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YIELD, YIELD COMPONENTS, AND NITROGEN PARTITIONING IN BAMBARA GROUNDNUT (VIGNA SUBTERRANEA), COMMON BEAN (PHASEOLUS VULGARIS), AND COWPEA (VIGNA UNGUICULATA) GROWN UNDER STRESS AND NON-STRESS SOIL MOISTURE CONDITIONS

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ABSTRACT

YIELD, YIELD COMPONENTS AND NITROGEN PARTITIONING IN BAMBARA GROUNDNUT(*Vigna subterranea*),COMMON BEAN (*Phaseolus vulgaris* L.), AND COWPEA (*Vigna unguiculata*) GROWN UNDER STRESS AND NON-STRESS SOIL MOISTURE CONDITIONS

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Globally, moisture stress is a major constraint in agricultural production resulting in millions of dollars in economic losses. A study was conducted in the rainshelter at the Kellogg Biological Research Station, Hickory Corners, Michigan, in 1995 and 1996 to evaluate the effect of moisture stress on yield, yield components and N partitioning in Bambara groundnut (*Vigna subterranea*) genotypes ZVS530 and ZVS564; common bean (*Phaseolus vulgaris*) genotypes Carioca, Natal Sugar and T3147-2; and cowpea (*Vigna unguiculata*) genotypes IT82D-889 and 475/89. The experiment was a split-plot in a randomized complete block design with moisture status as the main effect and species as the sub-plot. Moisture stress reduced yield by as much as 79% in common bean and 46% in cowpea. Cowpea genotypes aborted more seeds per pod than the other species Significant species differences were observed in seed weight, number of seeds per pod, number of pods per plant, and in N concentration of the different plant parts. Moisture stress did not significantly affect N concentration in any structures.

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CHAPTER 2

INTRODUCTION

Grain legumes are an important dietary component of many people in the 'developing world.' Grain legumes provide essential protein and vitamins and are an important source of fiber and calories in the human diet. In Zimbabwe, grain legumes are particularly important to the communal area and small scale farmers. Grain legumes are grown for their leaves, immature pods, and dry grain which are consumed in various preparations: fresh green leaves, dried and stored leaves, green peas, dry grain boiled with maize and various pastes (Nleya, 1992). Grain legumes store well and are often stored by farmers for domestic consumption. Only the excess production is sold for cash. The role of grain legumes in meeting human nutritional needs in Zimbabwe is likely to increase with the increasing cost of animal protein.

World wide, grain legumes are generally grown under rainfed conditions and often experience moisture stress during the growing season (Ehleringer et al., 1991). White and Singh (1991) estimated that more than 60% of common beans (*Phaseolus vulgaris*) grown in Latin America, Asia, and Africa suffer from water stress during crop growth. In Latin America alone, 93% of the common bean growing areas experience moisture stress (Fairbairn, 1993). Nearly one third of the world's common beans are produced in the central highlands of Mexico and northeastern Brazil, areas where drought is a common occurrence. Yield losses

caused by drought result in the economic loss of millions of dollars for the common bean producing regions of the world. The intensity of drought stress and the phenological stage of development at which drought occurs is unpredictable and differs for each year and region. Thus, moisture stress influences crop yield in different ways in different regions (Acosta-Gallegos and Adams, 1991). Various authors have proposed definitions of drought. Hall (1993) defines drought as occurring when water supply in the soil is sufficiently less than the maximum tendency of plants to lose water, as determined by the evaporative demand of the atmosphere. Drought stress in this review is defined as insufficient soil moisture to sustain plant growth and development. Drought may be terminal, when there is a gradual decrease of soil moisture as the plant matures, or intermittent in which moisture stress persists for seven days or longer and occurs once or several times in the growing season (Levitt, 1972).

Most communal area and small scale farmers in Zimbabwe are located in areas that experience inadequate and ineffective rainfall for crop production. Some of the rainfall occurs outside the growing season and is subsequently lost through evapotranspiration, while rainfall during the season often comes as sporadic storms and results in excessive runoff.

LITERATURE REVIEW

The effect of moisture stress on plant growth and development

Moisture stress affects cell membrane structure, modifying viscosity and permeability (Izzo et al., 1989) and results in decreased cell elongation (Hsiao, 1973). Above ground biomass and leaf area index are reduced due to reduced leaf-area expansion and premature senescence (Acosta-Gallegos and Shibata, 1989). Moisture stress interferes with nutrient uptake and alters plant hormone levels (Bradford and Hsiao, 1982). Moisture stress has the greatest effect on the plant tissue which is growing most rapidly at the time the stress occurs (Aspinall et al., 1964). The effect of moisture stress on seed yield depends on the phenological stage of development during the moisture deficit and on the intensity and duration of the deficit. In legumes, the reproductive stages from flower set through pod development and maturity are the most sensitive to moisture stress (Acosta-Gallegos and Shibata, 1989). Moisture stress in common beans during the reproductive stage reduced yield twice as much as moisture stress during the vegetative phase (Acosta-Gallegos and Shibata, 1989). In cowpea, (*Vigna unguiculata*), a 35% reduction in yield was observed when moisture stress was imposed at flowering and a 69% reduction when it was imposed at the pod fill stage (Shouse et al., 1981). Meckel et al. (1984) reported that the vegetative stage of soybean (*Glycine max*) was more sensitive to moisture stress than the seed

development stage. However, differences in seed yield between stressed and non-stressed plants of the same variety vary markedly from year to year, depending upon the phenological stage at which moisture stress occurs (Hoogenboom et al., 1987).

