09	14.39	1.06
9-39-1	16.81	5.51	2.81
	ns	*	ns
WATER		-	
Stress	10.21	3.40	2.11
Non-stress	16.62	16.50	1.92
	ns	**	ns
<u>Upper leaves</u>			
8-42-M-2 (S)	18.02	13.14	2.49
9-39-1 "	7.89	11.00	1.22
8-42-M-2 (NSD)	14.02	10.61	1.66
9-39-1 "	11.11	11.05	0.95
	ns	ns	ns
GENOTYPE			
8-42-M-2	16.31	12.06	2.28
9-39-1	9.50	11.03	1.10
	*	ns	ns
WATER			
Stress	12.95	12.07	1.76
Non-stress	12.36	10.86	1.13
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

** p = 0.01 * p = 0.05 ¹ = R₂/R₃ ² = R₅ ³ = R₇

the lower leaves at 29 DAS (R_2) and in the upper leaves at 21 DAS (R_3). This indicates that by these dates, 8-42-M-2 was remobilizing less N from the leaves to developing seeds or other plant parts than 9-39-1. Although not significant, the differences between ^{15}N content in the upper and lower reproductive structures under stress and non-stress were quite interesting. 9-39-1 maintained the level of ^{15}N remobilization to the upper and lower reproductive structures under stress and non-stress treatments at 65 DAS, but the level of remobilization was reduced under stress in 8-42-M-2 (Table 4). In addition, 9-39-1 remobilized ^{15}N to the seeds at a faster rate under the stress than non-stress treatment. The ability of 9-39-1 to increase its N remobilization rate under stress and its ability to maintain the amount of N remobilized may partly explain its greater yield stability (4.6% yield reduction due to stress) over 8-42-M-2 (51.4% yield reduction).

1992

Eventhough four genotypes were planted in 1992, only two were analyzed for ^{15}N because of lack of funds to analyze all four genotypes. The genotypes N81017 (resistant and high yielding) and 8-25-2 (susceptible and low yielding) were choosen for analysis because they had not previously been used in ^{15}N studies and because 9-39-1 and 8-42-M-2 were used in another study in 1988. Thus, the 1988 and 1990 results would provide information about the latter two genotypes and the 1991 and 1992 results would provide information about the former two genotypes.

There were no differences between stress and non-stress treatments or between genotypes in ^{15}N content in the roots, stems, leaves or reproductive structures (Tables 5-8). This was to be expected since there was only a mild drought stress in 1992.

TABLE 4. The Effect of Soil Water Changes on ^{15}N Content in Bean Reproductive Parts in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	21 ¹	29 ²	65 ³
<u>Lower reproductive</u>		%	
8-42-M-2 (S)	4.44	20.81	26.07
9-39-1 "	4.37	16.20	34.14
8-42-M-2 (NSD)	5.50	22.39	40.64
9-39-1 "	3.75	5.83	34.52
	ns	ns	ns
GENOTYPE			
8-42-M-2	5.00	21.60	32.31
9-39-1	4.06	11.02	34.33
	ns	+	ns
WATER			
Stress	4.41	- 18.50	30.10
Non-stress	4.63	14.11	37.14
	ns	ns	ns
<u>Upper reproductive</u>			
8-42-M-2 (S)	5.62	3.71	13.89
9-39-1 "	1.27	4.42	10.18
8-42-M-2 (NSD)	2.80	5.03	18.76
9-39-1 "	1.39	2.02	10.74
	ns	ns	ns
GENOTYPE			
8-42-M-2	4.21	4.37	16.33
9-39-1	1.32	3.22	10.46
	ns	ns	ns
WATER			
Stress	3.44	4.06	12.03
Non-stress	2.20	3.53	14.75
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

+ p = 0.1 ¹ = R_2/R_3 ² = R_5 ³ = R_7

TABLE 5. The Effect of Soil Water Changes on ^{15}N Content in Bean Roots Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	<u>DAYS AFTER STRESS WAS IMPOSED</u>	
	37 ¹	47 ²
	%	
N81017 (S)	1.22	0.56
8-25-2 "	0.75	0.55
N81017 (NSD)	1.23	0.66
8-25-2 "	1.63	0.60
	ns	ns
	GENOTYPE	
N81017	1.23	0.61
8-25-2	1.19	0.58
	ns	ns
	WATER	
Stress	0.99	0.56
Non-stress	1.43	0.63
	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₅ Pod filling

² = R₇ Maturity

TABLE 6. The Effect of Soil Water Changes on ^{15}N Content in Bean Stems Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT		DAYS AFTER STRESS WAS IMPOSED	
		37 ¹	47 ²
<u>Lower stem</u>		%	
N81017	(S)	9.42	8.97
8-25-2	"	8.44	9.63
N81017	(NSD)	7.52	9.28
8-25-2	"	11.16	10.51
		ns	ns
GENOTYPE			
N81017		8.47	9.13
8-25-2		9.80	10.07
		ns	ns
WATER			
Stress		8.93	9.30
Non-stress		9.34	9.90
		ns	ns
<u>Upper stem</u>			
N81017	(S)	3.35	1.88
8-25-2	"	1.53	2.37
N81017	(NSD)	2.61	1.95
8-25-2	"	2.82	9.48
		ns	ns
GENOTYPE			
N81017		2.98	1.91
8-25-2		2.17	5.93
		ns	ns
WATER			
Stress		2.71	2.12
Non-stress		2.44	5.71
		ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₅ ² = R₇

TABLE 7. The Effect of Soil Water Changes on ^{15}N Content in Bean Leaves Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED	
	37¹	47²
<u>Lower leaves</u>		
	%	
N81017 (S)	11.11	6.98
8-25-2 "	13.95	6.54
N81017 (NSD)	10.60	3.23
8-25-2 "	13.20	9.44
	ns	ns
GENOTYPE		
N81017	10.86	5.11
8-25-2	13.57	8.00
	ns	ns
WATER		
Stress	12.53	6.76
Non-stress	11.90	6.34
	ns	ns
<u>Upper leaves</u>		
N81017 (S)	13.92	9.21
8-25-2 "	4.44	18.56
N81017 (NSD)	6.17	18.46
8-25-2 "	18.47	8.00
	ns	ns
GENOTYPE		
N81017	9.49	14.49
8-25-2	11.46	14.04
	ns	ns
WATER		
Stress	8.50	14.55
Non-stress	12.32	13.98
	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₅ ² = R₇

TABLE 8. The Effect of Soil Water Changes on ^{15}N Content in Bean Reproductive Parts Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1992.

TREATMENT		DAYS AFTER STRESS WAS IMPOSED	
		37¹	47²
<u>Lower reproductive</u>		%	
N81017	(S)	59.08	54.06
8-25-2	"	66.30	55.64
N81017	(NSD)	70.74	57.67
8-25-2	"	42.81	76.98
		ns	ns
GENOTYPE			
N81017		64.91	55.87
8-25-2		54.56	66.31
		ns	ns
WATER			
Stress		62.69	54.85
Non-stress		56.77	67.33
		ns	ns
<u>Upper reproductive</u>			
N81017	(S)	7.78	10.01
8-25-2	"	6.75	20.92
N81017	(NSD)	7.00	13.63
8-25-2	"	27.37	8.47
		ns	ns
GENOTYPE			
N81017		7.39	11.82
8-25-2		17.06	14.70
		ns	ns
WATER			
Stress		7.19	15.47
Non-stress		17.19	11.05
		ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₅ ² = R₇

In 1990, moisture stress tended to reduce ^{15}N content in the roots, lower stem and lower leaves indicating that there was greater N remobilization to the seeds under stress. The resistant genotype, 9-39-1, remobilized more N to the seeds and other plant parts than the susceptible genotype, 8-42-M-2. There were no differences in 1992 because there was minimal stress. The difference in N remobilization between resistant and susceptible genotypes, and between stress and non-stress indicate that N remobilization may contribute to yield stability.

^{15}N content for most plant parts was not statistically different even though numerical differences existed. This is due to the very high coefficient of variation which ranged from 60 to 200%. Harris (1993) also reported very high coefficient of variation ranging from 107 to 171% in ^{15}N recovery in red clover.

Nitrogen Concentration

1990

Moisture stress significantly decreased N concentration in the roots at 29 DAS (Table 9) The stress treatment significantly reduced N concentration at 21 and 29 DAS in the lower and upper stems (Tables 9) and in the lower and upper leaves (Tables 10). These results may be due to greater N remobilization from the roots, stems and leaves under stress and/or reduced N fixation under stress or greater nitrogen use efficiency. Moisture stress reduced N concentration in the lower reproductive structures at 29 and 65 DAS and in the upper reproductive structures at 29 DAS (Table 11). Egli et al. (1983) reported decreased N concentration in soybean leaves in response to moisture stress. At physiological maturity, the resistant and low yielding genotype 9-39-1 had a significantly

TABLE 9. The Effect of Soil Water Changes on N Concentration in Bean Roots and Stems in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI, 1990

TREATMENT (DAP)	ROOTS			LOWER STEM			UPPER STEM		
	21 ¹	29 ²	65 ³	21 ¹	29 ²	65 ³	21 ¹	29 ²	65 ³
8-42-M-2 (S)	1.26	1.01	1.00	1.73 bc	1.08	0.69	1.75	1.34	0.86
9-39-1	1.19	0.90	1.12	1.56 c	1.04	1.03	1.49	1.35	1.34
8-42-M-2 (NSD)	1.26	1.17	0.93	1.84 ab	1.57	0.86	2.20	1.76	0.87
9-39-1	1.43	1.12	1.07	2.02 a	1.48	1.20	2.32	1.85	1.72
GENOTYPE	ns	ns	ns	*	ns	ns	ns	ns	ns
8-42-M-2	1.26	1.09	0.96	1.79	1.32	0.77	1.97	1.55	0.87
9-39-1	1.31	1.01	1.10	1.79	1.26	1.12	1.90	1.60	1.56
WATER	ns	ns	+	ns	ns	*	ns	ns	***
Stress	1.22	0.95	1.06	1.65	1.06	0.86	1.62	1.35	1.07
Non-stress	1.34	1.15	1.00	1.93	1.53	1.03	2.26	1.80	1.29
	ns	*	ns	**	**	ns	**	**	ns

S = Stress NSD = Non-stress ns = not significant
***, **, *, + Different letters within a column indicate significant difference at p = 0.01, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.
¹ = R₂/R₃ ² = R₅ ³ = R₇

TABLE 10. The Effect of Soil Water Changes on N Concentration in Bean Leaves in the Rainshelter at the MSU Agronomy Farm in East Lansing. MI. 1990.

TREATMENT		DAYS AFTER STRESS WAS IMPOSED		
		21 ¹	29 ²	65 ³
<u>Lower leaves</u>			%	
8-42-M-2	(S)	4.33	2.90 b	1.06
9-39-1	"	3.76	2.44 c	1.66
8-42-M-2	(NSD)	4.57	3.68 a	1.22
9-39-1	"	4.39	3.56 a	1.87
		ns	+	ns
GENOTYPE				
8-42-M-2		4.45	3.29	1.14
9-39-1		4.07	3.00	1.76
		*	**	*
WATER				
Stress		4.05	- 2.67	1.40
Non-stress		4.43	3.62	1.59
		*	***	ns
<u>Upper leaves</u>				
8-42-M-2	(S)	4.48	4.04	1.08
9-39-1	"	5.22	3.21	1.73
8-42-M-2	(NSD)	5.66	4.81	0.99
9-39-1	"	5.47	4.58	1.60
		ns	ns	ns
GENOTYPE				
8-42-M-2		5.07	4.41	1.05
9-39-1		5.34	3.89	1.67
		ns	**	ns
WATER				
Stress		4.85	3.61	1.45
Non-stress		5.56	4.70	1.45
		+	***	ns

S = Stress NSD = Non-stress ns = not significant

***, **, *, + Different letters within a column indicate significant differences at p = 0.001, 0.01, 0.05 or 0.1 respectively according to DMRT

¹ = R₂/R₃ ² = R₅ ³ = R₇

TABLE 11. The Effect of Soil Water Changes on N Concentration in Bean Reproductive Parts in the Rainshelter at the MSU Agronomy Farm in East Lansing. MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	21 ¹	29 ²	65 ³
<u>Lower Reproductive</u>		%	
8-42-M-2 (S)	4.71	2.37	2.14 b
9-39-1 "	4.48	2.30	1.91 b
8-42-M-2 (NSD)	4.66	3.11	2.74 a
9-39-1 "	4.40	3.87	3.03 a
	ns	ns	+
GENOTYPE			
8-42-M-2	4.69	2.74	2.44
9-39-1	4.44	3.09	2.47
	+	ns	ns
WATER			
Stress	4.59	2.34	2.02
Non-stres	4.53	3.49	3.88
	ns	**	***
<u>Upper Reproductive</u>			
8-42-M-2 (S)	4.13	3.14	2.38
9-39-1 "	4.19	2.59	2.71
8-42-M-2 (NSD)	4.12	3.93	2.29
9-39-1 "	4.20	4.20	2.53
	ns	ns	ns
GENOTYPE			
8-42-M-2	4.13	3.53	2.34
9-39-1	4.19	3.40	2.62
	ns	ns	ns
WATER			
Stress	4.16	2.87	2.55
Non-stress	4.17	4.06	2.41
	ns	*	ns

S= Stress NSD= Non-stress ns= not significant

***, **, + Different letters within a column indicate

significant differences at p= 0.001, 0.01 or 0.1 respectively according to DMRT

¹= R₂/R₃ ²= R₅ ³= R₇

higher N concentration than 8-42-M-2, the susceptible and high yielding genotype in the roots, lower and upper stems, and lower leaves indicating that 9-39-1 may have remobilized less N to the seeds and other plant parts or may have utilized nitrogen less efficiently than 8-42-M-2. There was a significant reduction in N concentration under stress in the lower leaves at 21 and 29 DAS (Table 10), in the upper leaves at 29 DAS (Table 10) and in the lower reproductive structures at 29 and 65 DAS (Table 11).

1992

Since there was a mild drought stress in 1992, there were no differences between stress and non-stress treatments except at 47 DAS in the lower leaves (Table 14), where the stress treatment had a significantly higher N concentration than the non-stress treatment. N81017 had a significantly higher N concentration than 8-25-2 at 37 DAS in the upper leaves. Although not significant, there was a tendency for N81017 to have a lower N concentration than 8-25-2 in the roots, stems, leaves and reproductive structures (Tables 12-15).

In 1990 moisture stress reduced N concentration in the roots, stem, leaves and reproductive structures, indicating that the utilization of N under stress was probably more efficient than under the non-stress treatment. The resistant genotype, N81017 had lower N concentration in the seeds than the susceptible genotype, 8-25-2 which may partly explain its greater yield potential. Lynch and White (1992) reported that total N allocation to the seeds dominated the reproductive N budget in beans.

TABLE 12. The Effect of Soil Water Changes on N Concentration in Bean Roots Using Plastic at the Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED	
	37 ¹	47 ²
	%	
N81017 (S)	1.05	0.88
8-25-2 "	1.21	0.99
N81017 (NSD)	1.18	0.98
8-25-2 "	1.24	1.04
	ns	ns
GENOTYPE		
N81017	1.12	0.93
8-25-2	1.22	1.01
	ns	ns
WATER		
Stress	1.13	0.94
Non-stress	1.21	1.01
	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₅ ² = R₇

TABLE 13. The Effect of Soil Water Changes on N Concentration in Bean Stems Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT		DAYS AFTER STRESS WAS IMPOSED	
		37 ¹	47 ²
<u>Lower Stem</u>		%	
N81017	(S)	1.49	1.69
8-25-2	"	1.69	2.02
N81017	(NSD)	1.56	1.69
8-25-2	"	1.98	2.25
		ns	ns
	GENOTYPE		
N81017		1.52	1.69
8-25-2		1.84	2.13
		ns	ns
	WATER		
Stress		1.59	1.85
Non-stress		1.77	1.97
		ns	ns
<u>Upper Stem</u>			
N81017	(S)	1.65	1.66
8-25-2	"	2.02	1.96
N81017	(NSD)	1.93	1.85
8-25-2	"	1.89	2.41
		ns	ns
	GENOTYPE		
N81017		1.79	1.75
8-25-2		1.96	2.19
		ns	ns
	WATER		
stress		1.84	1.81
Non-stress		1.91	2.13
		ns	ns

S= Stress NSD= Non-stress ns= not significant

¹= R₅ ²= R₇

TABLE 14. The Effect of Soil Water Changes on N Concentration in Bean Leaves Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED	
	37 ¹	47 ²
<u>Lower Leaves</u>		
	%	
N81017 (S)	4.03	3.51
8-25-2 "	4.13	3.44
N81017 (NSD)	3.75	2.88
8-25-2 "	3.84	3.07
	ns	ns
GENOTYPE		
N81017	3.89	3.19
8-25-2	3.98	3.26
	ns	ns
WATER		
Stress	4.08	- 3.47
Non-stress	3.79	2.98
	ns	+
<u>Upper Leaves</u>		
N81017 (S)	4.81	3.46
8-25-2 "	4.32	4.11
N81017 (NSD)	4.86	4.17
8-25-2 "	4.32	4.11
	ns	ns
GENOTYPE		
N81017	4.84	3.82
8-25-2	4.32	4.11
	+	ns
WATER		
Stress	4.57	3.92
Non-stress	4.59	4.14
	ns	ns

S = Stress NSD = Non-stress ns = not significant

+ p = 0.1 ¹ = R₅ ² = R₇

TABLE 15. The Effect of Soil Water Changes on N Concentration in Bean Reproductive Parts Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1992.

TREATMENT		DAYS AFTER STRESS WAS IMPOSED	
		37 ¹	47 ²
<u>Lower Reproductive</u>		%	
N81017	(S)	3.63	3.62
8-25-2	"	3.93	3.88
N81017	(NSD)	3.67	3.63
8-25-2	"	3.88	4.29
		ns	ns
GENOTYPE			
N81017		3.65	3.62
8-25-2		3.90	4.09
		ns	ns
WATER			
Stress		3.78	3.75
Non-stress		3.78	3.96
		ns	ns
<u>Upper Reproductive</u>			
N81017	(S)	3.67	3.80
8-25-2	"	4.05	4.29
N81017	(NSD)	3.72	3.88
8-25-2	"	3.79	4.31
		ns	ns
GENOTYPE			
N81017		3.70	3.84
8-25-2		3.92	4.30
		ns	ns
WATER			
Stress		3.86	4.05
Non-stress		3.76	4.10
		ns	ns

S = stress NSD = Non-stress ns = not significant

¹ = R₅ ² = R₇

Biomass Accumulation

Total plant dry weight increased with plant growth but was reduced by moisture stress in most cases although the reduction was not statistically significant. In 1990, there was a tendency for the dry weight of 9-39-1 to decrease under stress and that of 8-42-M-2 to increase under stress at physiological maturity (Fig 1). There was a significant difference between the harvest index (HI) of 9-39-1 (HI= 0.64) and 8-42-M-2 (HI= 0.74) which may partly explain the low yield potential of 9-39-1 and the high yield potential of 8-42-M-2. In 1992, the dry weight of N81017 and 8-25-2 was decreased by stress at 37 DAS. The total dry weight decreased with time which could be due to excessive moisture that increased with time in 1992. The harvest index of N81017 and 8-25-2 were not significantly different in 1992. In 1992 it was 0.56 for N81017 and 0.53 for 8-25-2. The actual numbers for dry matter accumulation of the different plant parts are shown in appendix C (Tables 1-7). As would be expected, within each growing season the genotype that accumulated the most biomass also tended to accumulate the most nitrogen. Muchow et al (1993) reported similar results in the accumulation and partitioning of biomass and nitrogen in soybean, mungbean and cowpea.

COWPEAS

In 1990 cowpeas were replanted because of poor germination and the genotype B005-C was late maturing. As a result it flowered late in the season so it was not labelled with ¹⁵N-Urea. Only TVX 3236 was labelled. In 1992 excess moisture and low temperature delayed plant growth and cowpeas were more affected than beans.

FIG. 1. TOTAL PLANT DRY WEIGHT IN 1990

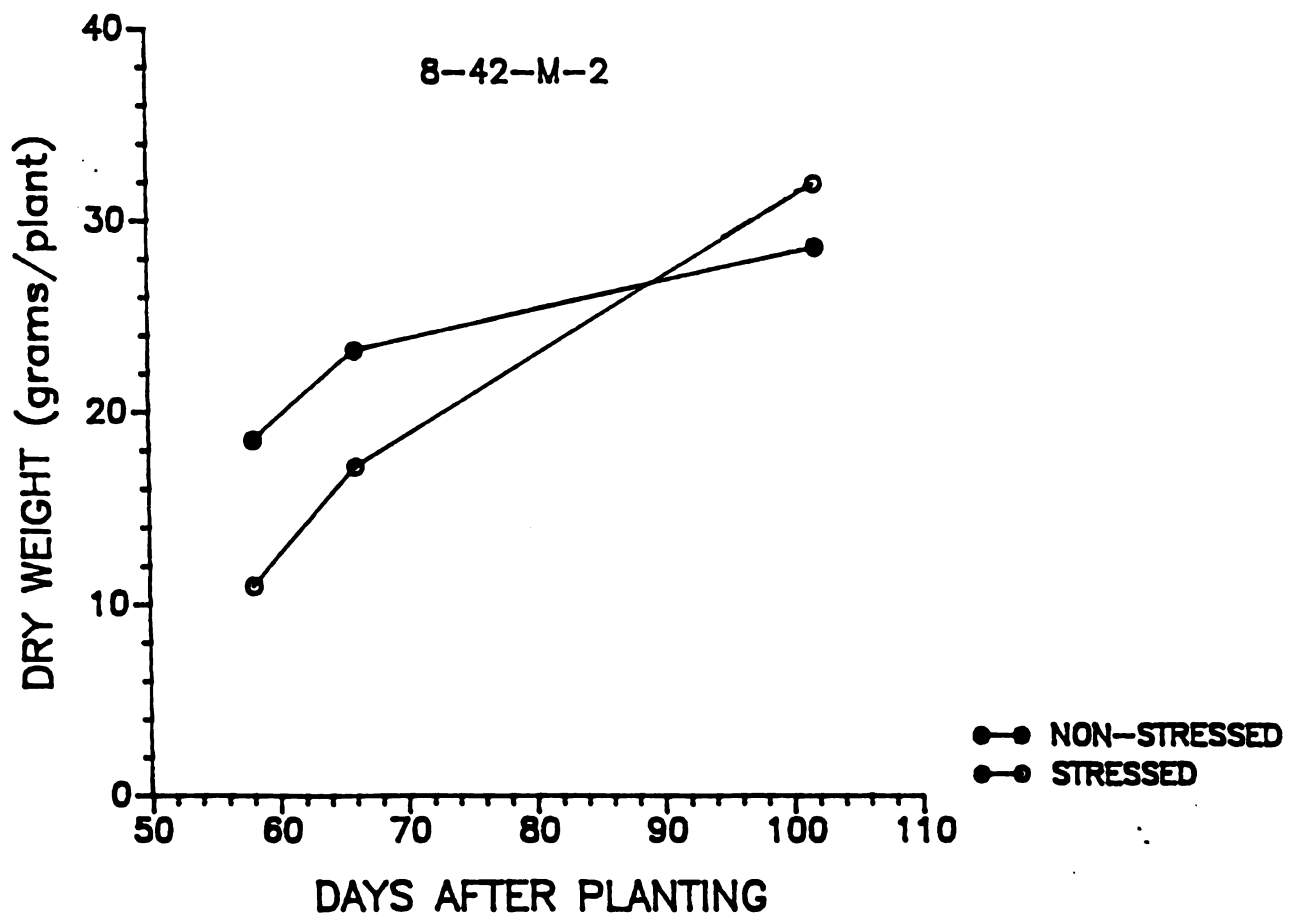
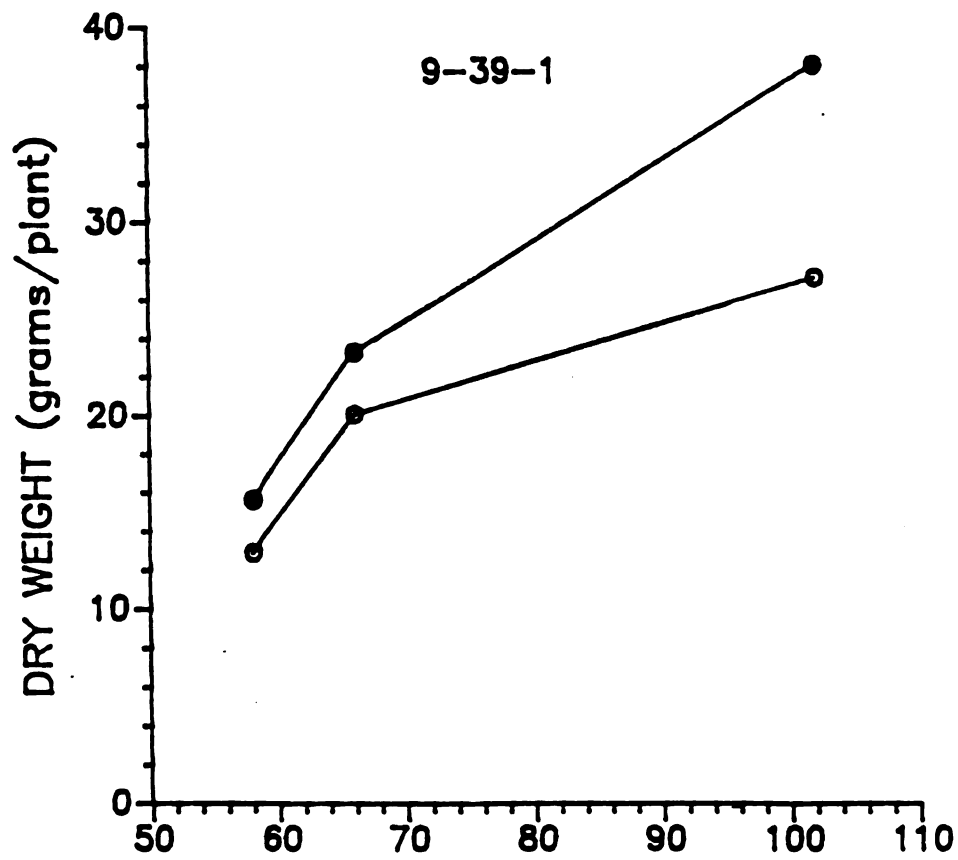
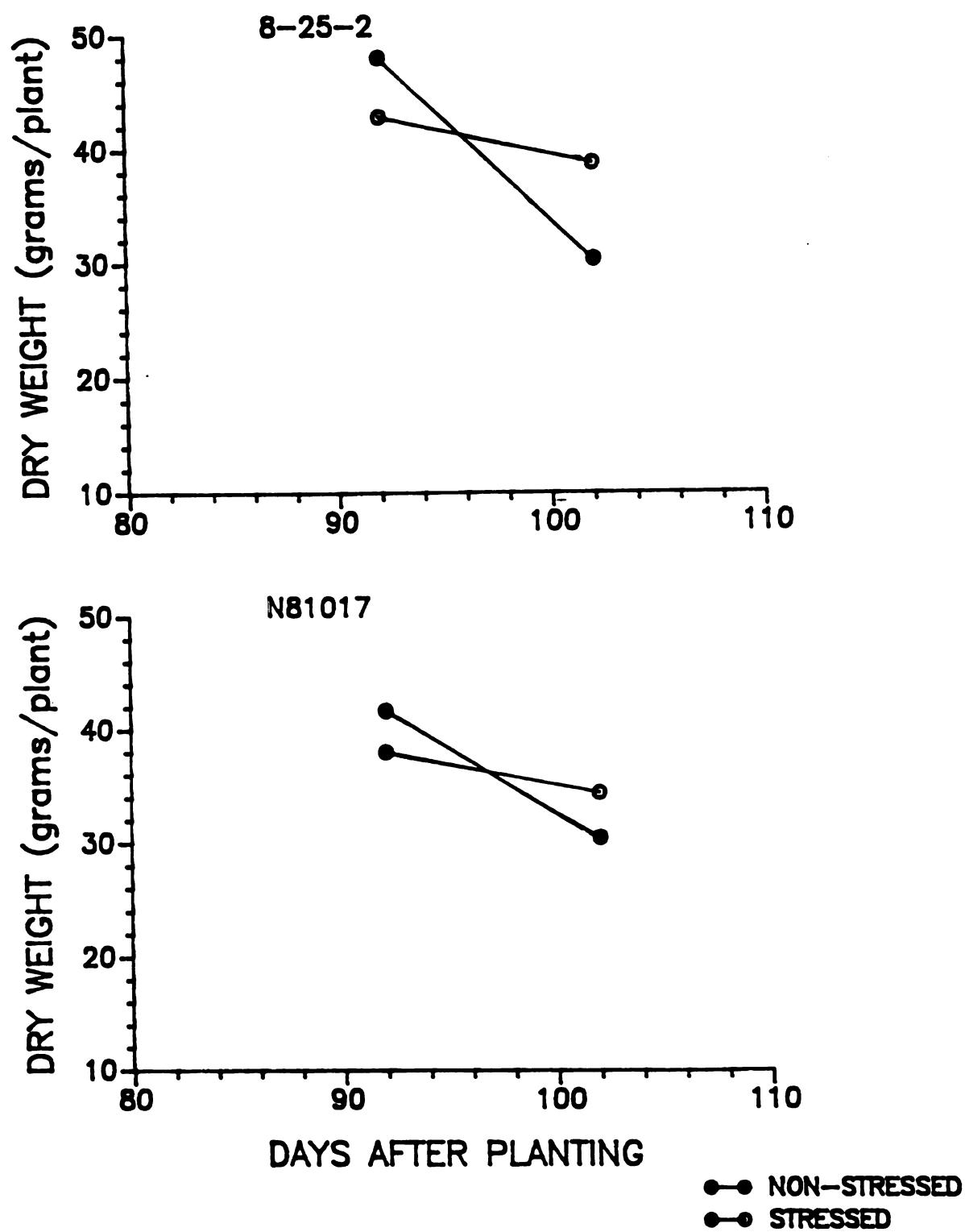


FIG. 2. TOTAL DRY WEIGHT IN BEANS IN 1992



Consequently, they flowered late and were not labelled.

¹⁵N Content

There was no significant difference in the ¹⁵N content between the stress and non-stress treatments of TVX 3236 in 1990 except in the lower stem at flowering (Table 16) where the non-stress treatment contained a greater proportion of ¹⁵N than the stress treatment. There was a tendency for a reduction of ¹⁵N content in plant structures under stress except in the reproductive structures where stress tended to increase the proportion of ¹⁵N content. These results support the theory of more N being remobilized from other plant parts to the seeds under stress.

N Concentration

There were no significant differences between the stress and non-stress treatment in the upper stem, lower leaves, and lower and upper reproductive structures in TVX 3236 (Table 17) in 1990. At 49 DAS in the roots, the stress treatment had a significantly higher N concentration than the non-stress treatment. Similarly, the upper leaves had a higher N concentration under stress at 13 DAS but the lower stem had reduced N concentration under stress at 33 DAS.

Biomass Accumulation

Moisture stress decreased plant dry weight but only significantly in the upper leaves at 13 DAS (Table 18) in 1990. However, the reproductive structures tended to have more dry weight at 33 DAS under stress. There was no reproductive data at 49 DAS because cowpea pods were damaged by frost.

TABLE 16. The Effect of Soil Water Changes on ^{15}N Content in Cowpea TVX 3236 in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990

TREATMENT		<u>DAYS AFTER STRESS WAS IMPOSED</u>		
		13 ¹	33 ²	49 ³
%				
Roots	(S)	7.59	5.87	5.16
	(NSD)	2.22	6.01	5.29
		ns	ns	ns
Upper Stem	(S)	8.89	6.52	8.01
	(NSD)	8.82	21.95	5.53
		ns	ns	ns
Lower Stem	(S)	7.55	16.39	8.98
	(NSD)	13.80	34.64	27.61
		*	ns	ns
Upper Leaves	(S)	6.90	3.20	3.40
	(NSD)	4.63	6.32	4.74
		ns	ns	ns
Lower Leaves	(S)	11.58	10.23	1.35
	(NSD)	14.52	25.00	9.01
		ns	ns	ns
Upper Reproductive	(S)	8.69	14.99	--
	(NSD)	4.33	7.42	--
		ns	ns	
Lower Reproductive	(S)	6.36	20.99	--
	(NSD)	6.42	4.38	--
		ns	ns	

* p(0.05)

S = Stress NSD = Non-stress ns = not significant

¹ = R₁ Flowering ² = R_{3/4} Early pod filling stage

³ = R_{5/6} Late pod filling stage

TABLE 17. The Effect of Soil Water Changes on N Concentration in Cowpea TVX 3236 in the Rainshelter at the MSU Agronomy Farm in East Lansing, MI. 1990

TREATMENT		DAYS AFTER STRESS WAS IMPOSED		
		13 ¹	33 ²	49 ³
		%		
Roots	(S)	1.79	1.92	3.21
	(NSD)	2.01	2.19	1.86
		ns	ns	*
Upper Stem	(S)	1.67	1.50	2.40
	(NSD)	2.57	2.64	1.65
		ns	ns	ns
Lower Stem	(S)	1.49	1.19	2.16
	(NSD)	2.50	2.46	1.93
		ns	+	ns
Upper Leaves	(S)	3.63	2.51	2.24
	(NSD)	3.41	3.60	2.84
		+	ns	ns
Lower Leaves	(S)	3.61	2.86	2.54
	(NSD)	3.81	3.79	2.94
		ns	ns	ns
Upper Reproductive	(S)	3.47	3.00	--
	(NSD)	3.24	3.14	--
		ns	ns	
Lower Reproductive	(S)	3.91	3.25	--
	(NSD)	3.94	3.66	--
		ns	ns	

S = Stress NSD = Non-stress ns = not significant

*, + p = 0.05 or 0.1 respectively

¹ = R₁ ² = R_{3/4} ³ = R_{5/6}

TABLE 18. The Effect of Soil Water Changes on Cowpea TVX 3236 Dry Weight in the Rainshelter at the MSU Agronomy Farm in East Lansing. MI. 1990.

TREATMENT	DAYS AFTER STRESS WAS IMPOSED		
	13 ¹	33 ²	49 ³
grams/plant			
Roots (S)	1.21	1.34	1.01
(NSD)	1.95	2.90	2.66
	ns	ns	ns
Upper Stem (S)	1.50	1.41	1.20
(NSD)	1.65	2.05	2.43
	ns	ns	ns
Lower Stem (S)	7.36	13.25	4.19
(NSD)	16.69	28.06	29.86
	ns	ns	ns
Upper Leaves (S)	1.18	1.05	2.41
(NSD)	1.94	2.65	1.16
	+	ns	ns
Lower Leaves (S)	4.66	7.05	1.18
(NSD)	13.63	18.93	8.25
	ns	ns	ns
Upper Reproductive (S)	0.45	1.96	--
(NSD)	0.27	0.48	--
Lower Reproductive (S)	1.26	9.10	--
(NSD)	1.46	4.58	--
	ns	ns	

S = Stress NSD = Non-stress ns = not significant

+ p = 0.1

¹ = R₁ ² = R_{3/4} ³ = R_{5/6}

CONCLUSIONS

Differences were found between the stress and non-stress treatments and between resistant and susceptible genotypes in ^{15}N content, N concentration and dry weight in beans and cowpeas. In general, moisture stress reduced ^{15}N content in the stems and leaves of in both beans and cowpeas. These results suggest that beans and cowpeas remobilized more N from the leaves and stems to the seeds under moisture stress. N remobilization in the resistant genotypes (9-39-1 and N81017) was not affected by stress. N remobilization was reduced under stress for the susceptible and high yielding genotype, 8-42-M-2 and increased under stress for the susceptible and low yielding genotype, 8-25-2. These findings suggests N remobilization may contribute to yield stability.

Soil moisture stress decreased N concentration in beans and cowpeas. The high yielding bean genotypes (8-42-M-2 and N81017) utilized nitrogen more efficiently than the low yielding genotypes. ^{15}N studies may therefore be useful in estimating or explaining the plant's response to stress. However, because of the difficulty and time involved in labelling plants, sampling and analysis, it is not feasible to do many replications. Therefore ^{15}N would not be useful in evaluating a large number of genotypes.

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CHAPTER 4

THE EFFECT OF LEAFHOPPER DAMAGE ON DRY BEANS (Phaseolus vulgaris L.) AND COWPEAS (Vigna unguiculata (walp) L.).

ABSTRACT

Soil moisture stress adversely affects crop growth and productivity. This study was conducted to examine the effect of moisture stress on yield and yield components, leaf water, root growth, physiological parameters, and nitrogen partitioning and remobilization in beans (Phaseolus vulgaris L.) and cowpeas (Vigna unguiculata (walp) L.) under field conditions. The research was conducted in Michigan using a black plastic to impede water on mixed mesic ochroqualfs soil. Moisture stress was imposed at the late vegetative stage (V₉), 48 DAP.

Leafhopper damage decreased seed yield by decreasing the number of pods per plant in both beans and cowpeas. Leaf water retention capacity, leaf water content and root growth were also decreased by leafhopper damage in beans and cowpeas.

Leafhopper damage decreased photosynthetic rate and stomatal conductance in both beans and cowpeas. Genotypic differences were found only in cowpeas. Carbon isotope discrimination was not affected by leafhopper damage but genotypic differences were observed in both beans and cowpeas. Leafhopper damage increased the amount of ¹⁵N in the plant structures indicating less N remobilization under leafhopper stress. Leafhopper damage decreased N concentration and dry weight in both beans and

cowpeas.

INTRODUCTION

The leafhopper (*Empoasca* spp) is one of the most important pest in beans and cowpeas. Damage is most severe during hot, dry climatic conditions and during flowering and pod setting growth periods (Kornegay and Temple, 1986). Symptoms of leafhopper damage in beans are yellowing and downward curling of the leaves, followed by necrosis at the leaf tip and margins. Plant growth is stunted and pod number and seed weight are reduced. Under severe infestation the plant may die. In cowpeas, losses of 60% or more in seed yield have been reported due to leafhopper damage (Jackai and Daoust, 1986).

The objective of this study was to evaluate the effect of leafhopper damage on yield and yield components, leaf water status, root growth, photosynthesis, stomatal conductance, transpiration ratio, carbon isotope discrimination, and nitrogen partitioning and remobilization.

MATERIALS AND METHODS

A field study was conducted at the Agronomy Research Farm at Michigan State University in East Lansing during the summer of 1991. The soil type was a fine loamy, mixed mesic aeris ochraqualfs with a slope of 0-3% (USDA Soil Conservation Service Classification). The rainfall and temperature data are presented in Fig 1 and Table 1 of Appendix A.

The experimental design was a modified split plot with and with four replications. The main plot was the leafhopper infestation and genotypes were the subplots. The leafhopper factor was confounded by site difference in that all stressed plots were grouped together and all non-stressed plots were grouped together. Each plot had four rows of 2 m length. The bean spacing was 50 x 10 cm and the cowpea spacing was 75 x 20 cm which resulted in a plant density of 20 plants per m² for beans and 10 plants per m² for cowpeas. Four bean genotypes (9-39-1, 8-42-M-2, N81017 and 8-25-2) and four cowpea genotypes (TVX 3236, Blackeye, ER₇, and IT83S-742-2) were used. The bean genotypes were chosen based upon their previous performance in the MSU bean breeding program and their subsequent designation as either drought resistant or susceptible. The cowpea genotypes were chosen based upon their performance from a preliminary growth chamber study conducted in 1989 and their performance in field studies at ITTA and in Botswana. Genotype description is presented in Table 2 of Appendix A.