Inhibition of photosynthesis at low water potential coupled with low carbohydrate reserves at pollination caused developmental failure of the reproductive tissue due to a lack of substrate (Schussler and Westgate, 1991). With maize (*Zea mays*), Westgate and Grant (1989) showed that low water potential occurred in ovaries of water-deficient plants. At leaf water potentials that completely inhibited photosynthesis, ovary water potential was low enough to affect cell division, cell expansion, and metabolism of assimilates (Nicholas et al., 1985). Shussler and Westgate (1991) concluded that low ovary water potential may induce zygotic abortion directly by altering reproductive sink strength. Increased flower abortion and reduced pod numbers have been reported in cowpea (Hiler et al., 1972) and common bean (Stoker, 1974) under moisture stress, along with decreased individual seed weight .

Water limitation can hasten or delay phenological development of plants depending on severity of the water stress (Turk and Hall, 1980; Lawn, 1982; Rosenthal et al., 1987). In soybean, moisture stress has been reported to decrease the duration of reproductive development and consequently yield (Korte et al., 1983). Chickpea (*Cicer arietinum*) matured early under conditions of limited water

(Khanna-Chopra and Sinha, 1987). Turk and Hall (1980) and Lawn (1982) noted that the reproductive activity of cowpea may be hastened or delayed depending on phenological stage of development of the plant and intensity of the moisture stress. Determinate cowpea cultivars had little yield loss when moderate moisture stress was imposed during flowering because the pods matured before the stress became severe (Summerfield et. al., 1985). Thus, sensitive stages can escape midseason drought (Gwathmey and Hall, 1992).

Recovery from drought

Most leguminous species branch and have stem apices which tend to be protected by older leaves during conditions of moisture stress. The newer leaves have a more negative water potential and water moves from the older leaves to the apex. The water status of the apex was thus maintained at the expense of older leaves (Elston and Bunting, 1980). Singh et al. (1995) observed that the cowpea apex remained alive even after the rest of the plant was severely wilted. If the crop was re-watered, the terminal meristem regenerated to form new leaves, flowers and ultimately seed (Elston and Bunting, 1980; Singh et al., 1995). Indeterminate growth habit and protection of the apex were useful survival strategies in areas of erratic rainfall. These important survival mechanisms resulted in uneven maturing of the legumes and created difficulties in mechanical harvesting (Elston and Bunting, 1980).

Strategies of response to water stress

Water stress induced many morphological, phenological, anatomical, and physiological responses in plants (Ludlow, 1989). Often, the responses occurred simultaneously or in combinations. Ludlow (1989) referred to them as 'strategies.' He defined a strategy as a combination or grouping of mechanistically-linked responses and characteristics that comprised a particular type of behavior during periods of water stress.

Drought Escape

The drought escape strategy enabled plants to complete their life cycles during a short period of time before drought occurred (Hall,1993). Seeds germinated quickly after rain, grew and developed rapidly, flowered, and produced seed before the water supply was exhausted (Ludlow, 1989). The time from germination to maturity was short and approximated the average length of the growing season for the particular environment. Cultivars grown by West African farmers had phenologies that shortened as the rainfall decreased from the coast towards the desert (Dancette and Hall, 1979). In the Sahel, newly developed early cultivars of cowpea flowered within 30 days of sowing and produced substantial yield by 55 days, at which time traditional varieties had only begun to flower. The photoperiod sensitivity of these plants permitted flowering to coincide with the average date to the end of the rainy season (Ludlow and Muchow, 1990). This ensured a relatively high grain yield as pests and diseases were avoided and

sufficient time was provided to fill grain before soil moisture reserves were exhausted.

Drought escape can also be enhanced through phenotypic plasticity and varietal intercropping. It is a conservative survival strategy that occurs at the expense of yield. The benefit is that some seed is obtained to ensure species survival from year to year.

Avoidance

Plants that exhibited drought avoidance had tissue that was very sensitive to dehydration. These plants avoided water deficits whenever a water shortage occurred. Processes that aided in greater dehydration avoidance included low stomatal conductance, paraheliotropic leaf orientation, less leaf area, deeper roots that exploited water in deeper soil profiles, higher root/shoot ratio, greater osmotic adjustment, and little photosynthetic adjustment (Hall, 1993; Ludlow, 1989). For example Siratro (*Macroptilium atropurpureum),* a tropical legume had deep roots for maximum water uptake (Sheriff et al., 1986). It closed its stomates under dry, hot conditions and paraheliotropic movement occurred after stomatal closure (Ludlow et al., 1983). If moisture stress continued, smaller dark green leaves were produced with a hairy abaxial surface. The smaller leaves had a larger convective heat exchange which moderated the increase of leaf temperature above air temperature when stomata were closed. Under extreme moisture stress, leaves died back progressively up the stem from the oldest to the youngest, followed by

basipetal stem die back leaving only the crowns to survive prolonged droughts (Ludlow, 1989). Cowpea was intolerant of desiccation and its avoidance techniques involved stomatal regulation of water loss (Bates and Hall, 1982). Leaf area was reduced by leaf senescence, abscission, and cessation of new leaf expansion (Turk and Hall, 1980; Akyeampong, 1986). This avoidance technique ensured water conservation by the remaining vegetative tissue and hence plant survival. However, drought avoidance negatively affected photosynthetic capacity and yield potential. In extreme cases, both yield and survival of the plant was threatened by complete defoliation (Gwathmey and Hall, 1992). All the characteristics of drought avoidance did not appear in any one plant.