Plots were hand planted using a hoe to open rows and 40 or 20 seeds were planted per row for beans and cowpeas respectively, along with abundant inoculant. The bean inoculum was Rhizobium phaseoli and the cowpea inoculum was Rhizobium Cowpea miscellany nitrogen EL.

Planting and Management Practices

The experiment was planted on June 15. Fertilizer was applied as water soluble Pro-sol (20-20-20) on July 27 and August 14 at the rate of 27 pounds per 450 gallons of water. All plots received a total of 116.4 mm of irrigation on June 21 and July 15 before stress was imposed. On August 27 the non-stressed plots received 42.7 mm of irrigation.

The total rainfall during the growing season (June 15-Oct 20) was 294.9 mm. Sevin was applied on June 23 and August 15 to alleviate a severe leafhopper problem.

Soil moisture was monitored regularly in all plots at three depths (0-30, 30-60, 60-90 cm) using a neutron probe. Undisturbed soil core samples were taken at the same depths to develop a soil moisture desorption curve which was used to convert the volumetric moisture content into water potential.

Leaf Water Status

Relative water content (RWC), leaf water content (LWC) and leaf water retention capacity (LWRC) were determined. Weather permitting, measurements were made every two weeks after stress was imposed. Three plants per plot at the same growth stage were tagged and marked A, B and C. The center leaflet of the youngest fully developed leaf was placed in a plastic bag marked A₂, B₂ or C₂ depending on whether it was from plant A, B or C respectively. With the leaf face-up, the leaflet on the right was labelled A₃, B₃ or C₃ and the leaflet on the left was labelled A₁, B₁ or C₁. RWC, LWC and LWRC measurements were made on samples marked number 1, 2 and 3 respectively. Immediately after leaf detachment, the samples were placed in ziplock bags and stored on ice in a cooler until their fresh weight was recorded.

RWC: Each sample was weighed and placed in a petri dish and covered with distilled water. After 4 hrs, turgid weight was recorded. The leaves were then oven dried at 70° C for 24 hrs to determine the dry weight. RWC was computed as: $(Fw - Dw) / (Tw - Dw) * 100$.

LWC: The fresh weight was recorded. Then, leaves were oven dried as described above.

LWC was computed as: $(Fw - Dw) / Dw * 100$.

LWRC: After the fresh weight was recorded, samples were left uncovered in a dark environment at room temperature for 48 hrs. After 48 hrs, air dry weight (Dw_1) was recorded, leaves were oven dried at 70° C for 72 hrs, and the dry weight (Dw_2) was recorded. LWRC was computed as: $(Fw - Dw_1) / (Fw - Dw_2) * 100$.

Leafhopper Damage

The stressed plots were located next to another bean field which was heavily infested with leafhopper. Severe leafhopper damage was done to the plots which were next to the infested field. As a result, the stressed plots were due to leafhopper damage. This was not initially planned as part of the experiment.

Root Growth

Root measurements were made by using a minirhizotron camera. Only live roots were counted. This provided information on root distribution along the soil profile. Root growth rate was calculated from root counts of two successive recording dates as follows: $(\text{root count on date 1} - \text{root count on date 2}) / \text{number of days between date 1 and date 2}$ which was reported as number of roots/cm²/day. Each plot had one 6 inch diameter tube inserted at a 45° angle into the center row to a depth of 3 feet and measurements were taken, weather permitting, every 30 days. Two readings were taken during the season.

At physiological maturity seed yield and yield components were recorded. All measured parameters were analysed by MSTAT microcomputer statistical package for agricultural sciences or by the SAS package.

Photosynthesis

Three plants per plot were tagged and measurements were taken from these plants on the uppermost fully expanded leaf. The ADC-LCA 2 photosynthesis system (The Analytical Development Co. Ltd., Hoddesdon. UK) was used under the following conditions (Flow rate= 400 ml m⁻¹, Leaf temperature= 30±2°C, Vapor pressure deficit= 3 KPa, ambient CO₂= 350±10 µl l⁻¹, and photosynthetically active radiation (PAR) ≥ 1000 µmol m⁻² s⁻¹). The leaf was enclosed in a leaf chamber and exposed to incoming solar radiation. Readings were recorded at approximately the same photosynthetically active radiation (PAR). Each reading took approximately 30 seconds before a stable value was recorded. Measurements were taken between 10 am and 2 pm EDT on a cloudless day. Photosynthesis, stomatal conductance and transpiration ratio were calculated from a program developed by Moon and Flore (1986), (Appendix B1).

Carbon Isotope Discrimination

Samples for carbon isotope discrimination were taken during the pod filling growth stage (R₅) on five plants per plot. Five leaves were sampled from each plant so 25 leaves were detached from each plot. The uppermost fully expanded leaves were sampled and samples were bulked for each plot. The samples were oven dried at 60°C for five days before grinding. The samples were sent to the laboratory of Dr James Ehleringer at the University of Utah, Salt Lake City, UT, USA for analysis via mass spectrometry.

^{15}N Measurement

Ten plants per plot from the border rows were labelled with ^{15}N on August 2. Five plants of approximately the same growth stage were tagged from each border row then marked 1 to 10 in alternating rows so that the odd numbered plants were in one row and the even numbered plants were in another row. Plants were labelled at the late vegetative stage (V_9).

Treating Plants with ^{15}N

^{15}N -urea was used to label the plants. Plants were labelled in the morning between 8 am and 12 noon. Upon labelling, each plant was covered with plastic so that the entire trifoliolate was separated from the rest of the plant. The trifoliolate was dipped into the solution of 0.35 % N and 0.001 % ortho L-77 surfactant for a few seconds then removed. The plastic around the plant prevented the solution from dripping onto the plant or the soil. Control plants were treated with surfactant only. As soon as the leaf was dry, the plastic was removed, rinsed with water, and dried in the sun. The petiole of the labelled leaf was tagged and a flag was placed in front of the plant for easy identification. After a minimum of two hours, the labelled plant was recovered with plastic as before and the leaf was dipped in water to remove all urea from the outside of the leaf.

Sampling Plants

A screw driver was used to loosen the soil around the labelled plant and the plant was pulled from the soil with as much root as possible. The plant was cut at the soil line to separate the roots. The labelled leaf and its petiole were separated from the rest of the plant, washed with water to remove all soil, and placed in a bag for drying. A separate

container was used to wash soil from the remainder of the plant. A tape measurer was used to determine the height of each plant and to determine the middle of the plant for separation into upper and lower leaves, upper and lower stems, and upper and lower reproductive parts (flowers and/or pods). Each plant part was bagged separately for drying.

Two labelled plants were sampled the day after treatment in order to determine how much ^{15}N -urea entered the plant. Two labelled plants were subsequently sampled at flowering and pod development (R_1/R_2), pod filling (R_3) and physiological maturity (R_7).

Sample Analysis

The samples were oven dried for 48 hrs at 72°C before grinding in a Udy mill grinder. The dry weight was also recorded. Extreme care was taken not to contaminate plant parts. Whirlpak bags were used to collect samples from the grinder. After each sample was ground, the entire grinder, working surface, and the instruments were carefully cleaned. Compressed air was used to clean the grinder.

Samples were analyzed for N and ^{15}N using a gas chromatography mass spectrometer (ANCA-MS, Europa Scientific, Crewe. U.K) after conversion of sample N to N_2 by Dumas combustion in a roboprep CN analyzer. Ammonium sulfate (0.3663 atom % ^{15}N) Whatman number 1 filter paper was used as a reference standard.

RESULTS AND DISCUSSION

I. YIELD AND YIELD COMPONENTS, LEAF WATER STATUS AND ROOT GROWTH

Soil Moisture

Soil moisture content decreased with increasing number of days after planting for both the stress and non-stress treatments at all depths (Fig 1). The leafhopper stress treatment had lower moisture content than the non-stress treatment at the 30 and 60 cm depth. There were no significant differences between the stress and non-stress treatment at the 90 cm depth.

BEANS

Yield data

There was a significant difference in yield between the leafhopper stress and non-stress treatment (Table 1). Leafhoppers damage bean plants by extracting plant juices, plugging vascular tissue and possibly injecting a toxin into the plant. Leaf margins turn yellow while leaves are crinkled and reduced in size. Heavy attacks may result in stunted growth (van Schoonhoven et al., 1978). All of these symptoms were noted in the leafhopper-stressed plots and none occurred in the control plots. Pods per plant were significantly reduced by leafhopper damage (Table 1). The genotypes 8-42-M-2 and N81017 were higher yielding than 9-39-1 and 8-25-2. Stress significantly reduced yield. These results agree with previous reports indicating that leafhopper affected yield by

FIG 1. % VOLUMETRIC SOIL MOISTURE CONTENT IN 1991

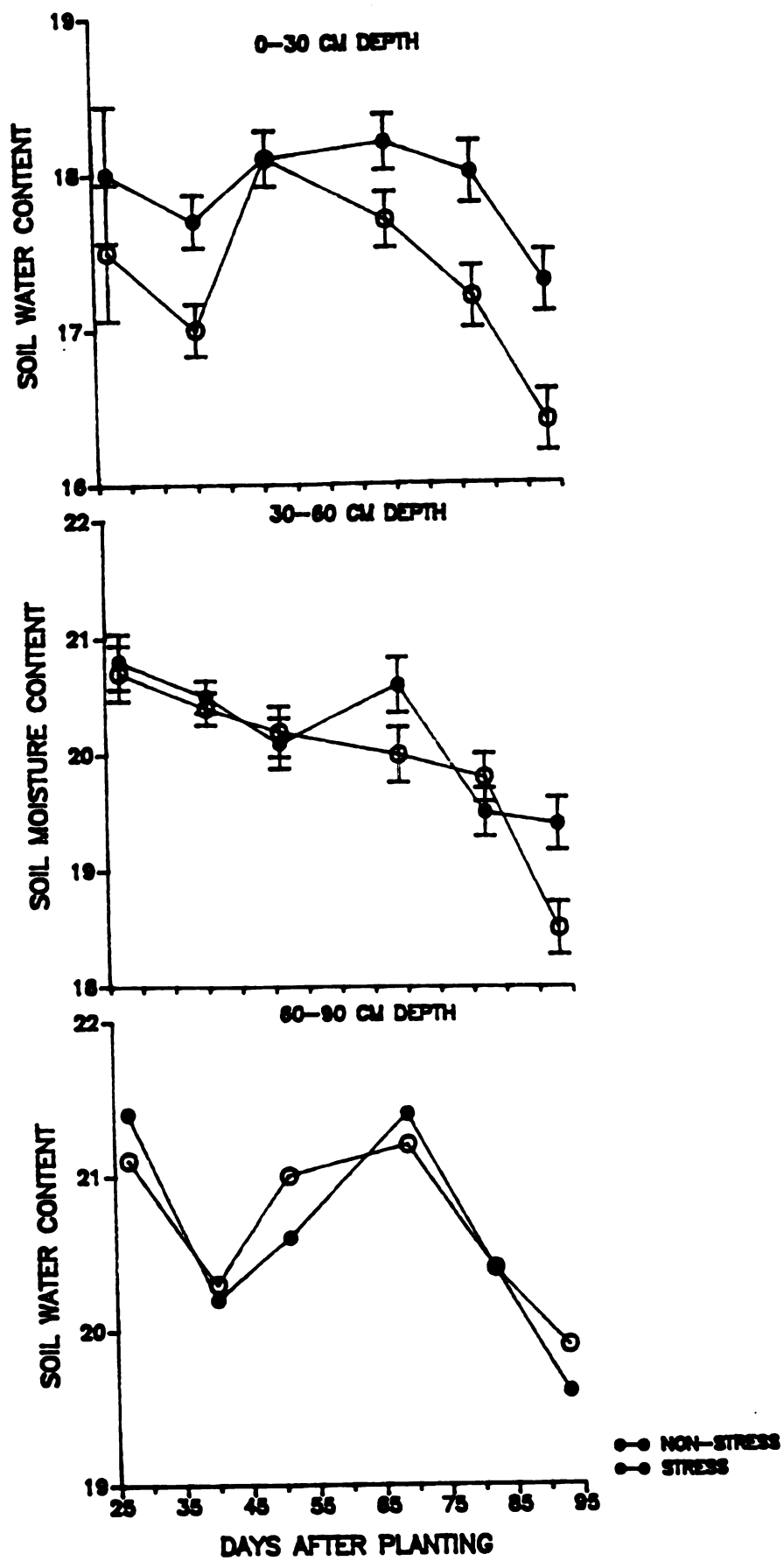


TABLE 1. Yield and Yield Components of Bean Genotypes Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	SEEDS PER POD	PODS PER PLANT	YIELD (Kg/Ha)	GEOMETRIC MEAN	% YIELD REDUCTION
8-42-M-2 (S) (NSD)	6	11	2189.8		
	6	12	3092.9	2602.4	29.2
9-39-1 (S) (NSD)	5	9	938.9		
	6	12	1533.3	1199.8	38.8
N81017 (S) (NSD)	5	11	2223.5		
	6	17	2644.8	2425.0	15.9
8-25-2 (S) (NSD)	5	10	988.4		
	5	12	1873.5	1360.8	47.2
GENOTYPE					
	ns	ns	ns		
8-42-M-2	6	12	2641.3 a		
9-39-1	5	10	1236.1 b		
N81017	6	14	2434.2 a		
8-25-2	5	11	1430.9 b		
LEAFHOPPER					
	ns	ns			
Stress	5	13 a	1585.1 a		
Non-stress	6	10 b	2286.1 b		
	ns	+	**		

S = Stress NSD = Non-stress ns = not significant
 **, + Different letters within a column indicate significant difference at p = 0.01 or 0.1 respectively according to DMRT.

reducing the number of pods per plant, seeds per pod, 100 seed weight and the number of empty pods per plant (van Schoohoven et al., 1978; Kornegay and Temple, 1986; Jackai and Daoust, 1986). The genotype 9-39-1 had a higher yield reduction (38.8%) than 8-42-M-2 (29.2%). This suggests that 9-39-1 may be more sensitive to leafhopper damage than is 8-42-M-2.

A significantly high correlation was observed between yield and pods per plant (Table 2).

Leaf Water Status

There were no differences between genotypes but leafhopper damage decreased RWC at 38, 52 and 80 days after planting (Table 3). Leafhopper damage also significantly decreased LWRC at 38, 52 and 66 DAP (Table 4). The two low yielding genotypes, 9-39-1 and 8-25-2 had a higher RWC than the high yielding, drought susceptible genotype (N81017) at 66 DAP. The drought susceptible and low yielding genotype, 8-25-2 had a higher LWRC than 9-39-1 at 80 DAP. LWC was significantly lower under leafhopper damage at 66 DAP (Table 5).

Root Growth

Leafhopper damage did not significantly reduce root growth rate (Table 6) but there was a tendency for root growth rate to be reduced under stress (52%). The resistant genotypes (9-39-1 and N81017) had a lower root growth rate than the susceptible genotypes (8-42-M-2 and 8-25-2).

Figures 1 and 2 show root distribution of four bean genotypes at 61 and 75 days after planting. There was a tendency for more root growth under the non-stress treatment

TABLE 2. Yield and Yield Component Correlations, 1991.

	Yield	PPP	SPP
Yield	---	0.65***	0.001
PPP		---	-0.16
SPP			---

PPP= Pods per plant

SPP= Seeds per pod

*** p= 0.001

TABLE 3. Relative Water Content in Beans Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING			
	38 ¹	52 ²	66 ³	80 ⁴
%				
N81017 (S)	81.5	85.1 bc	86.1	85.8
9-39-1 "	80.6	88.4 b	82.7	86.9
8-42-M-2 "	81.5	82.5 c	86.9	87.9
8-25-2 "	81.9	86.6 bc	85.8	85.5
N81017 (NSD)	89.1	94.4 a	90.8	91.4
9-39-1 "	90.6	88.1 b	89.2	90.6
8-42-M-2 "	91.7	94.5 a	90.4	89.5
8-25-2 "	96.0	94.8 a	82.1	91.5
	ns	+	ns	ns
GENOTYPE				
N81017	85.3	88.2	88.4	88.6
9-39-1	85.6	88.3	86.0	88.8
8-42-M-2	86.6	86.5	88.7	88.7
8-25-2	88.9	90.7	83.9	88.5
	ns	ns	ns	ns
LEAFHOPPER				
Stress	81.4	85.7	85.4	86.5
Non-stress	91.8	93.7	88.1	90.8
	***	***	ns	***

S = Stress NSD = Non-stress ns = not significant

***, + Different letters within a column indicate significant difference at $p = 0.001$ or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V_5)

² Late vegetative stage (V_8)

³ Flowering and pod development stage (R_1/R_2)

⁴ Pod filling stage (R_5/R_6)

TABLE 4. Leaf Water Retention Capacity in Beans Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING			
	38 ¹	52 ²	66 ³	80 ⁴
	%			
N81017 (S)	95.1	93.4	92.6 c	98.0
9-39-1 "	95.0	96.1	96.2 ab	93.8
8-42-M-2 "	92.4	93.3	94.6 b	95.5
8-25-2 "	91.2	95.0	96.2 ab	98.6
N81017 (NSD)	97.3	97.7	97.1 a	97.2
9-39-1 "	97.1	96.6	97.5 a	96.4
8-42-M-2 "	97.6	96.2	97.7 a	95.5
8-25-2 "	95.8	96.8	96.7 a	97.7
	ns	ns	+	ns
GENOTYPE				
N81017	96.2	95.6	94.8 b	97.6 ab
9-39-1	96.0	96.4	96.8 a	95.1 b
8-42-M-2	95.0	94.7	96.1 ab	95.5 ab
8-25-2	93.5	95.9	96.4 a	98.5 a
	ns	ns	+	*
LEAFHOPPER				
Stress	93.4	94.5	94.9	96.5
Non-stress	97.0	96.8	97.2	96.7
	**	**	***	ns

S = Stress NSD = Non-stress ns = not significant

***, **, *, + Different letters within a column indicate significant difference at p = 0.001, 0.01, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₈)

³ Flowering and pod development stage (R₁/R₂)

⁴ Pod filling stage (R₅/R₆)

TABLE 5. Leaf Water Content in Beans Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING			
		38 ¹	52 ²	66 ³	80 ⁴
		%			
N81017	(S)	76.3 ab	82.1	81.3	81.4 ab
9-39-1	"	75.3 ab	82.3	82.9	79.0 bc
8-42-M-2	"	75.2 ab	81.5	81.3	80.2 abc
8-25-2	"	78.4 a	81.8	80.7	79.9 abc
N81017	(NSD)	78.2 a	83.6	86.4	82.5 a
9-39-1	"	78.3 a	83.1	85.0	82.3 a
8-42-M-2	"	76.5 ab	83.7	85.2	78.4 c
8-25-2	"	72.7 b	81.3	84.5	81.3 ab
		*	ns	ns	+
GENOTYPE					
N81017		77.3	82.9	83.8	81.9 a
9-39-1		76.8	82.7	84.0	80.6 ab
8-42-M-2		75.9	82.6	83.2	79.3 b
8-25-2		75.6	81.6	82.6	80.6 ab
		ns	ns	ns	+
LEAFHOPPER					
Stress		76.3	81.9	81.5	80.1
Non-stress		76.4	82.9	85.5	81.1
		ns	ns	***	ns

S = Stress NSD = Non-stress ns = not significant

***, *, + Different letters within a column indicate significant difference at $p = 0.001$, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₈)

³ Flowering and pod development stage (R₁/R₂)

⁴ Pod filing stage (R₅/R₆)

TABLE 6. Root Growth Rate of Bean Genotypes Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT 8/15 - 8/29

roots/cm²/day

8-42-M-2	(S)	1.36
9-39-1	"	0.64
N81017	"	1.24
8-25-2	"	2.73

8-42-M-2	(NSD)	4.32
9-39-1	"	1.30
N81017	"	2.45
8-25-2	"	4.45
		ns

GENOTYPE

8-42-M-2	2.84
9-39-1	0.97
N81017	1.93
8-25-2	3.59
	ns

LEAFHOPPER

Stress	1.51
Non-stress	3.13
	ns

S= Stress NSD= Non-stress

ns= not significant

for all genotypes except 8-42-M-2 at 61 DAP at the 30 cm depth. At the 60 cm depth there were more roots under stress in 9-39-1 and N81017, both resistant genotypes. 8-25-2 had more roots under stress at the 90 cm depth (Fig 1). At 75 DAP, all genotypes had more root growth under the non-stress treatment at the 30 cm depth. At the 60 cm depth, root count was similar for both the stress and non-stress treatment except for N81017 which had more roots in the non-stress treatment. The high yielding and resistant genotype, N81017 had the same root count at the 80 cm depth under stress and non-stress treatments. 9-39-1 and 8-25-2 both low yielding had decreased roots under stress at the 80 cm depth and 8-42-M-2, high yielding and susceptible (Fig 2).

COWPEAS

Yield data

There were significant reductions in seeds per pod, pods per plant and yield due to leafhopper damage (Table 7). IT83S-742-2 had a high number of seeds per pod, pods per plant, and the highest yield. Blackeye had the lowest number of seeds per pod, pods per plant and the lowest yield. Nevertheless, IT83S-742-2 had a higher (72%) yield reduction than Blackeye (61%) which was due to a low number of pods per plant under stress with IT83S-742-2. Significant differences in the levels of leafhopper damage between cowpea cultivars have been reported (Parh, 1983). Jackai and Daoust (1986) showed yield losses up to 60% in cowpeas due to leafhopper damage. TVX 3236 and Blackeye are considered to be drought resistant lines and ER₇ and IT83S-742-2 to be drought susceptible lines.

FIGURE 2. BEAN ROOT DISTRIBUTION AT 61 DAP IN 1991

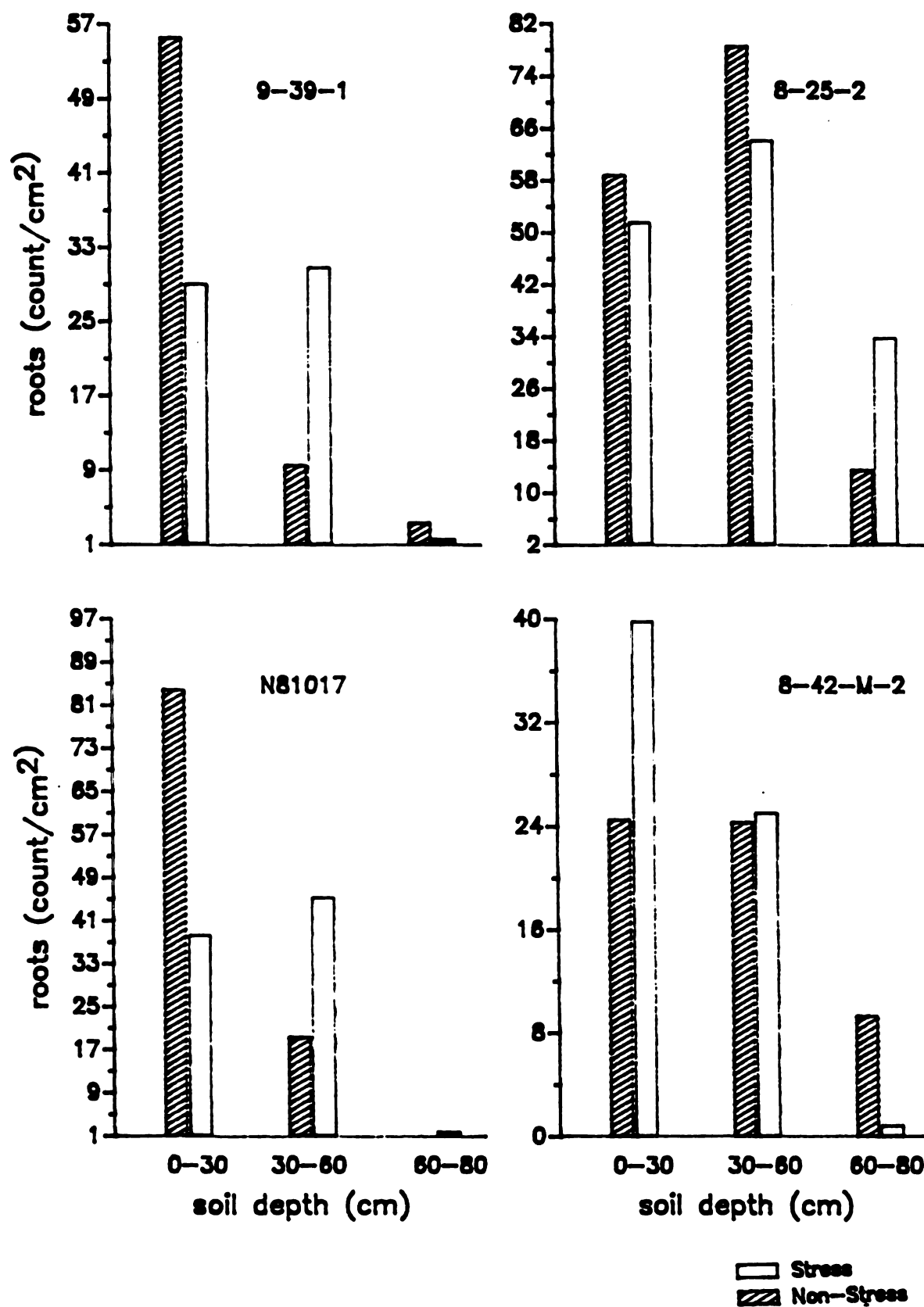


FIGURE 3. BEAN ROOT DISTRIBUTION AT 75 DAP IN 1991

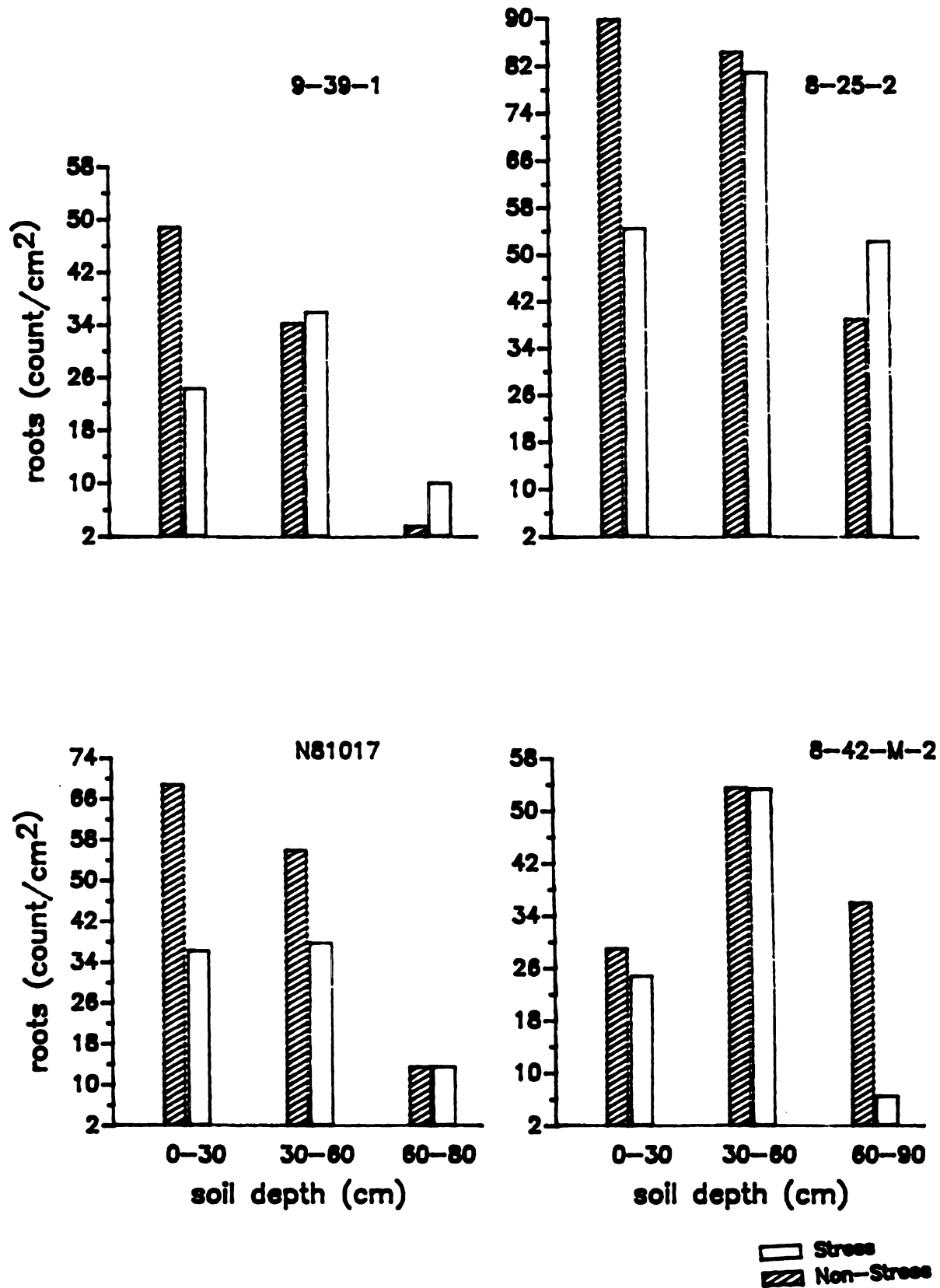


TABLE 7. Yield and Yield Components of Cowpea Genotypes Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing. MI. 1991.

TREATMENT	SEEDS PER POD	PODS PER PLANT	YIELD (Kg/Ha)	GEOMETRIC MEAN	% YIELD REDUCTION
TVX 3236 (S) (NSD)	7 b 11 a	2 15	71.1 cd 736.4 b	228.8	90.3
BLACKEYE (S) (NSD)	6 b 8 b	2 4	39.1 d 100.6 cd	62.7	61.1
ER ₇ (S) (NSD)	8 b 11 a	5 19	161.7 cd 823.5 b	364.9	80.4
IT83S-742-2 (S) (NSD)	12 a 11 a +	7 27 ns	367.6 c 1319.3 a +	696.4	72.1
GENOTYPE					
TVX 3236	9 ab	9 bc	403.8 b		
BLACKEYE	7 c	3 c	76.0 c		
ER ₇	9 ab	12 ab	492.6 b		
IT83S-742-2	11 a *	18 a **	911.5 a ***		
LEAFHOPPER					
Stress	8 b	4 b	162.5 b		
Non-Stress	10 a **	17 a ***	787.9 a ***		

S = Stress NSD = Non-stress ns = not significant ***, **, *, + Different letters within a column indicate significant difference at $p = 0.001, 0.01, 0.05$ or 0.1 respectively according to DMRT.

Leaf Water Status

Leafhopper damage significantly decreased RWC at 38 and 66 days after planting (Table 8). There were genotypic differences at all sampling dates except at 52 DAP. Blackeye consistently had a significantly lower RWC than all other genotypes. This may partly explain the low yield observed with Blackeye. Stressed plants had a significantly lower LWC at 66 and 80 DAP (Table 9). There were also genotypic differences at 52, 66 and 80 DAP. For LWRC, the difference with the stress treatment was significantly lower than the non-stress treatment at 52 and 66 DAP (Table 10). TVX 3236 had a significantly lower LWRC than other genotypes at 66 DAP and Blackeye had a lower LWRC at 80 DAP.

Root Growth

There were no differences between genotypes but there was a significantly higher root growth rate under the non-stress treatment (Table 11). Blackeye had more roots at the top 30 cm under stress at 61 DAP (Fig 3). Blackeye and TVX 3236 had more roots under stress at the 60 cm depth at 61 DAP. At 75 DAP only Blackeye had more roots under stress at the 30 cm depth (Fig 4). In general, root count decreased with increasing soil depth.

TABLE 8. Relative Water Content in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING			
	38 ¹	52 ²	66 ³	80 ⁴
	%			
TVX 3236 (S)	88.5	96.0 a	90.8	91.7
BLACKEYE "	74.9	82.0 a	80.3	89.3
ER ₇ "	85.8	87.8 a	89.2	91.8
IT83S-742-2 "	82.4	93.7 a	91.1	94.1
TVX 3236 (NSD)	95.5	91.4 a	94.4	94.3
BLACKEYE "	74.0	90.3 a	88.5	88.1
ER ₇ "	88.2	96.4 a	95.0	92.2
IT83S-742-2 "	92.0	65.0 b	93.2	94.6
	ns	*	ns	ns
GENOTYPE				
TVX 3236	91.5 a	94.2	92.6 a	93.1 a
BLACKEYE	74.4 b	84.8	84.4 b	88.7 b
ER ₇	87.0 a	90.7	92.1 a	92.0 ab
IT83S-742-2	86.6 a	84.1	92.2 a	94.4 a
	***	ns	**	**
LEAFHOPPER				
Stress	82.9	89.5	87.9	91.7
Non-stress	86.5	85.8	92.8	92.3
	+	ns	**	ns

S= Stress NSD= Non-stress ns= not significant

***, **, *, + Different letters within a column indicate significant difference at p= 0.001, 0.01, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₃)

² Late vegetative stage (V₈)

³ Flowering and pod development stage (R₁/R₂)

⁴ Pod filling stage (R₅/R₆)

TABLE 9. Leaf Water Content in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing. MI. 1991.

TREATMENT	DAYS AFTER PLANTING			
	38 ¹	52 ²	66 ³	80 ⁴
	%			
TVX 3236 (S)	73.4 b	84.9	83.9 b	80.9
BLACKEYE "	80.8 a	84.4	85.2 ab	82.4
ER ₇ "	79.2 a	81.3	84.9 b	80.2
IT83S-742-2 "	76.9 ab	82.2	81.2 c	81.5
TVX 3236 (NSD)	77.9 ab	85.4	87.4 a	82.6
BLACKEYE "	77.8 ab	83.9	84.7 b	84.5
ER ₇ "	73.2 b	82.9	85.8 ab	81.2
IT83S-742-2 "	76.6 ab	82.5	85.4 ab	80.8
	+	ns	+	ns
GENOTYPE				
TVX 3236	75.6	85.1 a	85.7 a	81.7 ab
BLACKEYE	79.3	84.1 ab	84.9 a	83.4 a
ER ₇	76.2	82.1 b	85.3 a	80.7 b
IT83S-742-2	76.7	82.3 b	83.3 b	81.1 ab
	ns	**	+	**
LEAFHOPPER				
Stress	77.6	83.2	83.8	81.2
Non-stress	76.4	83.7	85.8	82.3
	ns	ns	**	+

S = Stress NSD = Non-stress ns = not significant

******, *****, **+** Different letters within a column indicate significant difference at $p = 0.01$, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₃)

² Late vegetative stage (V₈)

³ Flowering and pod development stage (R₁/R₂)

⁴ Pod filling stage (R₃/R₆)

TABLE 10. Leaf Water Retention Capacity in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING			
	38 ¹	52 ²	66 ³	80 ⁴
	%			
TVX 3236 (S)	97.4	91.4	78.2 d	91.0
BLACKEYE "	96.5	92.3	88.9 c	82.6
ER ₇ "	97.4	94.0	90.6 bc	91.6
IT83S-742-2 "	97.3	95.5	92.6 abc	97.4
TVX 3236 (NSD)	97.1	96.1	90.2 bc	93.1
BLACKEYE "	97.7	97.1	93.2 abc	89.9
ER ₇ "	98.3	95.6	96.3 a	94.4
IT83S-742-2 "	95.3	94.0	94.4 ab	92.8
	ns	ns	+	ns
GENOTYPE				
TVX 3236	97.3	93.8	84.2 b	92.1 a
BLACKEYE	97.1	94.6	91.0 a	86.2 b
ER ₇	97.9	94.8	93.4 a	93.0 a
IT83S-742-2	96.3	93.3	93.5 a	95.1 a
	ns	ns	***	*
LEAFHOPPER				
Stress	97.1	92.5	87.6	93.5
Non-stress	97.1	95.7	93.5	92.5
	ns	***	***	ns

S= Stress NSD= Non-stress ns= not significant

***, *, + Different letters within a column indicate significant difference at p= 0.001, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₃)

² Late vegetative stage (V₈)

³ Flowering and pod development stage (R₁/R₂)

⁴ Pod filling stage (R₅/R₆)

TABLE 11. Root Growth Rate of Cowpea Genotypes Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT 8/15 - 8/29