Drought Tolerance

Dehydration tolerance indicates the plant's ability to maintain vital functions as the relative water content decreases (Hall, 1993). These plants exhibited moderate to high osmotic adjustment. Osmotic adjustment assisted in the maintenance of turgor, which in turn assisted maintenance of carbon acquisition by sustaining stomatal opening, photosynthesis and leaf expansion. If carbon acquisition is to continue, water loss becomes inevitable and is often described as 'the necessary evil.' This is especially harmful if water uptake cannot match water loss (Ludlow, 1987). In some cases, this results in death of the plant.

Osmotic adjustment

The exact role of osmotic adjustment in drought resistance is not fully understood and has been questioned (Blum, 1989). Morgan (1984) working with wheat concluded that genotypes selected for a greater capacity for osmotic adjustment under moisture stress yielded more under drought stress than those exhibiting less osmotic adjustment. Grumet et al. (1987) found that barley populations with greater capacity for constitutive osmotic adjustment grew and yielded less under drought stress than those of lower capacity. They suggested that induced osmotic adjustment rather than constitutive osmotic adjustment can be used in the selection for drought resistance.

Quick Screening methods for drought tolerance

Identifying a quick, reliable and inexpensive method of screening for drought resistance in plants remains a great challenge to crop physiologists. Several plant physiological responses and genes have been suggested as possible screening tools, but none has been defined as conclusive. Lynch (1995) suggested identifying mechanisms of tolerance and selecting for that mechanism directly or indirectly through molecular markers. Yield has traditionally been used as the main component to evaluate plant performance under drought conditions. The disadvantage is that yield trials are costly to run and results are often variable (Lynch, 1995). Singh et al. (1995) concluded that selecting for drought using physiological parameters is expensive, time consuming, and difficult to use when

screening large number of lines or segregating lines.

Screening method for drought tolerance using growth boxes

Singh et al. (1995) developed a screening method which determined drought tolerant genotypes during the early vegetative stage. The method used boxes lined with polyethylene sheets containing a 1:1 sand and soil mixture. Plants were watered until partial emergence of the trifoliate leaf, at which time water was withheld and percentage wilting and the number of days to permanent wilting of each cultivar was determined and scored. The surviving plants were re-watered to check their ability to regrow (Singh et al., 1995).

Criteria for evaluating the effect of moisture stress on yield

Four classes of genotypes can be identified based on the ability of the genotypes to tolerate moisture stress. Group A genotypes yield well under both non-stress and stress environments,. Group B genotypes yield well only under non-stress conditions. Group C genotypes yield relatively well under stress conditions, and group D genotypes yield poorly under both non-stress and stress conditions (Fernandez, 1993). Various indices have been developed in attempts to assess yield performance under moisture stress.

Mean productivity

Mathematically the mean productivity (MP) can be expressed as $MP = (Y_s + Y_p)/2$ where Y_s is the yield in stress environment and Y_p the potential yield of a given genotype in a non-stress environment. The MP tends to select genotypes for

higher yield potential (Fernandez 1993). Genotypes chosen for MP qualities increase yield under both non-stress and stress conditions. However the MP cannot separate genotypes that yield well under both stress and non-stress conditions from those yielding well only under non-stress conditions (Fernandez, 1993)

Geometric mean

The geometric mean (GM) separates genotypes that yield well both under stress and non-stress environments from those that yield well only under non-stress, those yielding relatively well under stress, and those yielding poorly under both stress and non-stress conditions (Fernandez, 1993). GM can be expressed as $GM = (Y_s * Y_p)^{1/2}$

The drought susceptibility index (DSI)

The drought susceptibility index is reported to estimate drought tolerance. A value of one is reported to equal average resistance, values lower than one represent greater than average resistance, and values greater than one indicate susceptibility (Fischer and Maurer, 1978). The DSI of individual genotypes is calculated as $DSI = [1-(Y_s/Y_p)]/DII$. The DII is calculated as $DII = 1 - Y_s/Y_p$ with Y_s representing the average ;yield of all genotypes under stress and Y_p representing the average yield of all genotypes under non-stress conditions.

The stress tolerance index (STI)

The stress tolerance index (STI) has been developed as an alternative to the DSI. STI is reported to measure both stress tolerance and yield potential. With STI, the

higher the value, the greater the stress tolerance and the higher the yield. Genotypes chosen based upon high STI exhibit high yield potential and high yield in stress environments (Fernandez, 1993). Fernandez (1993) expresses the STI as $[(Y_p)(Y_s)]/(Y_p)^2$.