roots/cm²/day

TVX 3236	(S)	0.64
BLACKEYE	"	1.59
ER ₇	"	2.05
IT83S-742-2	"	0.86

TVX 3236	(NSD)	3.25
BLACKEYE	"	2.50
ER ₇	"	3.70
IT83S-742-2	"	3.87
		ns

GENOTYPE

TVX 3236	2.13
BLACKEYE	2.05
ER ₇	2.88
IT83S-742-2	2.38
	ns

LEAFHOPPER

Stress	1.33
Non-stress	3.34
	*

S= Stress NSD= Non-stress

ns= not significant

*** p= 0.05**

FIG 4. COWPEA ROOT DISTRIBUTION AT 61 DAP IN 1991

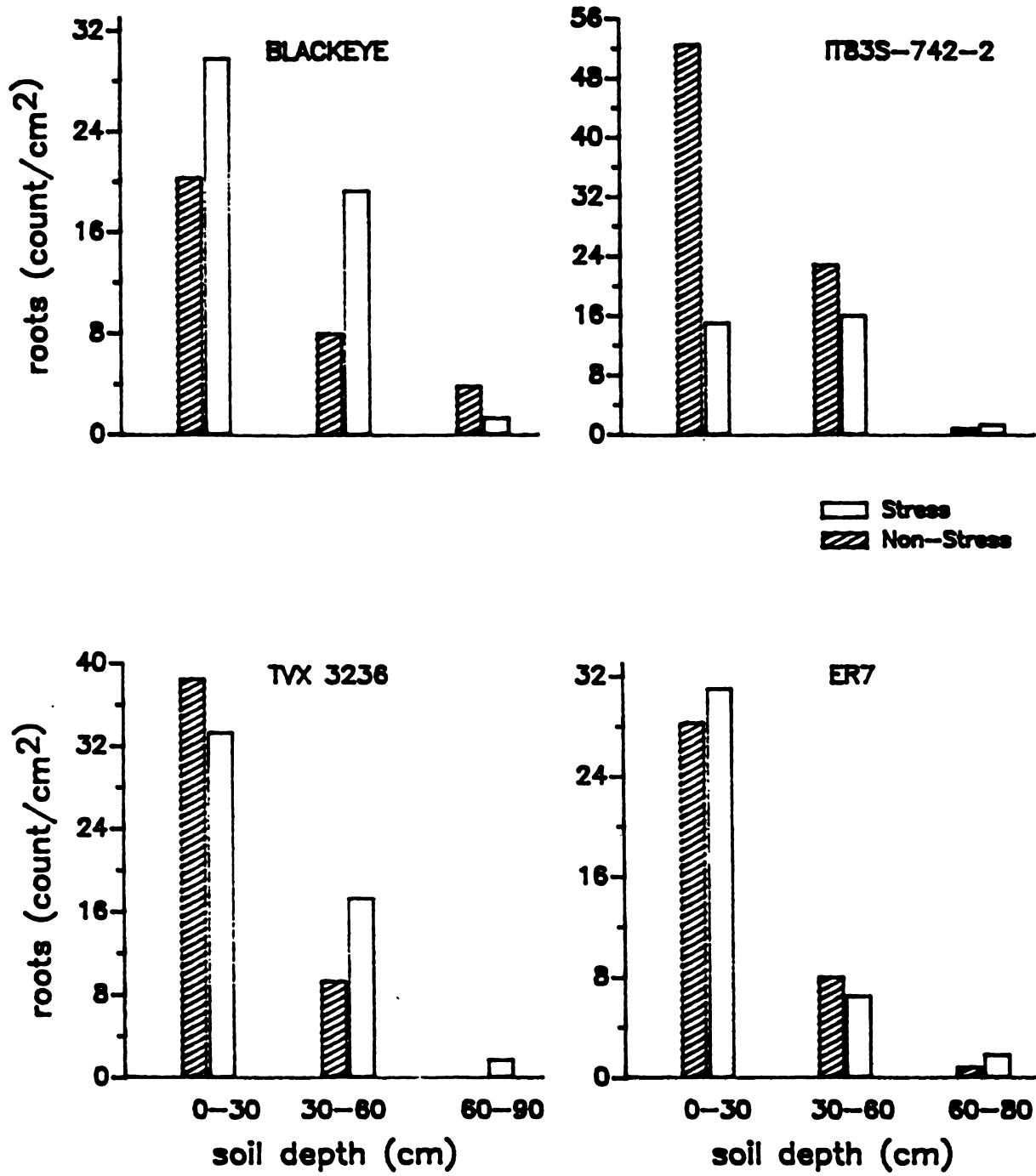
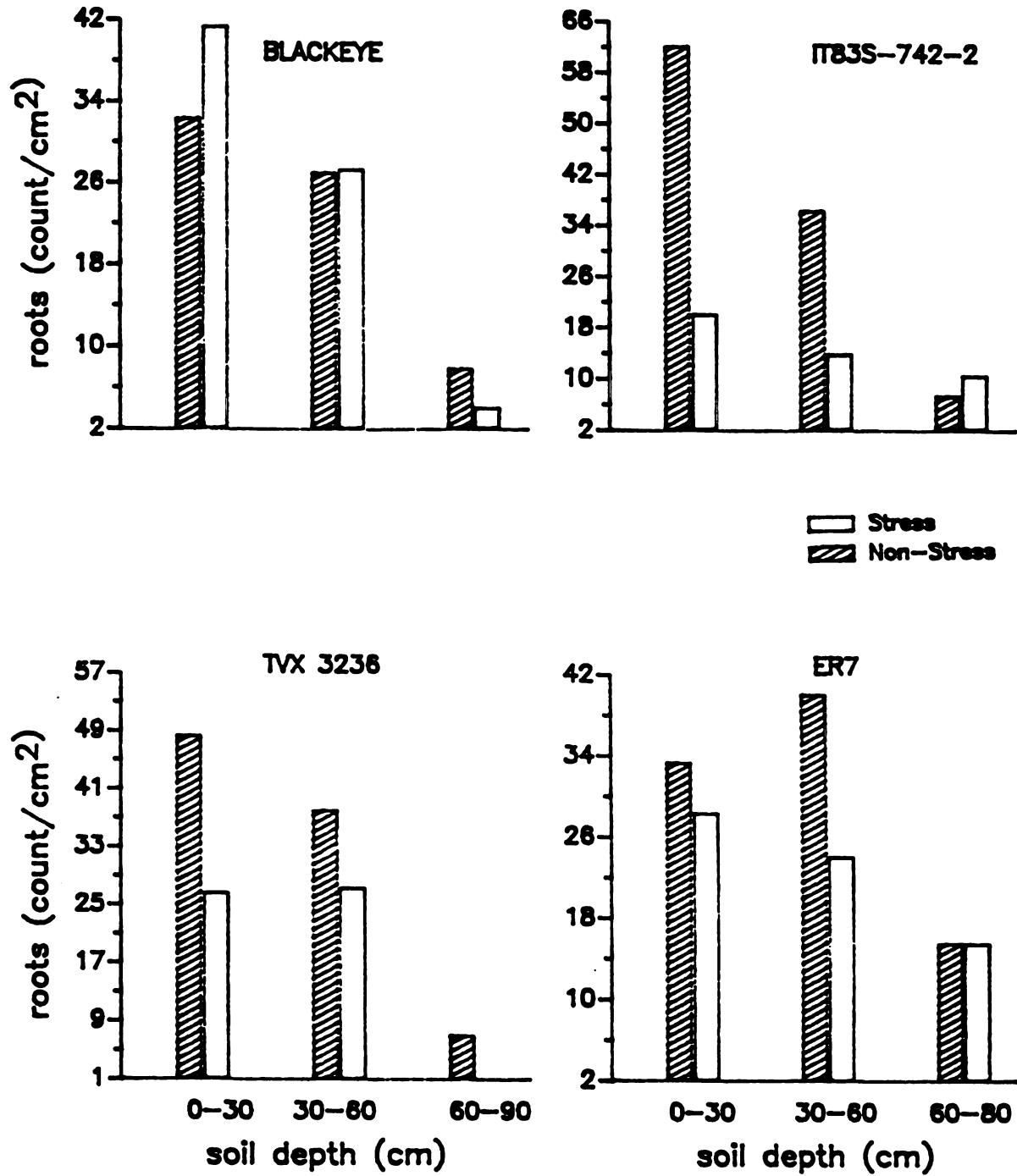


FIG 5. COWPEA ROOT DISTRIBUTION AT 75 DAP IN 1991



II. PHOTOSYNTHESIS, STOMATAL CONDUCTANCE, TRANSPIRATION RATIO AND CARBON ISOTOPE DISCRIMINATION.

BEANS

Photosynthesis

Leafhopper damage decreased the rate of photosynthesis at 40 and at 70 days after planting (Table 12). At 57 DAP, the genotype 8-25-2, susceptible and low yielding, had the highest photosynthetic rate (Table 12) although it was not significantly different from that of N81017 (resistant and high yielding). Both 8-42-M-2, drought susceptible and high yielding, and 9-39-1, resistant and low yielding had a lower photosynthetic rate than 8-25-2.

Transpiration Ratio

There were no significant differences between stress and non-stress treatments in the transpiration ratio. Genotypic differences were found only at 57 days after planting. The susceptible and low yielding genotype, 8-25-2 had a lower transpiration ratio than the other genotypes (Table 13).

Stomatal Closure

There were no differences between stress and non-stress treatments except at 40 days after planting (Table 14) where the stress treatment had a lower stomatal conductance than the non-stress treatment. There were no genotypic differences.

TABLE 12. CO₂ Assimilation Rate in Beans Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	40 ¹	57 ²	70 ³
	$\mu\text{mols m}^{-2} \text{ s}^{-1}$		
8-42-M-2 (S)	9.8	17.4 d	12.2
9-39-1 "	5.5	20.8 acbd	12.7
N81017 "	6.6	17.8 cd	15.5
8-25-2 "	7.6	21.1 abc	15.6
8-42-M-2 (NSD)	8.8	18.1 bcd	16.9
9-39-1 "	8.5	16.6 d	16.0
N81017 "	13.3	22.3 ab	17.2
8-25-2 "	10.0	22.5 a	15.7
	ns	*	ns
GENOTYPE			
8-42-M-2	9.3	17.7 b	16.2
9-39-1	6.9	18.7 b	14.4
N81017	9.9	20.0 ab	14.7
8-25-2	8.8	21.8 a	15.7
	ns	*	ns
LEAFHOPPER			
Stress	7.4	19.2	14.0
Non-stress	10.2	19.9	16.5
	*	ns	*

S = Stress NSD = Non-stress ns = not significant

* Different letters within a column indicate significant difference at $p = 0.05$ according to Duncan Multiple Range Test

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₉)

³ Flowering and pod development stage (R₁/R₂)

TABLE 13. Transpiration Ratio in Beans Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	40 ¹	57 ²	70 ³
	mmols H ₂ O/mmols CO ₂		
8-42-M-2 (S)	449.0	334.7 abcd	456.4
9-39-1 "	777.9	304.5 bcd	532.8
N81017 "	600.3	384.8 a	455.6
8-25-2 "	3240.1	276.3 d	396.6
8-42-M-2 (NSD)	421.8	356.3 abc	417.5
9-39-1 "	456.0	380.0 ab	425.8
N81017 "	391.8	316.0 abcd	408.2
8-25-2 "	491.1	280.9 cd	473.5
	ns	*	ns
GENOTYPE			
8-42-M-2	435.4	345.5 a	436.9
9-39-1	616.9	342.2 a	497.3
N81017	496.1	350.4 a	431.9
8-25-2	1865.6	278.6 b	435.1
	ns	*	ns
LEAFHOPPER			
Stress	1266.8	325.1	460.3
Non-stress	440.2	333.3	431.3
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

*, + Different letters within a column indicate significant difference at p = 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₉)

³ Flowering and pod development stage (R₁/R₂)

TABLE 14. Stomatal Conductance in Beans Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	40 ¹	57 ²	70 ³
	mmols m ⁻² s ⁻¹		
8-42-M-2 (S)	82.7	157.5	265.2
9-39-1 "	82.8	176.2	235.6
N81017 "	77.7	192.9	187.7
8-25-2 "	95.2	161.9	218.8
8-42-M-2 (NSD)	137.7	160.3	244.8
9-39-1 "	147.0	153.7	234.8
N81017 "	180.4	191.0	233.8
8-25-2 "	150.0	164.6	270.7
	ns	ns	ns
GENOTYPE			
8-42-M-2	110.2	159.9	225.0
9-39-1	114.9	164.9	235.2
N81017	129.0	191.9	210.7
8-25-2	122.6	163.2	244.7
	ns	ns	ns
LEAFHOPPER			
Stress	84.6	172.6	226.8
Non-stress	153.8	167.4	246.0
	*	ns	ns

S= Stress NSD= Non-stress ns= not significant

* p=0.05

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₉)

³ Flowering and pod development stage (R₁/R₂)

Carbon Isotope Discrimination

Carbon isotope discrimination was not reduced by leafhopper damage but genotypic differences were observed (Table 15). Genotypic variability in CID has been reported in soybeans (*Glycine max* L.) (Ashley, 1991) and peanuts (*Arachis hypogaea* L.) (Brown and Bryd, 1991). 9-39-1 (resistant and low yielding) had a lower CID value than N81017 (resistant and high yielding) and 8-42-M-2 (susceptible and low yielding).

COWPEAS

Photosynthesis

At 57 days after planting, there was a difference between the stress and non-stress treatment (Table 16). Leafhopper damage reduced photosynthesis by 24 %. Genotypic differences were observed at 57 and 70 DAP. Blackeye had the lowest photosynthetic rate. This may explain the low genotypic yield reported for Blackeye (76 Kg/ha).

Transpiration Ratio

There was no difference between the stress and non-stress treatments except at 40 days after planting where the transpiration ratio was higher due to leafhopper damage (Table 17). Blackeye had the highest transpiration ratio at 57 DAP.

Stomatal Conductance

Leafhopper damage decreased stomatal conductance by 40% at 40 days after planting, by 20% at 57 DAP and by 15% at 70 DAP (Table 18). At 57 DAP Blackeye had the lower stomatal conductance than TVX 3236. This corresponds with a low photosynthetic rate at 57 DAP (Table 16).

**TABLE 15. Carbon Isotope Discrimination in Beans
Subjected to Leafhopper Infestation at the MSU
Agronomy Farm in East Lansing, MI. 1991.**

<u>TREATMENT</u>		<u>DELTA</u>
N81017	(S)	20.4
9-39-1	"	19.6
8-42-M-2	"	20.6
8-25-2	"	20.0
N81017	(NSD)	20.4
9-39-1	"	19.9
8-42-M-2	"	20.4
8-25-2	"	20.3
		ns
GENOTYPE		
N81017		20.4 a
9-39-1		19.7 b
8-42-M-2		20.5 a
8-25-2		20.2 ab
		*
LEAFHOPPER		
Stress		20.2
Non-stress		20.3
		ns

S= Stress NSD= Non-stress ns= not significant

* Different letters within a column indicate significant difference at $p = 0.05$ according to Duncan Multiple Range Test.

TABLE 16. CO₂ Assimilation Rate in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		40 ¹	57 ²	70 ³
$\mu\text{mols m}^{-2} \text{ s}^{-1}$				
TVX 3236	(S)	2.8 b	29.7	17.1 ab
BLACKEYE	"	4.4 ab	9.7	15.1 bc
ER ₇	"	11.0 a	15.4	16.1 bc
IT83S-742-2	"	6.1 ab	17.7	13.4 bc
TVX 3236	(NSD)	9.9 ab	26.6	19.0 ab
BLACKEYE	"	6.1 ab	11.8	10.6 c
ER ₇	"	5.3 ab	19.6	17.4 ab
IT83S-742-2	"	6.5 ab	25.4	22.8 a
		*	ns	*
GENOTYPE				
TVX 3236		6.3	23.7 a	18.1 a
BLACKEYE		5.3	10.8 c	12.9 b
ER ₇		8.1	17.5 b	16.7 a
IT83S-742-2		6.3	21.5 ab	18.1 a
		ns	**	*
LEAFHOPPER				
Stress		6.9	18.1	15.4
Non-stress		6.1	20.9	17.5
		ns	***	ns

S= Stress NSD= Non-stress ns= not significant

***, **, * Different letters within a column indicate significant difference at $p = 0.001$, 0.01 or 0.05 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₉)

³ Flowering and pod development (R₁/R₂)

TABLE 17. Transpiration Ratio in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		40 ¹	57 ²	70 ³
mol H ₂ O/ mol CO ₂				
TVX 3236	(S)	3297.9 a	292.1	370.3
BLACKEYE	"	781.8 b	478.8	408.2
ER ₇	"	407.7 b	330.3	384.2
IT83S-742-2	"	853.3 b	286.2	440.7
TVX 3236	(NSD)	421.1 b	240.0	411.3
BLACKEYE	"	649.8 b	589.4	886.6
ER ₇	"	717.1 b	350.5	424.1
IT83S-742-2	"	763.7 b	266.9	342.5
		*	ns	ns
GENOTYPE				
TVX 3236		1859.5	266.0 b	390.9
BLACKEYE		715.8	534.1 a	647.1
ER ₇		562.4	340.4 b	391.6
IT83S-742-2		808.5	276.6 b	391.6
		ns	*	ns
LEAFHOPPER				
Stress		1335.2	346.8	400.9
Non-stress		637.9	361.7	516.0
		*	ns	ns

S= Stress NSD= Non-stress ns= not significant

***, *, + Different letters within a column indicate significant difference at p= 0.001, 0.05 or 0.1 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₉)

³ Flowering and pod development stage (R₁/R₂)

TABLE 18. Stomatal Conductance in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	40 ¹	57 ²	70 ³
	mmols m ⁻² s ⁻¹		
TVX 3236 (S)	66.0	156.4	230.0 bc
BLACKEYE "	67.3	110.9	218.3 bc
ER ₇ "	51.4	128.4	222.7 bc
IT83S-742-2 "	78.0	127.4	193.9 c
TVX 3236 (NSD)	132.6	167.6	270.8 ab
BLACKEYE "	117.3	139.0	200.5 c
ER ₇ "	92.2	159.0	250.1 abc
IT83S-742-2 "	93.8	164.5	295.9 a
	ns	ns	*
GENOTYPE			
TVX 3236	99.3	162.0 a	250.4
BLACKEYE	92.3	125.0 b	209.4
ER ₇	71.8	143.7 ab	236.4
IT83S-742-2	85.9	145.9 ab	244.9
	ns	*	ns
LEAFHOPPER			
Stress	65.7	130.8	216.2
Non-stress	108.9	157.5	254.3
	**	**	*

S = Stress NSD = Non-stress ns = not significant

***, **, * Different letters within a column indicates significant difference at p = 0.001, 0.01 or 0.05 respectively according to Duncan Multiple Range Test.

¹ Early vegetative stage (V₅)

² Late vegetative stage (V₉)

³ Flowering and pod development stage (R₁/R₂)

Carbon Isotope Discrimination

Carbon isotope discrimination was not reduced by leafhopper damage but genotypic differences were observed (Table 17). Blackeye and IT83S-742-2 had a significantly lower CID value than ER₇. CID values have been proposed for predicting drought resistance and not resistance to leafhopper damage but it is interesting to note that CID did not separate the highest (IT83S-742-2) and the lowest (Blackeye) yielding genotypes.

III. NITROGEN PARTITIONING AND REMOBILIZATION

BEANS

¹⁵N Content

Even though four genotypes were planted, only two were analysed for ¹⁵N because of lack of funds to analyze all four genotypes. N81017 and 8-25-2 were chosen for analysis because they had not previously been used in ¹⁵N studies, because N81017 was resistant and high yielding and 8-25-2 was susceptible and low yielding, and because two years of ¹⁵N data had already been collected for 9-39-1 and 8-42-M-2.

¹⁵N content in the roots was not significantly affected by stress or genotype (Table 20). Leafhopper stress significantly increased ¹⁵N content in the lower stems during pod development and pod filling (69 and 86 DAP) by 48% and 53% respectively (Table 21). At physiological maturity (93 DAP) although not significant, ¹⁵N content was increased by 32% under stress. Leafhopper stress significantly increased ¹⁵N content in the upper

TABLE 19. Carbon Isotope Discrimination in Cowpeas Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

<u>TREATMENT</u>		<u>DELTA</u>
TVX 3236	(S)	19.5
BLACKEYE	"	19.6
ER ₇	"	20.1
IT83S-742-2	"	19.0
TVX 3236	(NSD)	19.6
BLACKEYE	"	19.1
ER ₇	"	19.7
IT83S-742-2	"	19.2
		ns
GENOTYPE		
TVX 3236		19.5 ab
BLACKEYE		19.4 b
ER ₇		19.9 a
IT83S-742-2		19.1 b
		**
LEAFHOPPER		
Stress		19.5
Non-stress		19.4
		ns

S= Stress NSD= Non-stress ns= not significant

** Different letters within a column indicate significant difference at $p = 0.01$ according to Duncan Multiple Range Test

TABLE 20. ^{15}N Content in Bean Roots Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		69¹	86²	93³
		%		
N81017	(S)	2.29	1.05	0.95
8-25-2	"	1.95	0.57	0.96
N81017	(NSD)	1.14	0.76	0.65
8-25-2	"	1.13	1.36	0.71
		ns	ns	ns
GENOTYPE				
N81017		1.71	0.91	0.80
8-25-2		1.54	0.97	0.83
		ns	ns	ns
LEAFHOPPER				
Stress		2.12	0.81	0.95
Non-stress		1.14	1.06	0.68
		ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

¹ = R₂/R₃ Flowering and early pod development

² = R₅ Pod filling

³ = R₇ Maturity

TABLE 21. ^{15}N Content in Bean Stems Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		69 ¹	86 ²	96 ³
<u>Lower stem</u>		%		
N81017	(S)	29.90	25.34	12.15
8-25-2	"	27.90	22.91	15.67
N81017	(NSD)	12.49	10.57	10.62
8-25-2	"	17.47	11.65	8.16
		ns	ns	ns
GENOTYPE				
N81017		21.20	17.95	11.38
8-25-2		22.68	17.28	11.91
		ns	ns	ns
LEAFHOPPER				
Stress		28.90	24.13	13.91
Non-stress		14.98	11.11	9.39
		**	*	ns
<u>Upper stem</u>				
N81017	(S)	13.75	6.41	1.90
8-25-2	"	8.16	3.59	2.18
N81017	(NSD)	3.96	7.32	0.97
8-25-2	"	5.49	8.20	0.60
		ns	ns	ns
GENOTYPE				
N81017		8.86	6.87	1.43
8-25-2		6.82	5.89	1.39
		ns	ns	ns
LEAFHOPPER				
Stress		10.96	5.00	2.04
Non-stress		4.73	7.76	0.79
		ns	+	*

S = Stress NSD = Non-stress ns = not significant

+ p(0.1) * p(0.05) ** p(0.01)

¹ = R₂/R₃ ² = R₅ ³ = R₇

stem at 69 and 93 DAP. This suggests that more N was being remobilized to the stem from the labelled leaf under stress. There were no genotypic differences in ^{15}N content in the lower or upper stems. There was a significant increase of 61% and 62% in ^{15}N content in the lower leaves under stress at 86 and 93 DAP (Table 22). Stress significantly increased ^{15}N content in the upper leaves at 69 and 93 DAP. The genotype N81017 contained a significantly higher level of ^{15}N than did 8-25-2 in the upper leaves under stress conditions at 93 DAP indicating less N remobilization to seeds. There were no differences between stress and non-stress in the lower or upper reproductive structures, or between genotypes (Table 23). However, the leafhopper x genotype interaction was significant in the upper reproductive structures at 86 DAP. Stress increased ^{15}N content by 560% in 8-25-2 indicating greater N remobilization under stress.

Leafhopper damage increased ^{15}N content in the stem and leaves. ^{15}N content for most plant parts was not statistically different even though numerical differences existed. This is due to the very high coefficient of variation which ranged from 60 to 200%. Harris (1993) also reported very high coefficient of variation ranging from 107 to 171% in ^{15}N recovery in red clover.

Nitrogen Concentration

There was no significant difference in N concentration between the leafhopper stress and non-stress treatment in the roots but N81017 tended to have a lower root N concentration than 8-25-2 (Table 24). The stress treatment significantly increased N concentration at 86 and 93 DAP in the lower stem (Table 25). The drought susceptible genotype, 8-25-2 had a significantly higher N concentration than the drought resistant

TABLE 22. ^{15}N Content in Bean Leaves Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
<u>Lower leaves</u>		%	
N81017 (S)	41.01	32.92	16.04
8-25-2 "	47.02	32.26	11.38
N81017 (NSD)	32.70	19.56	4.79
8-25-2 "	23.60	5.71	5.50
	ns	ns	ns
GENOTYPE			
N81017	36.86	26.23	10.41
8-25-2	35.29	18.99	8.44
	ns	ns	ns
LEAFHOPPER			
Stress	44.02	32.59	13.71
Non-stress	28.43	12.63	5.14
	ns	+	+
<u>Upper leaves</u>			
N81017 (S)	20.20	8.49	4.21 a
8-25-2 "	17.50	4.96	1.65 b
N81017 (NSD)	5.50	7.99	1.28 b
8-25-2 "	9.19	5.28	1.53 b
	ns	ns	*
GENOTYPE			
N81017	12.85	8.24	2.54
8-25-2	13.35	5.12	1.60
	ns	ns	+
LEAFHOPPER			
Stress	18.85	6.73	2.75
Non-stress	7.34	6.64	1.39
	**	ns	*

S = Stress NSD = Non-stress ns = not significant

**, *, + Different letters within a column indicate significant difference at $p = 0.01$, 0.05 or 0.1 respectively according to DMRT

¹ = R_2/R_3 ² = R_5 ³ = R_7

TABLE 23. ^{15}N Content in Bean Reproductive Parts Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
<u>Lower reproductive</u>		%	
N81017 (S)	12.84	28.46	41.83
8-25-2 "	11.18	18.02	46.91
N81017 (NSD)	17.34	29.64	36.91
8-25-2 "	23.04	33.57	33.93
	ns	ns	ns
GENOTYPE			
N81017	15.09	29.05	39.37
8-25-2	17.11	25.79	40.03
	ns	ns	ns
LEAFHOPPER			
Stress	12.01	23.24	43.99
Non-stress	20.19	31.60	35.42
	ns	ns	ns
<u>Upper reproductive</u>			
N81017 (S)	3.29	1.66 ab	7.05
8-25-2 "	1.39	4.87 a	5.91
N81017 (NSD)	2.24	4.01 ab	6.87
8-25-2 "	3.00	0.87 b	6.61
	ns	*	ns
GENOTYPE			
N81017	2.77	3.00	6.96
8-25-2	2.20	2.58	6.26
	ns	ns	ns
LEAFHOPPER			
Stress	2.34	2.44	6.48
Non-stress	2.62	3.27	6.74
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

* Different letters within a column indicate significant difference at $p = 0.05$ according to Duncan Multiple Range Test.

¹ = R_2/R_3 ² = R_5 ³ = R_7

TABLE 24. N Concentration in Bean Roots Subjected to Leafhopper Infestation at the Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
	%		
N81017 (S)	1.33	1.43	1.01
8-25-2 "	1.88	1.36	1.17
N81017 (NSD)	1.37	1.13	0.91
8-25-2 "	1.75	1.36	1.17
	ns	ns	ns
GENOTYPE			
N81017	1.35	1.28	0.96
8-25-2	1.82	1.32	1.10
	**	ns	ns
LEAFHOPPER			
Stress	1.61	1.40	0.96
Non-stress	1.56	1.21	1.09
	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

** p = 0.01

¹ = R₂/R₃ ² = R₅ ³ = R₇

TABLE 25. N Concentration in Bean Stems Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
Lower Stem			
	%		
N81017 (S)	2.49	2.50	1.57
8-25-2 "	3.15	3.00	2.32
N81017 (NSD)	1.81	1.23	1.27
8-25-2 "	2.82	2.36	1.79
	ns	ns	ns
GENOTYPE			
N81017	2.15	1.87	1.42
8-25-2	2.99	2.68	2.06
	*	*	*
LEAFHOPPER			
Stress	2.82	2.75	1.95
Non-stress	2.32	1.80	1.53
	ns	**	+
Upper Stem			
N81017 (S)	3.31	2.73	1.85
8-25-2 "	4.58	3.05	3.06
N81017 (NSD)	3.20	3.12	1.64
8-25-2 "	3.98	3.42	1.95
	ns	ns	ns
GENOTYPE			
N81017	3.25	2.93	1.74
8-25-2	4.28	3.23	2.50
	ns	ns	*
LEAFHOPPER			
Stress	3.94	2.89	2.46
Non-stress	3.59	3.67	1.79
	ns	ns	+

S = Stress NSD = Non-stress ns = not significant

**, *, + p = 0.01, 0.05 or 0.1 respectively

¹ = R₂/R₃ ² = R₅ ³ = R₇

genotype, N81017 at all sampling dates suggesting that 8-25-2 was probably not utilizing N as efficiently as N81017. Leafhopper stress significantly increased N concentration in the upper stem at physiological maturity. The resistant and high yielding genotype, N81017 had lower N concentration than the susceptible and low yielding genotype 8-25-2 at 93 DAP in the upper stem (Table 25). Stress significantly increased N concentration in the lower leaves at 69 and 86 DAP and in the upper leaves at 86 DAP (Table 26). 8-25-2 had a significantly higher N concentration in the lower leaves at 69 and 93 DAP. There was a significant increase in N concentration in the lower and upper reproductive structures at 69 DAP under stress (Tables 27). 8-25-2 had a significantly higher N concentration than N81017 at 69 and 93 DAP in the lower reproductive structures (Table 27).

Leafhopper damage increased N concentration in the roots, stem, leaves and reproductive structures. This suggests that the utilization of N was less efficient due to leafhopper damage. The resistant genotype, N81017 had a lower N concentration in the seeds than the susceptible genotype, 8-25-2. This suggestion of greater N use efficiency may explain its greater yield performance.

Biomass Accumulation

Total plant dry weight increased with plant growth but was reduced under stress. Leafhopper damage decreased the dry weight of both N81017 and 8-25-2 (Fig 6). The harvest index of N81017 was 0.61 and that of 8-25-2 was 0.64. The actual numbers for dry matter accumulation of the different plant parts are shown in Appendix C (Tables 1-7).

TABLE 26. N Concentration in Bean Leaves Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing. MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
Lower Leaves			
	%		
N81017 (S)	4.54	3.97	2.73
8-25-2 "	4.82	4.53	3.26
N81017 (NSD)	3.79	3.43	2.62
8-25-2 "	4.26	3.45	3.13
	ns	ns	ns
GENOTYPE			
N81017	4.16	3.70	2.68
8-25-2	4.54	3.99	3.19
	+	ns	**
LEAFHOPPER			
Stress	4.68	4.25	2.99
Non-stress	4.03	3.44	2.88
	*	+	ns
Upper Leaves			
N81017 (S)	5.14	4.84	2.23
8-25-2 "	6.48	4.92	1.10
N81017 (NSD)	4.77	3.56	1.28
8-25-2 "	5.91	3.55	2.30
	ns	ns	ns
GENOTYPE			
N81017	4.96	4.20	1.76
8-25-2	6.19	4.23	1.61
	ns	ns	ns
LEAFHOPPER			
Stress	5.81	4.88	1.67
Non-stress	5.34	3.55	1.72
	ns	***	ns

S= Stress NSD= Non-stress ns= not significant

**, *, + p= 0.01, 0.05 or 0.1 respectively

¹= R₂/R₃ ²= R₅ ³= R₇

TABLE 27. N Concentration in Bean Reproductive Parts Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

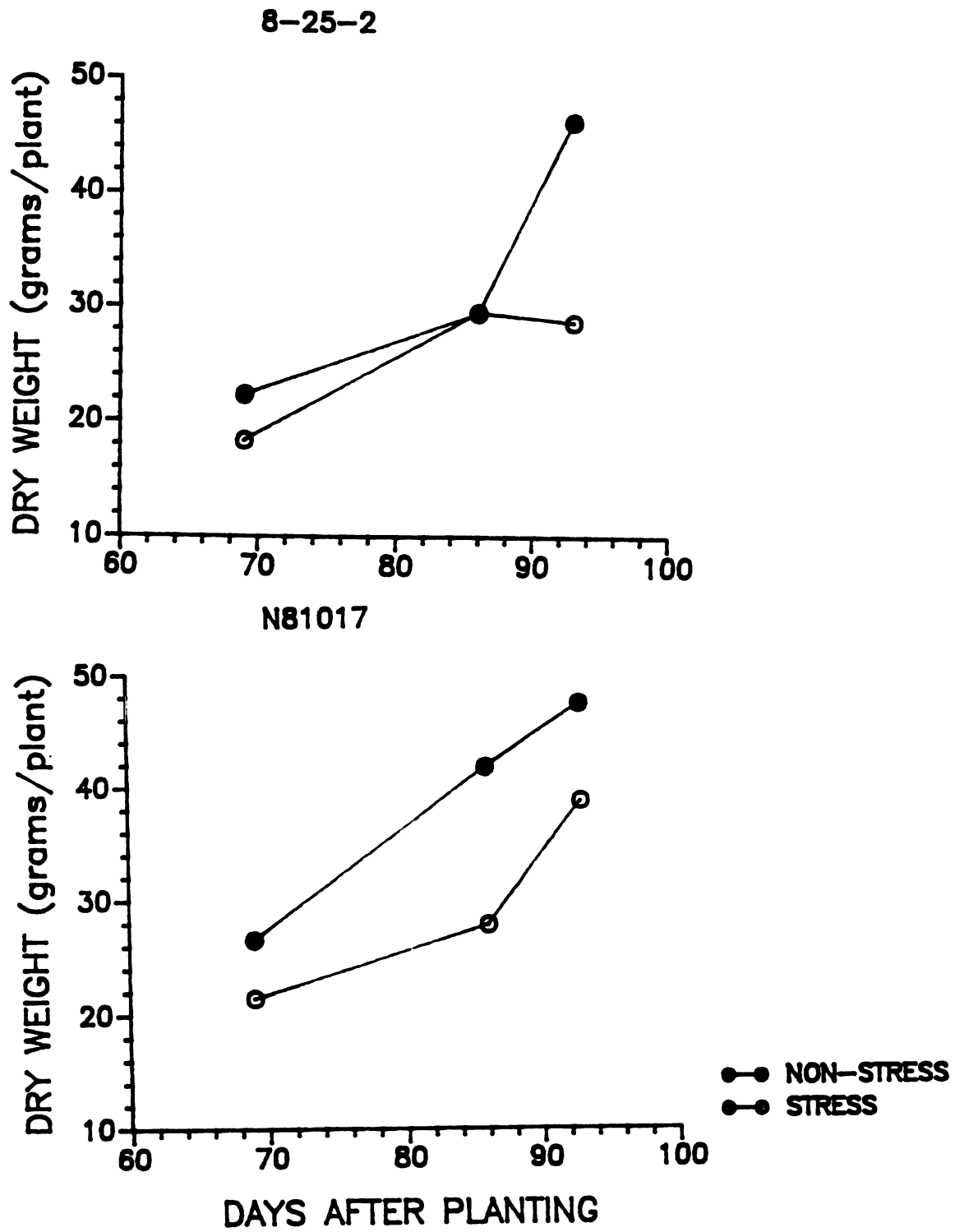
TREATMENT		DAYS AFTER PLANTING		
		69 ¹	86 ²	93 ³
<u>Lower Reproductive</u>			%	
N81017	(S)	4.87	4.39	3.26 b
8-25-2	"	5.81	4.54	4.46 b
N81017	(NSD)	3.76	3.34	3.40 b
8-25-2	"	4.78	4.05	3.46 a
		ns	ns	+
GENOTYPE				
N81017		4.31	3.86	3.33
8-25-2		5.30	4.29	3.96
		**	ns	*
LEAFHOPPER				
Stress		5.34	4.46	3.86
Non-stress		4.27	3.69	3.43
		**	ns	ns
<u>Upper Reproductive</u>				
N81017	(S)	5.13	3.45	3.16
8-25-2	"	5.02	3.71	4.01
N81017	(NSD)	4.02	3.51	3.27
8-25-2	"	4.48	3.63	3.44
		ns	ns	ns
GENOTYPE				
N81017		4.58	3.48	3.22
8-25-2		4.75	4.17	3.73
		ns	ns	ns
LEAFHOPPER				
Stress		5.08	4.08	3.59
Non-stress		4.25	3.57	3.36
		*	ns	ns

S = Stress NSD = Non-stress ns = not significant

**, *, + Different letters within a column indicate significant difference at p = 0.01, 0.05 or 0.1 respectively according to DMRT

¹ = R₂/R₃ ² = R₅ ³ = R₇

FIG. 6. TOTAL DRY WEIGHT IN BEANS IN 1991



COWPEAS

^{15}N Content

Stress significantly increased the proportion of ^{15}N that was in the root at 86 DAP but there were no genotypic differences (Table 28). There was no significant difference between percentage of ^{15}N in the stress and non-stress treatment of the lower stems, but TVX 3236 contained a higher proportion of ^{15}N than IT83S-742-2 at physiological maturity suggesting that TVX 3236 remobilized less N from the lower stem. At 69 DAP, the stress treatment contained a greater proportion of ^{15}N the upper stem, and TVX 3236 contained more ^{15}N than IT83S-742-2 (Table 28). There was a significant increase in the proportion of ^{15}N under stress at 86 DAP in the lower leaves and at 69 and 86 DAP in the upper leaves (Table 29). TVX 3236 contained more ^{15}N in the lower leaves than IT83S-742-2 at physiological maturity. There were no differences between the stress and non-stress treatments in the lower or upper reproductive structures with regard to ^{15}N content (Table 30). IT83S-742-2 contained a greater proportion of ^{15}N in the lower reproductive structures than TVX 3236 at 86 DAP. These results suggest that IT83S-742-2 remobilized greater amount of N to the seeds.

N Concentration

Leafhopper damage significantly increased N concentration at 69 and 93 DAP in the roots and upper stems, and at all sampling dates in the lower stem (Table 31). At 93 DAP, TVX 3236 had a significantly higher N concentration than IT83S-742-2 in the roots, lower and upper stems. There was a significant increase in N concentration in the lower and upper leaves at 69 and 86 DAP under stress, and TVX 3236 had a higher leaf

TABLE 28. ¹⁵N Content in Cowpea Roots and Stems Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing. MI. 1991.

TREATMENT (DAP)	ROOTS			LOWER STEM			UPPER STEM		
	69 ¹	86 ²	93 ³	69 ¹	86 ²	93 ³	69 ¹	86 ²	93 ³
%									
TVX 3236 (S)	2.10	5.41	2.77	14.87	37.10	37.73	13.60	7.18	3.24
IT83S-742-2 "	2.48	3.82	4.44	10.50	20.08	37.73	11.04	6.65	2.68
TVX 3236 (NSD)	2.01	2.42	3.94	16.62	16.93	29.05	6.52	9.91	8.17
IT83S-742-2 "	1.68	1.88	1.58	8.71	9.65	5.02	3.22	5.90	1.08
ns									
GENOTYPE									
TVX 3236	2.05	3.91	3.27	15.87	23.65	31.94	10.06	8.74	5.35
IT83S-742-2	2.08	2.85	3.01	9.61	14.96	6.62	7.13	6.22	1.88
ns									
LEAFHOPPER									
Stress	2.29	4.62	3.61	12.37	25.88	13.03	12.32	6.91	2.96
Non-stress	1.84	2.15	2.59	12.66	13.29	15.99	4.87	7.91	4.11
ns									
*									
ns									

ns									
ns									

S= Stress NSD= Non-stress ns= not significant

***, *, + p= 0.001, 0.05 or 0.1 respectively

¹= Flowering (R₁) ²= Early pod fill (R₂) ³= Late pod fill (R₃)

TABLE 29. ^{15}N Content in Cowpea Leaves Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		69 ¹	86 ²	93 ³
<u>Lower Leaves</u>		%		
TVX 3236	(S)	26.55	44.15	20.38
IT83S-742-2	"	21.42	41.68	8.90
TVX 3236	(NSD)	33.34	24.61	14.92
IT83S-742-2	"	11.87	15.30	7.76
		ns	ns	ns
GENOTYPE				
TVX 3236		29.94	32.99	18.04
IT83S-742-2		15.96	28.49	8.41
		ns	ns	+
LEAFHOPPER				
Stress		24.35	42.74	14.64
Non-stress		22.60	19.96	11.34
		ns	*	ns
<u>Upper Leaves</u>				
TVX 3236	(S)	16.53	9.19	7.24
IT83S-742-2	"	14.97	7.44	1.30
TVX 3236	(NSD)	9.71	4.68	2.76
IT83S-742-2	"	3.70	4.05	1.42
		ns	ns	ns
GENOTYPE				
TVX 3236		13.12	6.93	5.32
IT83S-742-2		9.33	5.75	1.34
		ns	ns	ns
LEAFHOPPER				
Stress		15.75	8.31	4.27
Non-stress		6.70	4.37	2.33
		*	+	ns

S = Stress NSD = Non-stress ns = not significant

*, + p = 0.05 or 0.1 respectively

¹ = R₁ ² = R₃ ³ = R₆

TABLE 30. ^{15}N Content in Cowpea Reproductive Organs Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
<u>Lower Reproductive</u>		%	
TVX 3236 (S)	0.53	4.06	2.38
IT83S-742-2 "	2.37	18.77	15.70
TVX 3236 (NSD)	2.20	5.59	8.54
IT83S-742-2 "	6.62	7.66	28.04
	ns	ns	ns
GENOTYPE			
TVX 3236	1.48	4.82	5.46
IT83S-742-2	4.50	13.22	23.93
	ns	+	ns
LEAFHOPPER			
Stress	1.58	11.42	9.04
Non-stress	4.41	6.63	21.54
	ns	ns	ns
<u>Upper Reproductive</u>			
TVX 3236 (S)	0.70	0.18	--
IT83S-742-2 "	0.84	0.79	--
TVX 3236 (NSD)	1.68	6.27	--
IT83S-742-2 "	0.79	3.79	--
	ns	ns	
GENOTYPE			
TVX 3236	1.29	3.22	--
IT83S-742-2	0.82	2.79	--
	ns	ns	
LEAFHOPPER			
Stress	0.80	0.49	--
Non-stress	1.23	4.62	--
	ns	ns	

+ p(0.1) ¹ = R₁ ² = R₃ ³ = R₆

S = Stress NSD = Non-stress ns = not significant

TABLE 31. N Concentration in Cowpea Roots and Stems Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT (DAP)	ROOTS			LOWER STEM			UPPER STEM		
	69 ¹	86 ²	93 ³	69 ¹	86 ²	93 ³	69 ¹	86 ²	93 ³
%									
TVX 3236 (S)	2.32	1.64	1.86	5.35	3.79 a	3.14	5.60	4.26	3.97
IT83S-742-2 *	2.36	1.69	1.53	4.99	4.04 a	2.96	5.95	4.63	3.22
TVX 3236 (NSD) IT83S-742-2 *	1.57	1.46	1.49	3.51	2.60 b	2.12	4.08	3.45	3.35
	1.83	1.32	1.04	3.76	1.93 c	1.65	4.94	3.59	1.87
GENOTYPE	ns	ns	ns	ns	*	ns	ns	ns	ns
TVX 3236	1.95	1.55	1.70	4.43	3.20	2.70	4.84	3.80	3.70
IT83S-742-2	2.09	1.50	1.28	4.37	2.98	2.30	5.44	4.03	2.54
LEAFHOPPER	ns	ns	+	ns	ns	+	ns	ns	*
Stress	2.34	1.66	1.69	5.17	3.92	3.05	5.78	4.45	3.59
Non-stress	1.70	1.39	1.23	3.63	2.26	1.85	4.51	3.52	2.50
	**	ns	*	***	***	***	*	ns	*

S = Stress NSD = Non-stress ns = not significant
 ***, **, *, + Different letters within a column indicate significant difference at p = 0.001, 0.01, 0.05 or 0.1 according to DMRT.
¹ = R₁ ² = R₃ ³ = R₆

lower and upper leaves at 69 and 86 DAP under stress, and TVX 3236 had a higher leaf N concentration than IT83S-742-2 in the lower leaves at 69 and 86 DAP (Table 32). Leafhopper stress significantly increased N concentration in the lower reproductive structures at 86 and 93 DAP, and upper reproductive structures at 93 DAP (Table 33). There were no genotypic differences in N concentration.