Nitrogen and its effect on drought tolerance

Nitrogen is an important component of the biochemical constituents that enhance yield producing processes (Sinclair and Horie, 1989). However, it is unclear whether nitrogen deficiency increases or decreases the sensitivity of plants to moisture stress (Bennett et al., 1989). Plants in soils with low nitrogen have reduced growth rates and low shoot to root ratios (Russel, 1977). It has been suggested that this may affect the balance between crop transpiration and nutrient and water absorption (Bennet et al., 1989). Physiological responses of crops have been reported to be altered by nitrogen deficiency (Bennet et al., 1986; Jones et al., 1986). Radin and Parker (1979) suggested that this may result in the alteration of plant characteristics associated with drought resistance. Radin and Parker (1979) observed that cotton (*Gossypium hirsutum*) grown under low nitrogen levels had a lower water use efficiency. They further suggested that the difference could be used to improve drought resistance. However, Viets (1962) observed that field plants grown under low nitrogen levels had lower aboveground shoots but similar rates of evapotranspiration as plants grown with adequate nitrogen. Bennett et al. (1989), working with maize, inferred that an interaction between moisture

stress and nitrogen deficiency reduces total biomass, seed weight accumulation, and nitrogen uptake.

Nitrogen contribution of legumes to the subsequent non-legume crops

It is generally believed that the advantages of growing legumes stem mostly from the fact that they fix their own nitrogen and leave some extra nitrogen for the subsequent crop (Bandyopadhyay and De, 1986 ; Senaratne and Hardarson, 1988). This is particularly true when legumes are grown as green manure crops (Heichel, 1987). Thus the beneficial residual effect is to some extent dependent on the aboveground biomass being returned to the soil. For a subsequent crop after a legume to benefit, the quantity of fixed nitrogen returned by the legume to the soil should be more than that of soil nitrogen in the harvested grain (Eaglesham et al., 1982). Zapata et al. (1987) reported that after the removal of pods and the return of straw to a soybean field, there was still a net nitrogen depletion of 54 Kg N ha^{-1} nitrogen. Senarate and Hardarson (1988) suggested that the nitrogen benefit to the subsequent crop after grain legumes may be a result of a lower uptake of mineral nitrogen by legumes relative to non-legumes and a carry-over of nitrogen from the legume residue. These factors lead to a larger uptake of soil nitrogen by the subsequent crops compared to crops grown after non-legumes. It is further debated whether the beneficial effect of legumes to subsequent crops is because of contribution of nitrogen by fixation or because of an overall rotational effect, which includes disease control, soil crumb structure improvements, and nitrogen

availability (Papastylianou and Puckridge, 1983; Heichel, 1987).

Legume/cereal intercropping studies such as maize/common bean, maize/cowpea or maize/soybean intercropping have shown that the closer the intimacy between the component crops, the more nitrogen the legume fixed (Rweyemamu, 1990). Finlay (1975), Willey (1979), and Rweyemamu (1990) reported transfer of nitrogen from the legume to the non-legume such that the depletion of nitrogen by the cereal stimulated the legume to fix more nitrogen.

Effect of moisture stress on nitrogen fixation

Moisture stress affects the growth, physiological activities, and nitrogen fixation capacity of plants (Abd-Alla and Abdel Wahab, 1995; Becana et al., 1986). Leghemoglobin metabolism, respiration, and ATP production are reduced by moisture stress (Becana et al., 1986). Hooda (1986) inferred that the reduction in nitrogenase activity of moisture stressed chickpea may be due to the decline in sucrose translocation to the nodules. Reduced nitrogenase activity may also be a result of leghemoglobin degradation (Pate et al., 1984). Pate and Atkins emphasized that adequate water is necessary for the maintenance of turgidity in legume nodules and for the influx of fixed carbon and efflux of nitrogen. While it is now generally believed that moisture stress can cause nodules to dehisce and accelerate nodule senescence, it should be noted that nodule functions can be impaired even before stress symptoms are visible on the aboveground foliage (DeVries et al., 1989; Abd-Alla and Abdel Wahab, 1995). High soil temperatures

are thought to reduce the symbiotic performance of common bean more than that of cowpea and soybeans (Piha and Munns, 1987).

Nitrogenase activity following moisture stress

Summerfield et al. (1976) and Wien et al. (1979) showed that nitrogenase activity in cowpea was depressed by moisture stress. Pararajasingham and Knievel (1980) suggested that nitrogenase activity should recover rapidly to pre-stress levels upon watering in order to maximize dinitrogen fixation. The recovery ability of nitrogenase activity in cowpeas upon re-watering remains unclear. Summerfield (1976) observed that cowpea nitrogenase activity did not recover from drought stress coinciding with the pre-flowering stage, while Wien et al. (1979) reported that nitrogenase activity may be higher in cowpea undergoing moisture stress at the vegetative stage than in control plants.

Nitrogen utilization, partitioning, and remobilization

Nitrogen is the major limiting nutrient required for plant growth, especially in agricultural systems (Date, 1973). Legumes are often grown in polycultures, creating a farming system that promotes biodiversity. Cowpeas, Bambara groundnut and soybean usually fix adequate nitrogen and will normally not require N fertilizer (Kurtz, 1976). Peoples et al. (1983) reported that up to 40% of the pod's nitrogen represents nitrogen fixed after flowering. Common bean is considered to be an inefficient nitrogen fixer and often needs to be fertilized (Westermann et al., 1981). Inefficient nitrogen fixation in common bean is mostly

caused by the failure to establish efficient symbioses in the field. Common bean begins to fix nitrogen at a considerably later vegetative stage than other legumes, such that periods of nitrogen stress are observed in common bean before nodules begin to actively fix nitrogen. A starter dose of N is mainly applied to avoid the nitrogen stress potential periods (Sprent and Thomas 1984). Determinate, early maturing bush-type common bean fixes the least nitrogen, while indeterminate climbing genotypes fix more nitrogen (Graham, 1981; Rennie and Kemp, 1983). Generally early maturing varieties are inferior users of photosynthates for biological nitrogen fixation (Piha and Munns, 1987). However it has been suggested that some common bean varieties (most likely type III) can acquire enough nitrogen, either through fixation or assimilation of mineral nitrogen, for the plant to achieve genetic yield potential under field conditions (Westermann et al., 1981).