Biomass Accumulation

Leafhopper damage significantly reduced dry weight of the roots and lower stem at 69 and 86 DAP (Table 34). TVX 3236 had a higher dry weight than IT83S-742-2 in the lower stem at 86 and 93 DAP. There were no differences between the stress and non-stress treatments or between genotypes in the upper stem. Leafhopper stress did not significantly decrease dry weight in the lower and upper leaves except at 69 DAP in the lower leaves (Table 35). TVX 3236 had a higher dry weight than IT83S-742-2 at 93 DAP in the lower and upper leaves. There was a significant decrease in dry weight at all sampling dates in the lower reproductive structures due to leafhopper damage (Table 36). IT83S-742-2 had a significantly higher dry weight than TVX 3236 in the lower reproductive structures at all sampling dates.

CONCLUSION

Leafhopper damage decreased seed yield by decreasing the number of pods per plant in both beans and cowpeas. Cowpeas were more susceptible to leafhopper damage than beans. Leafhopper damage decreased LWRC and LWC in beans and cowpeas. Genotypic differences in LWRC and LWC occurred in beans and cowpeas but did not

TABLE 32. N Concentration in Cowpea Leaves Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		69 ¹	86 ²	93 ³
<u>Lower Leaves</u>		%		
TVX 3236	(S)	7.16	6.31	4.74
IT83S-742-2	"	6.07	5.77	4.77
TVX 3236	(NSD)	5.41	4.51	4.06
IT83S-742-2	"	5.10	4.05	4.04
		ns	ns	ns
GENOTYPE				
TVX 3236		6.29	5.41	4.45
IT83S-742-2		5.58	4.91	4.40
		+	+	ns
LEAFHOPPER				
Stress		6.62	6.04	4.76
Non-stress		5.25	4.28	4.05
		**	***	ns
<u>Upper Leaves</u>				
TVX 3236	(S)	6.18	5.79	4.26
IT83S-742-2	"	6.49	5.92	4.46
TVX 3236	(NSD)	5.14	4.38	3.58
IT83S-742-2	"	5.17	3.88	3.64
		ns	ns	ns
GENOTYPE				
TVX 3236		5.66	5.09	3.97
IT83S-742-2		5.88	4.90	4.05
		ns	ns	ns
LEAFHOPPER				
Stress		6.33	5.85	4.36
Non-stress		5.16	4.13	3.61
		***	**	ns

S = Stress NSD = Non-stress ns = not significant

***, **, *, + p = 0.001, 0.01, 0.05 or 0.1 respectively

¹ = R₁ ² = R₃ ³ = R₆

TABLE 33. N Concentration in Cowpea Reproductive Organs Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing. MI. 1991.

TREATMENT	DAYS AFTER PLANTING		
	69 ¹	86 ²	93 ³
<u>Lower Reproductive</u>		%	
TVX 3236 (S)	4.83	5.09	4.51
IT83S-742-2 "	5.46	4.94	4.20
TVX 3236 (NSD)	5.02	4.32	3.97
IT83S-742-2 "	5.19	4.12	3.31
	ns	ns	ns
GENOTYPE			
TVX 3236	4.94	4.70	4.28
IT83S-742-2	5.33	4.53	3.75
	ns	ns	ns
LEAFHOPPER			
Stress	5.19	5.02	4.35
Non-stress	5.11	4.22	3.59
	ns	**	+
<u>Upper Reproductive</u>			
TVX 3236 (S)	5.08	3.45	4.08
IT83S-742-2 "	4.77	4.10	4.43
TVX 3236 (NSD)	4.20	4.02	3.65
IT83S-742-2 "	4.71	3.69	3.49
	ns	ns	ns
GENOTYPE			
TVX 3236	4.55	3.73	3.82
IT83S-742-2	4.74	3.86	3.89
	ns	ns	ns
LEAFHOPPER			
Stress	4.87	3.72	4.29
Non-stress	4.46	3.86	3.5
	ns	ns	+
S = Stress NSD = Non-stress ns = not significant			
**, + p = 0.01 or 0.1 respectively			
¹ = R ₁ ² = R ₃ ³ = R ₆			

TABLE 34. Dry Weight of Cowpea Roots and Stems Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT (DAP)	ROOTS			LOWER STEM			UPPER STEM		
	69 ¹	86 ²	93 ³	69 ¹	86 ²	93 ³	69 ¹	86 ²	93 ³
grams/plant									
TVX 3236 (S)	0.5	1.6	2.0	2.6	15.5 b	26.6	1.1	1.3	1.6
IT83S-742-2 "	0.8	1.7	2.0	4.2	15.0 b	13.6	1.1	1.6	1.6
TVX 3236 (NSD)	1.1	2.3	2.3	9.6	27.9 a	25.2	1.2	1.8	2.1
IT83S-742-2 "	1.4	2.2	2.3	8.9	18.7 b	18.1	1.2	1.6	1.6
GENOTYPE	ns	ns	ns	ns	+	ns	ns	ns	ns
TVX 3236	0.8	2.0	2.2	6.1	21.7	26.0	1.2	1.6	1.8
IT83S-742-2	1.1	1.9	2.1	6.5	16.8	15.8	1.2	1.6	1.6
LEAFHOPPER	**	ns	ns	ns	+	**	ns	ns	ns
Stress	0.6	1.6	2.0	3.4	15.2	20.1	1.1	1.5	1.6
Non-stress	1.3	2.3	2.3	9.2	23.3	21.1	1.2	1.7	1.9
	***	*	ns	***	**	ns	ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

***, **, *, + Different letters within a column indicate significant difference at p = 0.001, 0.01, 0.05 or 0.1 according to DMRT.

¹ = R₁ ² = R₃ ³ = R₆

TABLE 35. Dry Weight in Cowpea Leaves Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		69 ¹	86 ²	93 ³
<u>Lower Leaves</u>		grams/plant		
TVX 3236	(S)	4.4 c	14.0	14.9
IT83S-742-2	"	5.6 c	11.8	6.7
TVX 3236	(NSD)	11.7 a	16.6	13.2
IT83S-742-2	"	8.7 b	12.0	10.9
		**	ns	ns
GENOTYPE				
TVX 3236		8.0	15.3	14.2
IT83S-742-2		7.1	11.9	8.8
		ns	+	+
LEAFHOPPER				
Stress		5.0	12.9	10.8
Non-stress		10.2	14.3	11.9
		***	ns	ns
<u>Upper Leaves</u>				
TVX 3236	(S)	1.9	2.3	2.5
IT83S-742-2	"	1.9	2.3	1.8
TVX 3236	(NSD)	2.0	2.0	2.6
IT83S-742-2	"	1.9	2.0	1.7
		ns	ns	ns
GENOTYPE				
TVX 3236		2.0	2.2	2.5
IT83S-742-2		1.9	2.1	1.7
		ns	ns	*
LEAFHOPPER				
Stress		1.9	2.3	2.1
Non-stress		1.9	2.0	2.1
		ns	ns	ns

S = Stress NSD = Non-stress ns = not significant ¹ = R₁ ² = R₃ ³ = R₆
 ***, **, *, + Different letters within a column indicate significant difference at p =
 0.001, 0.01, 0.05 or 0.1 respectively according to DMRT.

TABLE 36. Dry Weight of Cowpea Reproductive Organs Subjected to Leafhopper Infestation at the MSU Agronomy Farm in East Lansing, MI. 1991.

TREATMENT		DAYS AFTER PLANTING		
		69 ¹	86 ²	93 ³
<u>Lower Reproductive</u>		grams/plant		
TVX 3236	(S)	0.2	1.1	4.7
IT83S-742-2	"	0.6	7.1	11.7
TVX 3236	(NSD)	0.8	6.5	14.4
IT83S-742-2	"	2.6	11.2	29.3
		ns	ns	ns
GENOTYPE				
TVX 3236		0.6	3.8	8.9
IT83S-742-2		1.6	9.2	20.5
		+	*	*
LEAFHOPPER				
Stress		0.4	4.1	8.2
Non-stress		1.7	8.9	22.9
		*	*	**
<u>Upper Reproductive</u>				
TVX 3236	(S)	0.1	0.3	0.2
IT83S-742-2	"	0.2	0.7	2.2
TVX 3236	(NSD)	0.2	0.6	3.3
IT83S-742-2	"	0.3	1.1	2.2
		ns	ns	ns
GENOTYPE				
TVX 3236		0.2	0.5	2.1
IT83S-742-2		0.2	1.0	2.2
		ns	ns	ns
LEAFHOPPER				
Stress		0.2	0.5	1.4
Non-stress		0.2	0.8	2.7
		ns	ns	ns

S = Stress NSD = Non-stress ns = not significant

**, *, + p = 0.01, 0.05 or 0.1 respectively

¹ = R₁ ² = R₃ ³ = R₆

coincide with yield potential or resistance. The lower yielding cowpea genotype, Blackeye consistently had lower RWC. Leaf damage reduced root growth rate in both beans and cowpeas. Resistant bean genotypes had a lower root growth rate than susceptible genotypes. There was no genotypic pattern of root growth in cowpeas in terms of drought resistance or susceptibility, and high or low yielding potential.

Leafhopper damage decreased the rate of photosynthesis in both beans and cowpeas. There were genotypic differences in the rate of photosynthesis only in cowpeas. The low yielding genotype, Blackeye had the lowest rate of photosynthesis. Leafhopper damage decreased stomatal conductance in both beans and cowpeas but genotypic differences were found only in cowpeas. Carbon isotope discrimination was not reduced by leafhopper damage but genotypic differences were observed for both beans and cowpeas. However, the CID values were not effective in separating high and low yielding genotypes in either species.

Differences were found between the stress and non-stress treatments and between resistant and susceptible genotypes in ^{15}N content, N concentration and dry weight in beans and cowpeas. Leafhopper damage increased the amount of ^{15}N in the plant structures suggesting that there was less N remobilization under leafhopper stress. The resistant bean genotype remobilized greater N under stress than the susceptible genotype.

Although this study was not intentionally designed to evaluate the effect of leafhopper damage on beans and cowpeas, these results provide useful information on the response of both species to leafhopper damage. This gives a basis for future studies on the effects of leafhopper damage on beans or cowpeas.

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APPENDIX A

FISCHER AND MAURER PROCEDURE

This approach involves yield of individual genotypes under drought stress (Y_s) and irrigated or non-stress conditions (Y_i). Data on the average yield of all genotypes under stress (Y_s) and non-stress (Y_i) conditions are used to calculate the drought intensity index (DII) as follows;

$$\text{DII} = 1 - Y_s/Y_i$$

The drought susceptibility index (DSI) of individual genotypes is calculated as;

$$Y_s = Y_i (1 - \text{DSI} \cdot \text{DII})$$

$$\text{so DSI} = [1 - (Y_s/Y_i)] / \text{DII}$$

Varieties with average resistance to drought have a DSI value of 1.0, values less than 1.0 indicate less susceptibility and greater resistance to drought with a value of $\text{DSI} = 0$ indicate maximum possible drought resistance.

TABLE 1. DAILY AIR TEMPERATURE (°C)

DATE	JUNE		JULY		AUG.		SEPT.		OCT.	
	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN	MAX	MIN
190	23.3	6.7	29.4	15.0	21.7	8.3	29.4	15.0	16.1	4.4
290	27.2	15.0	23.3	10.6	26.1	10.0	30.0	15.6	16.7	2.2
390	26.7	15.6	26.7	16.7	28.3	13.9	27.8	14.4	20.6	5.0
490	23.9	4.4	30.0	15.6	27.2	16.7	25.6	14.4	23.3	10.0
590	17.2	3.3	34.4	20.0	21.7	17.2	29.4	16.1	18.3	10.0
690	18.9	9.4	28.9	12.8	24.4	12.8	28.3	18.9	27.2	8.9
790	23.9	11.1	22.2	7.2	16.7	8.9	33.3	18.9	28.9	15.6
890	26.1	13.3	25.0	15.6	22.2	8.9	24.4	9.4	16.1	7.8
990	26.1	13.9	32.8	21.7	26.7	12.2	25.6	11.7	8.9	6.1
1090	23.9	12.8	29.4	16.7	28.3	12.2	26.7	17.2	7.8	5.6
1190	23.3	10.6	28.3	13.3	27.8	13.9	27.2	13.3	11.7	3.3
1290	25.6	14.4	18.9	13.9	26.7	14.4	26.7	12.2	14.4	-0.6
1390	25.6	15.6	24.4	11.7	22.2	16.1	30.6	14.4	14.4	-0.6
1490	32.2	20.0	22.2	13.3	20.0	10.0	28.9	16.7	16.7	2.8
1590	27.2	13.3	18.9	13.9	23.9	12.8	23.9	10.0	20.0	5.6
1690	27.8	13.3	25.0	14.4	27.2	16.7	17.2	10.0	15.0	3.3
1790	30.0	19.4	27.2	16.7	28.9	16.7	15.6	3.3	18.3	5.0
1890	32.2	19.4	29.4	18.3	27.2	18.9	15.6	1.7	25.0	8.3
1990	26.7	10.0	30.6	16.7	29.4	18.3	19.4	3.3	8.9	0.6
2090	24.4	11.1	30.6	18.9	19.4	13.3	16.1	5.6	10.0	-1.1
2190	24.4	15.0	24.4	18.9	18.9	13.9	21.7	6.7	16.7	5.0
2290	27.2	17.8	27.8	16.1	21.7	17.2	16.1	8.3	15.6	5.0
2390	20.0	13.9	19.4	11.1	22.2	16.7	17.2	6.1	13.3	-2.2
2490	16.1	10.6	23.9	12.2	22.8	16.1	12.2	3.9	14.4	-2.2
2590	22.8	6.1	26.7	12.2	27.8	16.1	17.8	7.8	13.3	0.0
2690	27.2	12.8	30.0	14.4	28.3	17.8	21.1	10.0	7.8	-3.9
2790	25.0	13.3	29.4	13.9	30.6	20.6	23.9	7.2	10.0	-3.3
2890	28.3	17.8	29.4	16.1	31.7	22.8	27.2	8.3	16.1	2.2
2990	24.4	17.8	30.6	16.7	32.2	15.0	27.8	11.1	8.3	-4.4
3090	27.8	18.3	30.0	21.1	27.8	15.6	16.7	10.0	11.7	-2.8
3190			24.4	12.8	29.4	12.8			19.4	5.6
191	30.6	18.9	25.0	15.6	27.8	14.4	27.8	7.8	27.2	9.4
291	27.8	16.7	28.3	17.2	28.9	15.6	24.4	11.7	20.0	10.0
391	21.1	14.4	29.4	17.2	31.1	17.2	28.3	11.7	23.9	12.8
491	26.7	8.9	31.1	17.2	22.2	15.0	27.2	12.2	22.2	10.0
591	20.0	12.2	27.8	17.8	23.3	10.6	23.9	7.2	19.4	10.0
691	23.9	7.2	28.3	15.6	23.9	8.3	26.1	10.6	15.6	2.8
791	26.1	10.6	33.3	21.1	25.6	12.2	28.3	12.2	8.9	2.2
891	27.2	11.1	31.7	17.8	25.6	16.1	30.0	15.6	12.2	1.7
991	27.2	11.1	25.6	12.2	16.7	13.3	30.6	15.6	20.6	3.9
1091	28.9	15.0	25.6	13.3	25.0	12.8	30.0	18.9	22.2	5.0
1191	28.9	17.8	27.8	15.6	25.6	12.2	25.0	9.4	16.7	5.0
1291	25.0	13.9	27.2	16.7	27.2	12.2	21.1	11.1	13.9	5.0
1391	27.2	8.3	24.4	16.1	27.8	12.8	20.0	13.9	11.7	-1.1
1491	25.6	13.3	23.3	15.6	28.3	13.3	22.2	12.8	12.8	-1.7