Deibert et al. (1979) estimated that soybeans obtain between 25 and 75% of their nitrogen from fixation. The wide variation in the estimated amount of nitrogen fixed by soybean is caused by factors such as the length of time that a cultivar actively conducts nitrogen fixation (Hardy, 1977).

Nitrogen partitioning and remobilization

Future improvements in yield may come, in part, from improvements in the partitioning and remobilization of assimilates into harvested components (Loomis et al., 1979). Remobilization may be defined as the net loss of nutrients from

living plant parts coincident with their accumulation elsewhere in the plant, mostly though not exclusively, in the reproductive parts (Loberg et al., 1984). The effect of water stress on nitrogen accumulation, partitioning and remobilization in different legumes is not well documented (DeVries et al., 1989). It is generally believed that moisture stress affects the total accumulation of nitrogen in many species, including cowpea, soybean, green gram, black gram, and lablab bean (Chapman and Muchow, 1985). Nevertheless, the relationship between the level or timing of water stress and the contribution of remobilized nitrogen to seed nitrogen in soybean was not always consistent. Egli et al. (1983) concluded that the quantity of remobilized nitrogen during the grain-fill stage is more related to the amount of nitrogen accumulated during the whole growing season than to the ability of the plants to fix nitrogen or to obtain mineral nitrogen during seed filling. Cure et al. (1985) showed a relatively more rapid decline in leaf nitrogen concentration when moisture stress was induced during the mid-seed-fill stage of soybean. In Nigeria, Wien et al. (1979) observed that water-stressed cowpea translocated more nitrogen to the pods than plants supplied with adequate moisture. Foster et al. (1995) reported that a greater proportion of seed nitrogen was obtained from remobilized leaf nitrogen under moderate moisture stress conditions in common bean, but that a severe moisture stress impaired N remobilization. They suggested that nitrogen remobilization helps to maintain yield stability during conditions of moderate moisture stress, but not under severe

or prolonged moisture stress. Severe moisture deficits reduced N harvest index and N use efficiency. Foster et al. (1995) concluded that drought susceptible common bean genotypes utilized nitrogen less efficiently than resistant genotypes. Peoples et al. (1983) showed that 60% of the nitrogen fixed before flowering is remobilized in cowpea. Selemat and Gardner (1985) inferred that nitrogen was remobilized from leaves to pods during periods of nitrogen stress in non-nodulating peanut cultivars *(Arachis hypogaea)*, but no remobilization occurred in the nodulated plants. Likewise DeVries et al. (1989) and Egli et al. (1983) showed that moisture stress had no effect on nitrogen concentration of leaves and stems of peanuts.

Zapata et. al (1987) reported that soybean pods and seeds contained up to 73% of the total nitrogen in the plant while they made up less than one third of the total dry matter. Seventy-one to 91% of total N was in the seed of common bean grown under moderate moisture deficits (Foster et al., 1995). Vegetative and reproductive growth occur simultaneously during flowering and fruit set in indeterminate soybean. During seed-fill stage, the seeds are the main sink and are the recipients of remobilized N (Zeiher et al., 1982). Yield components such as number of fruit and seeds are determined during flowering and fruit set, hence the portion of carbon and nitrogen partitioned to reproductive growth at that stage have direct influence on fruit set, seed number, and yield (Egli et al., 1985). Greer and Anderson (1965) suggested that competition between vegetative and

reproductive growth during flower set reduced fruit set. Loberg et al. (1984) suggested that determinate cultivars have less competition during the reproductive stage which results in higher yield.

Soybean remobilized more nitrogen to the seed than pigeon pea and peanut (Chapman and Muchow, 1985). Zeiher et al. (1982) estimated that contribution of remobilized nitrogen towards seed nitrogen at maturity ranged from 20 to 100% in soybean. Soybean leaf senescence and abscission have been termed as self-destructive (Sinclair and DeWit (1976)). DeVries et al. (1989) showed that peanut and pigeon pea retained a fair amount of leaves with moderate concentration of nitrogen up to harvest maturity. In fact, water stressed peanut leaves were slow to abscise and remained as a nitrogen source when the stress was relieved.

Total nitrogen in pigeon pea stems increased throughout the entire season, while the nitrogen in chickpea and soybean stems decreased during the reproductive stages (DeVries et al., 1989). Hooda et al (1986) observed that the nitrogen content of shoots and dry weight in chickpea did not decrease during seed fill, while the underground plant material showed only a small decrease in dry weight. They inferred that seed dry matter may be derived from current photosynthesis.

Moisture stress in Zimbabwe

In Zimbabwe, mid-season droughts (intermittent drought) occur in an unpredictable fashion. These droughts often coincide with reproduction and reduce yield. To optimize the stability of harvest, farmers practice `phased planting.' With phased planting, farmers distribute the planting of their crops over a long period, preferring to spread the risk instead of maximizing the yields. This technique is wide-spread in Zimbabwe even though there are substantial losses due to late planting. When mid-season drought occurs, the legumes are at various phenological stages of development so farmers are assured of some yield. The late planted crop often matures when the rains have tailed off and suffer from terminal drought. Since these legumes are minor crops and rank behind major crops such as maize, sorghum and groundnut, they are usually planted after the more important crops. Therefore, the growth period with adequate water is even shorter for legumes. Farmers need early maturing legume varieties.

Most of the soils in the communal areas and small scale commercial farms in Zimbabwe are coarse-grained sands derived from granite. They are generally deficient in available N, phosphorus, sulfur and organic matter. Consequently, they have poor physical structure and low water holding capacity (Mashiringwani, 1983; Mataruka, 1985). Continuous maize farming has further depleted the soil's fertility. Often farmers cannot afford to buy fertilizers to replenish the soil. Furthermore, management factors are aggravated by discriminatory land policies

that concentrate the population on marginal land (Whitlow, 1988). Most cultivated legumes have the ability to fix N under different conditions, but efficiency in N fixation differs (Piha and Munns, 1987). Differences occur even within species. Nitrogen-fixing legumes are potentially important for Zimbabwe's inherently low fertile soils and for the N needs of the subsequent non-leguminous crops that are grown in rotation.

High yielding germplasm of legumes have been selected under non-stress conditions and for high yielding areas; however, their performance under drought conditions generally has not been evaluated. Determination of the N fixation capacity of these legumes under drought stress conditions is essential. Drought tolerant germplasm is essential for enhanced yield under communal area and small scale farming conditions.

With maize and soybean, recommendations have been made for varieties that can be grown in the different natural regions of Zimbabwe. This has not been done for Bambara groundnut, common bean or cowpea. There is a great need for research that will enable the development of varietal recommendations for Bambara groundnut, common bean and cowpea for the natural regions.

Origin and History of Bambara groundnut

Bambara groundnut is of African origin but its exact center of origin is debatable. Marcgrav De Liebstad's report of 1648 is the oldest known literature where Bambara groundnut is recorded. It was then called 'Mandubi d'Angola'

implying that it originated in Africa (Begemann, 1988). In 1763, Linnaeus classified the crop as *Glycine subterranea.* Du Petut-Thours (1806) found Bambara groundnut in Madagascar and Mauritius where it was called 'Voandzou.' He coined the term *Voadzeia subterranea.* The name '*Voandzou'* is from a local name 'Voanjo.' 'Voa' means seed and 'anjo' means that which satisfies well (Rassel, 1960). *Vigna subterranea* is now the scientific name for Bambara groundnut. The word Bambara is the name of an ethnic group in West Africa and hence the word is capitalized. Bambara groundnut is grown in West, East and Southern Africa in countries such as Mali, Burkina Faso, Ghana, Togo, Benin, Chad, Cameroon, Tanzania, Malawi, Zambia, Zimbabwe, Madagascar, South Africa, Zaire, Ivory Coast, Sudan, Ethiopia, Kenya, Uganda, Mozambique, and Angola. It was introduced to Brazil, the Philippines and Indonesia in the seventeenth century. The crop is now also grown in Australia and in many countries in Asia and Latin America (Begemann, 1988).

Nutritional Value

Bambara groundnut is a very balanced food crop with regard to human nutritional needs. The dried seeds have 54.5 to 69.3% carbohydrates, 17 to 24.6% protein, 5.3 to 7.8% fat, and supply 367 to 414 Kcal per 100 g. The protein quality of Bambara groundnut is rich in lysine and methionine, but deficient in isoleucine. The biological value of Bambara groundnut is 56%. It has a digestibility value of 82.6% (Chomchalow, 1993) and is a good complementary

diet to cereal. Bambara groundnut is served in a variety of ways in different countries. In Zimbabwe, the fresh beans are boiled or served as a soup. Fresh beans are sweet and very tasty. In Nigeria, they are served as stem balls of flour rolled in leaves of 'akara,' balls of flour rolled up in oil, or as Bambara groundnut pancakes.

Bambara groundnut ranks high for adaptability and for the ability to tolerate harsh environmental conditions. It has demonstrated survivability in challenging arid environments although its yields have always been unpredictable (Anonymous, 1979). As a result myths and taboos have been associated with the crop in some ethnic groups. The crop's unpredictability has also been reported by researchers. Begemann (1988), working in Zambia, suggested that Bambara groundnut is a short-day plant. Linnemann et al. (1995), working in the Netherlands, concluded that Bambara groundnut genotypes originating from 'higher' latitudes (10-15^{0}N) are early maturing and show a weak response to photoperiod while genotypes from 'lower' latitudes (5-10^{0}N) are late maturing and show relatively more photosensitive response. The crop grows well in poor sandy soils that are marginal for other crops (Anonymous, 1979; IITA, 1988). According to some researchers, the crop 'prefers' poor soils. In nitrogen rich soils, the crop tends to produce too many leaves at the expense of pods and seeds (Anonymous, 1979; Chomchalow, 1993). The optimum daytime temperature for the crop is 20-28^{0}C. The optimum amount of precipitation for the crop is between 900 mm and

1200 mm, but the crop can grow in the precipitation range from 500 mm to 4100 mm. Bambara groundnut can generally withstand water logging except during fruiting and harvesting stages and can tolerate a pH as low as 4.3 (Anonymous, 1979).