1591	31.1	17.8	26.1	11.1	27.8	13.3	25.6	16.1	10.6	3.3
1691	32.2	19.4	28.9	13.9	29.4	16.1	31.7	22.2	7.2	-3.9
1791	26.7	12.8	30.6	19.4	30.0	19.4	26.7	11.1	13.3	-2.8
1891	28.3	16.1	30.6	18.9	25.0	13.3	22.8	11.1	21.7	5.0
1991	29.4	15.0	32.2	21.7	27.8	15.6	18.3	4.4	15.6	0.6
2091	30.6	15.0	32.8	22.2	23.3	14.4	13.9	1.7	7.2	-4.4
2191	31.1	15.6	33.3	22.8	23.9	8.9	14.4	-1.7	11.7	-3.9
2291	31.1	14.4	31.1	21.1	26.1	13.9	18.3	-0.6	17.2	3.9
2391	16.1	9.4	32.2	21.1	28.3	13.3	18.3	6.7	22.8	5.6
2491	23.3	9.4	31.7	14.4	25.0	13.9	16.1	2.8	25.6	14.4
2591	26.7	14.4	26.1	14.4	27.8	12.8	10.6	0.0	23.3	17.8
2691	29.4	16.1	23.9	10.6	30.6	12.8	13.3	3.9	18.3	12.8
2791	32.2	20.6	24.4	9.4	32.2	19.4	11.7	0.6	18.9	10.0
2891	31.7	20.0	25.6	13.3	31.7	17.2	12.2	-3.3	10.6	7.8
2991	31.1	21.7	25.6	14.4	33.3	19.4	16.7	-3.3	13.9	8.3
3091	32.2	19.4	20.0	14.4	33.9	19.4	17.8	-0.6	18.3	10.6
3191			23.3	11.1	32.2	17.8			14.4	5.6
192	22.8	7.8	26.7	13.9	25.6	11.1	23.9	7.8	17.8	2.2
292	24.4	10.0	29.4	16.1	25.0	10.0	20.0	10.6	23.9	3.9
392	26.1	9.4	30.0	16.7	23.3	14.4	25.0	14.4	26.1	11.7
492	27.8	9.4	23.9	13.3	22.8	12.2	24.4	8.3	20.6	11.1
592	24.4	15.6	26.1	15.0	24.4	9.4	27.8	11.1	16.7	3.3
692	21.7	16.1	24.4	10.6	25.6	8.3	27.8	13.3	18.3	0.0
792	24.4	14.4	24.4	10.6	28.9	9.4	26.1	18.3	22.8	0.0
892	23.9	10.6	27.2	14.4	23.9	17.8	20.6	18.3	17.8	3.9
992	23.9	12.2	26.1	17.8	31.7	16.1	20.6	7.8	17.2	7.8
1092	22.2	6.7	26.1	16.7	31.1	17.8	18.9	10.6	17.2	7.8
1192	25.0	8.9	26.1	14.4	25.0	12.8	17.8	7.8	11.7	7.8
1292	26.7	9.4	27.2	16.1	20.6	11.7	21.7	6.1	15.0	5.0
1392	29.4	12.8	26.1	15.6	19.4	11.1	23.3	8.3	12.8	1.1
1492	30.6	14.4	20.0	16.1	18.9	8.3	27.8	11.7	18.3	1.1
1592	27.2	13.3	21.1	13.3	21.7	11.1	28.3	13.3	16.7	8.9
1692	23.3	10.6	21.1	12.2	22.8	8.9	27.8	18.9	12.2	10.0
1792	27.2	15.6	22.2	14.4	23.9	7.8	25.6	20.0	9.4	9.4
1892	34.4	18.3	26.1	15.6	21.1	9.4	21.1	20.0	5.6	0.6
1992	25.6	10.0	25.6	12.2	22.2	20.0	16.7	5.6	6.7	-6.7
2092	15.6	5.0	26.7	16.7	23.3	6.7	20.0	3.3	5.6	-3.3
2192	13.9	5.6	23.9	8.3	25.6	6.7	23.9	6.1	10.6	-3.3
2292	17.2	2.8	20.6	10.6	26.1	8.9	19.4	15.6	16.1	-1.7
2392	20.6	7.8	21.1	10.6	28.3	12.2	15.0	0.6	23.3	0.0
2492	17.8	7.8	16.1	11.1	29.4	17.2	15.0	1.7	15.0	9.4
2592	20.0	10.6	23.3	12.2	31.1	19.4	17.2	2.8	12.8	0.0
2692	23.3	11.7	26.7	13.3	27.2	19.4	16.7	4.4	15.0	8.9
2792	23.3	10.0	26.7	15.6	18.3	15.0	11.7	10.0	12.8	-2.2
2892	21.7	5.6	23.9	9.4	15.0	11.7	12.2	7.2	16.7	-1.7
2992	26.1	10.6	27.8	14.4	21.1	7.2	8.9	1.7	9.4	1.7
3092	28.9	13.3	25.0	14.4	21.1	8.9	12.2	1.1	6.7	2.8
3192			20.0	14.4	21.7	12.2			9.4	-5.0

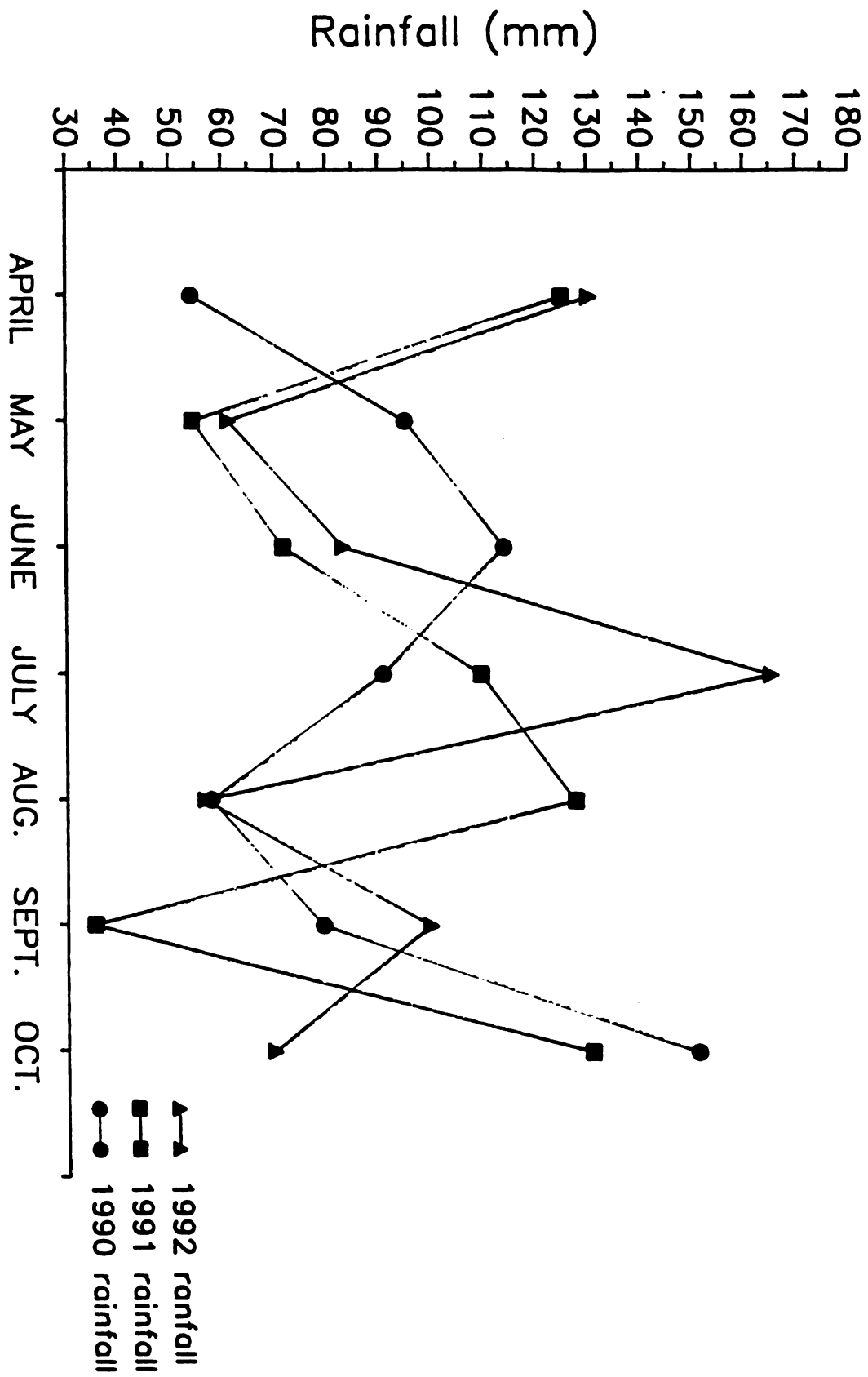


FIGURE 1. MONTHLY PRECIPITATION (mm) 1990–1992

TABLE 2. GENOTYPE DESCRIPTION

GENOTYPE	SOURCE	SEED COLOR	SEED SIZE
9-39-1	MSU ¹	white	small
8-25-2	"	brown	medium
N81017	"	white	"
8-42-M-2	"	off white	"
TVX 3236	IITA ²	tan	medium
IT83S-742-2	"	"	"
ER ₇	"	off white	small
BOO5-C	BOTSWANA	maroon	medium
BLACKEYE	"	white	"

¹ MSU- Michigan State University Bean Breeding Program. USA.

² IITA- International Institute of Tropical Agriculture, Ibadan. Nigeria.

APPENDIX B

Appendix B1: Photosynthesis Calculations

CO₂ Assimilation Rate (A)

$$A = f/s (C_e - C_o) [(1-X_e)/(1-X_o)]$$

Transpiration Rate (E)

$$E = f/s [(X_o - X_e)/(1 - X_o)]$$

Stomatal Conductance (g_s)

$$g_s = E / (X_s T_1 - X_o)$$

Where

s = leaf area

C_e = Mole fraction of CO₂ at chamber entrance

C_o = " " " " " " outlet

X_o = Mole fraction of water vapor at chamber outlet

X_e = " " " " " " entrance

X_s = " " " " " " saturation

f = air flow rate

T = Temperature recorded during measurement

Appendix B2: Light Interception Calculations

Variables measured

S - PAR reading from an upfacing ceptometer above crop canopy

R - Reflected PAR above canopy (ceptometer inverted above canopy)

T - Par reading from an upfacing ceptometer below crop canopy

U - Reflected PAR below canopy (ceptometer inverted below canopy)

Calculations

$t = T / S$ = light transmitted by the canopy

$r = R / S$ = light reflected to a sensor above the canopy

$r_s = U / T$ = reflectance of the soil surface

Light Intercepted (f)

$$f = 1 - t - r - tr_s$$

APPENDIX C

Calculations for ^{15}N data

Atom % and %N were obtained from the mass spectrometer data.

1. $\text{a.e} = \text{atom \% excess}$

$$= \text{atom \% in labelled plant} - \text{atom \% in control}$$

2. $\text{mg } ^{15}\text{N enrichment} = (\text{a.e}/100) * (\% \text{N}/100) * (\text{Dw}) * 1000$

a.e and %N were divided by 100 because they are percents. Multiplying by 1000 converts grams to milligrams since the dry weight (Dw) is in grams.

3. $\% ^{15}\text{N recovery} = (\text{mg N enrichment} / \text{mg } ^{15}\text{N applied}) * 100$

The amount applied was obtained when the plant was sampled one day after labeling. The total ^{15}N in the plant at that time was the total amount of ^{15}N that was applied.

TABLE 1. The Effect of Soil Water Changes on Root and Stem Dry Weight in Beans at the MSU Agronomy Farm. East Lansing. MI. 1990.

TREATMENT	ROOTS			LOWER STEM			UPPER STEM			
	21	29	65	21	29	65	21	29	65	
grams/plant										
8-42-M-2	(S)	0.79	0.84	1.02	4.41	5.36	4.08	0.57	1.12	1.36
9-39-1	"	0.85	1.02	1.16	3.93	5.65	6.42	1.50	1.59	1.44
8-42-M-2	(NSD)	1.02	1.10	0.88	6.93	8.26	5.06	1.60	2.03	0.81
9-3-1	"	0.81 ⁺	1.15	1.34	5.09	7.51	8.36	1.28	2.33	1.45
Genotype			ns	ns	ns	ns	ns	ns	ns	ns
8-42-M-2		0.90	0.97	0.95	5.67	6.81	4.57	1.09	1.58	1.13
9-39-1		0.83	1.09	1.25	4.51 ⁺	6.58	7.39	1.39	1.96	1.44
		ns	ns	ns		ns	ns	ns	ns	ns
WATER										
Stress		0.82	0.93	1.09	4.17	5.50	5.25	1.03	1.35	1.40
Non-stress		0.91 ^{**}	1.12 ⁺	1.10	6.01 ^{**}	7.88 ^{**}	6.71	1.44	2.88 [*]	1.17
				ns			ns	ns		ns

⁺ p(0.1) * p(0.05) ** p(0.01)

S= Stress NSD= Non-stress ns= non significant

TABLE 2. The Effect of Soil Water Changes on Leaf Dry Weight
Dry Weight in Beans in the Rainshelter at the MSU
Agronomy Farm in East Lansing. MI. 1990

TREATMENT	DAYS AFTER PLANTING		
	21	29	65
<u>Lower Leaves</u>			
	grams/plant		
8-42-M-2 (S)	3.69	4.31	1.09
9-39-1 "	4.86	4.74	1.96
8-42-M-2 (NSD)	6.05	5.39	0.63
9-39-1 "	5.57	6.52	1.91
	ns	ns	ns
Genotype			
8-42-M-2	4.87	4.85	0.83
9-39-1	5.22	5.63	1.92
	ns	ns	ns
Water			
STRESS	4.28	4.53	1.44
NON-STRESS	5.81	5.96	1.28
	*	+	ns
<u>Upper Leaves</u>			
8-42-M-2 (S)	0.87	1.46	0.97
9-39-1 "	0.97	2.22	0.69
8-42-M-2 (NSD)	2.33	2.77	0.22
9-39-1 "	2.10	3.68	0.38
	ns	ns	ns
Genotype			
8-42-M-2	1.60	2.12	0.52
9-39-1	1.54	2.95	0.48
	ns	+	ns
Water			
STRESS	0.92	1.84	0.83
NON-STRESS	2.21	3.22	0.31
	**	*	+

S= Stress NSD= Non-stress ns= not significant

**, *, + p=0.001, 0.05 or 0.1 respectively

TABLE 3. The Effect of Soil Water Changes on Reproductive Parts Dry Weight in Beans in the Rainshelter at the MSU Agronomy Farm in East Lansing. MI. 1990.

TREATMENT	DAYS AFTER PLANTING		
	21	29	65
<u>Lower reproductive</u>		grams/plant	
8-42-M-2 (S)	0.44	3.52	18.67
9-39-1 "	0.59	4.00	13.24
8-42-M-2 (NSD)	0.45	3.13	15.70
9-39-1 "	0.62	1.63	21.28
	ns	ns	ns
Genotype			
8-42-M-2	0.43	3.32	17.19
9-39-1	0.60	2.81	17.26
	ns	ns	ns
Water			
STRESS	0.50	3.76	15.96
NON-STRESS	0.53	2.38	18.49
	ns	ns	ns
<u>Upper Reproductive</u>			
8-42-M-2 (S)	0.15	0.54	4.75
9-39-1 "	0.17	0.86	2.26
8-42-M-2 (NSD)	0.14	0.54	5.33
9-39-1 "	0.14	0.49	3.34
	ns	ns	ns
Genotype			
8-42-M-2	0.14	0.54	5.04
9-39-1	0.16	0.68	2.80
	ns	ns	ns
Water			
STRESS	0.16	0.70	3.50
NON-STRESS	0.14	0.52	4.33
	ns	ns	ns

S= Stress

NSD= Non-stress

ns= not significant

TABLE 4. The Effect of Soil Water Changes on Bean Roots Dry Weight Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1991-92.

TREATMENT		1991			1992	
		21	38	45	37	47
		grams/plant			grams/plant	
N81017	(S)	1.20	1.29	1.53	1.57	1.58
8-25-2	"	0.80	0.94	1.16	0.98	0.86
N81017	(NSD)	0.96	0.96	1.05	1.95	1.56
8-25-2	"	0.74	0.87	0.96	0.96	0.70
Genotype		ns	ns	ns	ns	ns
N81017		1.08	1.13	1.29	1.76	1.57
8-25-2		0.77	0.90	1.06	0.97	0.77
		+	ns	+	**	+
		Leafhopper			Water	
STRESS		1.00	1.12	1.34	1.28	1.22
NON-STRESS		0.85	0.91	1.00	1.45	1.13
		ns	*	ns	ns	ns

S= Stress NSD= Non-stress ns= not significant

*, + p=0.05 or 0.1 respectively

TABLE 5. The Effect of Soil Water Changes on Bean Stem Dry Weight Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1991-92.

TREATMENT	1991			1992	
	21	38	45	37	47
<u>Lower Stem</u>	grams/plant			grams/plant	
N81017 (S)	8.26	10.11	9.08	8.21	9.22
8-25-2 "	6.36	5.74	7.21	6.69	9.69
N81017 (NSD)	7.07	7.92	8.17	9.57	11.27
8-25-2 "	5.41	7.36	6.31	7.42	8.01
	ns	ns	ns	ns	+
Genotype					
N81017	7.67	9.01	8.62	8.89	10.24
8-25-2	5.89	6.55	6.76	7.06	8.85
	ns	ns	+	ns	ns
	Leafhopper			Water	
STRESS	7.31	7.93	8.14	7.45	9.46
NON-STRESS	6.24	7.64	7.24	8.50	9.64
	ns	ns	ns	ns	ns
<u>Upper Stem</u>					
N81017 (S)	1.42	1.66	1.26	1.49	1.47
8-25-2 "	1.29	1.35	1.11	1.00	1.31
N81017 (NSD)	1.74	1.47	1.40	1.25	1.28
9-25-2 "	1.42	1.15	1.03	1.12	1.63
	ns	ns	ns	ns	ns
Genotype					
N81017	1.58	1.56	1.33	1.37	1.37
8-25-2	1.36	1.25	1.07	1.06	1.47
	+	+	*	ns	ns
	Leafhopper			Water	
STRESS	1.36	1.50	1.18	1.24	1.39
NON-STRESS	1.58	1.31	1.21	1.19	1.46
	+	ns	ns	ns	ns

S= Stress NSD= Non-stress ns= not significant

*, + p= 0.05 or 0.1 respectively

TABLE 6. The Effect of Soil Water Changes on Bean Leaf Dry Weight Using Plastic at the MSU Agronomy Farm in East Lansing, MI. 1991-92.

TREATMENT	1991			1992	
	21	38	45	37	47
Low Leaves					
	grams/plant			grams/plant	
N81017 (S)	6.96	6.12	3.24	6.01	4.64
8-25-2 "	6.73	3.41	2.68	6.38	3.19
N81017 (NSD)	7.23	5.56	5.38	7.18	5.82
8-25-2 "	7.24	5.76	2.93	4.84	3.06
	ns	ns	ns	ns	ns
Genotype					
N81017	7.09	5.84	4.31	6.59	5.23
8-25-2	6.98	4.58	2.81	5.61	3.10
	ns	ns	ns	ns	*
	Leafhopper			Water	
STRESS	6.84	4.76	2.96	6.19	3.92
NON-STRESS	7.24	5.66	4.15	6.01	4.41
	ns	ns	ns	ns	ns
Upper Leaves					
N81017 (S)	1.75	1.79	1.28	1.99	1.15
8-25-2 "	1.66	1.47	2.30	1.67	1.12
N81017 (NSD)	2.48	1.78	2.23	1.84	1.21
8-25-2 "	2.26	1.44	1.10	1.43	1.48
	ns	ns	ns	ns	ns
Genotype					
N81017	2.11	1.78	1.76	1.91	1.18
8-25-2	1.96	1.45	1.61	1.55	1.30
	ns	ns	ns	ns	ns
	Leafhopper			Water	
STRESS	1.71	1.63	1.72	1.83	1.13
NON-STRESS	2.67	1.61	1.67	1.64	1.35
	*	ns	ns	ns	ns

S= Stress

NSD= Non-stress

ns= not significant

* p= 0.05

TABLE 7. The Effect of Soil Water Changes on Bean Reproductive Parts Dry Weight Using Plastic at the MSU Agronomy Farm in East Lansing. MI. 1991-92

TREATMENT		1991			1992	
		21	38	45	37	47
<u>Lower Reproductive</u>		grams/plant			grams/plant	
N81017	(S)	6.29	15.71	28.98	16.66	21.76
8-25-2	"	4.86	13.48	27.29	16.56	20.09
N81017	(NSD)	1.63	6.36	19.06	18.42	24.42
8-25-2	"	0.95	10.82	15.89	13.06	13.82
		ns	ns	ns	ns	ns
Genotype						
N81017		3.96	11.04	24.02	17.54	23.09
8-25-2		2.90	12.15	21.59	14.81	16.95
		ns	ns	ns	ns	ns
		Leafhopper			Water	
STRESS		5.58	14.60	28.13	16.61	20.93
NON-STRESS		1.29	8.59	17.48	15.74	19.12
		***	*	*	ns	ns
<u>Upper Reproductive</u>						
N81017	(S)	0.71	5.02	1.87	2.14	3.07
8-25-2	"	0.53	3.02	3.78	1.20	2.57
N81017	(NSD)	0.33	3.80	1.39	1.54	2.56
8-25-2	"	0.23	2.07	0.46	1.65	1.78
		ns	ns	ns	ns	ns
Genotype						
N81017		0.52	4.41	1.63	1.84	2.81
8-25-2		0.38	2.55	2.12	1.42	2.17
		ns	*	ns	ns	ns
		Leafhopper			Water	
STRESS		0.62	4.02	2.83	1.67	2.82
NON-STRESS		0.28	2.94	0.92	1.59	2.17
		*	ns	ns	ns	ns

S= Stress NSD= Non-stress ns= not significant

***, * p= 0.001 or 0.05 respectively

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