Problems associated with Bambara groundnut production

Bambara groundnut yields are generally low. Yields range from 150 - 6000 kg/ha of shelled seed, depending on location (Chomchalow, 1993). Low yields reflect low-densities because farmers mainly intercrop Bambara groundnut with other crop plants (Anonymous, 1979). Late earthing, poor earthing practices such as incomplete covering of developing pods and damage to developing pods, and poor weeding are other problems often encountered in Bambara groundnut production. Earthing is the process of building up the soil around the base of the plant so the developing pods are not exposed to light.

Bambara groundnut is repeatedly described as disease and pest resistant (Chomchalow, 1993). It has also been argued that the reason it does not seem to be attacked by pests may be because it has been grown only in isolated fields and intercropped with non-related crops. It can be inferred from this theory that Bambara groundnut farmers ensured that the crop did not become susceptible to pests by having multiple crops in isolated fields. This is a sound example of Bambara groundnut farmers having practiced what the rest of the world now realizes as aspects of sustainable cropping system. Bambara groundnut has the

potential to become a stable, low cost and profitable food crop, but the crop needs to be promoted because many people even, in tropical Africa, are unaware of it (IITA, 1988). The negative aspects such as low yield can be addressed through research (Anonymous, 1979).

Status of Bambara groundnut production in Zimbabwe

Bambara groundnut is one of the most neglected legumes in terms of research and development in Zimbabwe. In the past, it has been considered a traditional crop. It is generally thought to be one of the most drought tolerant of all legumes grown in Zimbabwe. Zimbabwe is divided into five natural ecological regions based on the elevation above sea level, temperature and the amount of rainfall. Natural regions one and two have the highest rainfall, the highest elevation, and the lowest temperature. Natural regions III and IV are generally semi-intense farming regions. Bambara groundnut grows well on the poor and sandy soils, which predominant in natural regions III-IV. Bambara groundnut is suitable for several cropping systems and crop rotations (Chomchalow, 1993).

Cowpea

Cowpea originated in West Africa and was taken to India by the Sabaen trade route (Smartt and Hymowitz, 1985). In India, the cowpea produced two new distinct forms, 'cylindrica,' an erect growing forage type and 'sesquipedalis,' a long podded type (Smartt and Hymowitz, 1985). Cowpea was probably introduced into the United States about the 1700 by the Spanish or Portuguese (Blackhurst

and Miller, 1980; Smartt and Hymowitz, 1985).

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CHAPTER 1

MOISTURE STRESS EFFECTS ON YIELD AND YIELD COMPONENTS OF BAMBARA GROUNDNUT, COMMON BEAN, AND COWPEA

ABSTRACT

Legumes are often grown in semi-arid regions under agriculturally challenging conditions. The objectives of the study were (i) to compare the effects of moisture stress on yield and performance of Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), and cowpea (*Vigna unguiculata)* in the field and (ii) to assess the use of a greenhouse screening procedure as an indication of drought tolerance. The field study included three common bean lines (Carioca, Natal Sugar, and T3147), two cowpea lines (IT82D-889 and 475/89), three Bambara groundnut treatments (inoculated and uninoculated ZVS 530 and inoculated ZVS 546), and a non-nodulating isoline of the soybean (*Glycine max*) Harasoy grown under stress and non-stress moisture conditions in a rainshelter in MI in 1995 and 1996. For the greenhouse screening, common bean, cowpea, and Bambara groundnut were planted in 1.5 m square boxes at Michigan State University on June 18 and August 20, 1996. The boxes had a depth of 12 or 20 cm and were lined with plastic and filled with a 1:1 mixture of sand:soil. Moisture stress reduced the number of pods per plant in

cowpea and soybean, but not in common bean. Cowpea was more drought tolerant than common bean, although common bean produced a higher yield than cowpea. STI was a better predictor of yield performance than DSI. Species and genotypes differed in yield, seed weight, pod and seed number, and the effect of moisture deficit on each yield component.

INTRODUCTION

Herbaceous legumes have wide adaptability, are grown worldwide, and are of great economic importance (Adams and Pipoly III, 1980). Their high protein content and amino acid composition make them excellent complements for cereal diets, which are high in starch. Legumes are often grown in dry locations where agriculturally challenging conditions exist (Elston and Bunting, 1980). The extent to which moisture stress reduces yield depends on species, the phenological stage of development when moisture stress occurs, the degree of yield component compensation, and the severity and duration of the moisture stress (Korte et al., 1983).

Bambara groundnut (*Vigna subterranea*) is grown by farmers in Africa, Asia, South America and Australia, although it is a relatively unknown legume (Anonymous 1979; Chomchalow, 1993). Bambara groundnut is believed to be one of the most drought tolerant legumes, to be very disease and pest resistant, and to thrive on poor soils. It is often grown under conditions that are marginal for other crops.

Terminal moisture stress reduces yield components such as the number of pods per plant, number of seeds per pod, and individual seed weight (Kadhem et al., 1985). Water limitation can hasten or delay phenological development of plants, depending on the severity of the limitation (Rosenthal et al, 1987). In soybean, moisture stress has been reported to decrease the duration of reproductive

development, the length of the seed-filling period (Korte et al., 1985), and consequently yield. Chickpea is also known to mature early under conditions of limited water (Khanna-Chopra and Sinha, 1987). Turk et al. (1980) and Lawn (1982) observed that the reproductive activity of cowpea may be hastened or delayed depending on the time and intensity of the moisture deficit. Gwathmey and Hall (1992) concluded that the sensitive stages can thus escape the mid-season drought. The reproductive stage is reported to be the most sensitive stage to moisture stress in most legumes. In soybean, moisture stress reduced the effective seed filling period, but did not reduce seed growth rate (Meckel et al., 1984). Differences between seed yield in stressed and non-stressed plants, even in the same variety, tend to vary markedly from year to year, depending on the phenological stage at which moisture stress occurs (Huck et al., 1986).

There is a need to develop rapid, reliable, and relatively inexpensive methods to screen for drought tolerant lines in legumes. Yield is often used as a parameter to evaluate drought tolerance. However, yield trials are costly to run and results may be highly variable (Lynch, 1995). Other methods such as osmotic adjustment, observations of plant physiological responses, and genes have been suggested as possible screening tools, but these methods have not always produced consistent and reliable results.

The objectives of the study were (i) to compare the effect of moisture stress on yield and performance of Bambara groundnut, common bean, and cowpea in

the field and (ii) to assess the use of a greenhouse screening procedure as an indication of drought tolerance.

MATERIALS AND METHODS

Field Study

Two cowpea genotypes (IT82D-889 and 475/89), two Bambara groundnut genotypes (ZVS 530 and ZVS 564), three common bean genotypes (Carioca, T3147-2, and Natal Sugar), and a non-nodulating soybean (Harosoy) (*Glycine max*) were planted on a Spinks sandy soil (Psammentic Hapludalfs, sandy, mixed, mesic) in a rainshelter at the Kellogg Biological Station in Hickory Corners, Michigan in 1995 and 1996. The experimental design was a modified split-plot in a randomized complete block with two moisture treatments (stressed and non-stressed) as the main plots, genotype as the sub-plot and four replications. The four row plots were each 2 m long and 0.5 m wide with intra-row spacings of 8, 15 and 25 cm for common bean, Bambara groundnut and cowpea, respectively. The genotype T 3147-2 was obtained from the breeding program of Dr. James Kelly in the Department of Crop and Soil Sciences at Michigan State University in East Lansing, MI and the non-nodulating Harosoy from Dr. J. E. Harper at USDA-ARS in Urbana, IL. All other species and cultivars were obtained from the Department of Research and Specialist Services in Zimbabwe. Neutron probe access tubes were installed vertically to a depth of 1 m between the two center

rows of each plot prior to planting. Forty kg of N per hectare was broadcast using 19-19-19 fertilizer. Common bean was inoculated with a granular form of *Rhizobium phaseoli*, cowpea with *Rhizobium* cowpea miscellany nitrogen EL, and Bambara groundnut with *Voandzeia* Special 1. The cowpea and Bambara groundnut inoculum were obtained from Nitragin ™ Inoculants and were manufactured by Liphatech, Inc. In 1995, three applications of fungicide (Benlate for anthracnose and Sevin for Japanese beetles) at 1.12 kg ha^{-1} were made at two-week intervals beginning on July 14. In 1996, two applications of Benlate were used. Terminal moisture stress was initiated on all the legumes when common bean reached the R1 stage of development (Singh, 1982) on July 29 in 1995 and July 21 in 1996.

Separate Analysis of Bambara Groundnut

The yield and yield component data for Bambara groundnut treatments were analyzed separately from the rest of the treatments. None of the Bambara groundnut genotypes reached maturity under the Michigan climatic conditions. All of the Bambara groundnut treatments were at approximately the same stage of maturity at harvest time, hence, it was decided to compare the Bambara groundnut treatments only to each other.

Greenhouse Study to Assess Drought Tolerance

Common bean, cowpea, and Bambara groundnut were planted in wooden boxes, an adaptation of a procedure by Singh et al. (1995) in the greenhouse at

Michigan State University at East Lansing, MI on June 18 and August 20, 1996. The square boxes were 1.5 m in length with a depth of either 12 cm or 20 cm. The boxes were lined with plastic and filled with a 1:1 mixture of sand:soil. The experiment was a split-plot in a randomized block design with box depth as main plot and genotype as sub-plot. Cowpea (IT82D-889 and 475/89), Bambara groundnut (ZVS 530 and ZVS 564), and common bean (Carioca, Natal Sugar and T3147-2) genotypes were grown in rows 7 cm apart with an intra-row spacing of 5 cm. All genotypes were planted to a depth of 2 cm at 2 plants per station. They were later thinned to one plant per station. All species were watered until the partial appearance of the first trifoliate leaf in common bean. Percent wilting on a daily basis and the number of days it took for the plants to die in each row was recorded.

RESULTS AND DISCUSSION

Yield

The Zimbabwean genotype Natal Sugar did not reach maturity in 1995; hence it was not included in the 1996 study. The yield for common bean and cowpea ranged from 237 to 1437 kg ha^{-1} (Figures 1 and 2), with higher yields in 1995 than in 1996. Under adequate soil moisture conditions, the common bean genotypes had the highest yields with T3147-2 having yields as high as 1437 kg ha^{-1} in 1995 (Figure 1). The cowpea genotype 475/89 had a significantly higher

Figure 1. Yield of common bean (*Phaseolus vulgaris*), soybean (*Glycine max*), and cowpea (*Vigna unguiculata*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Research Station, MI. 1995.

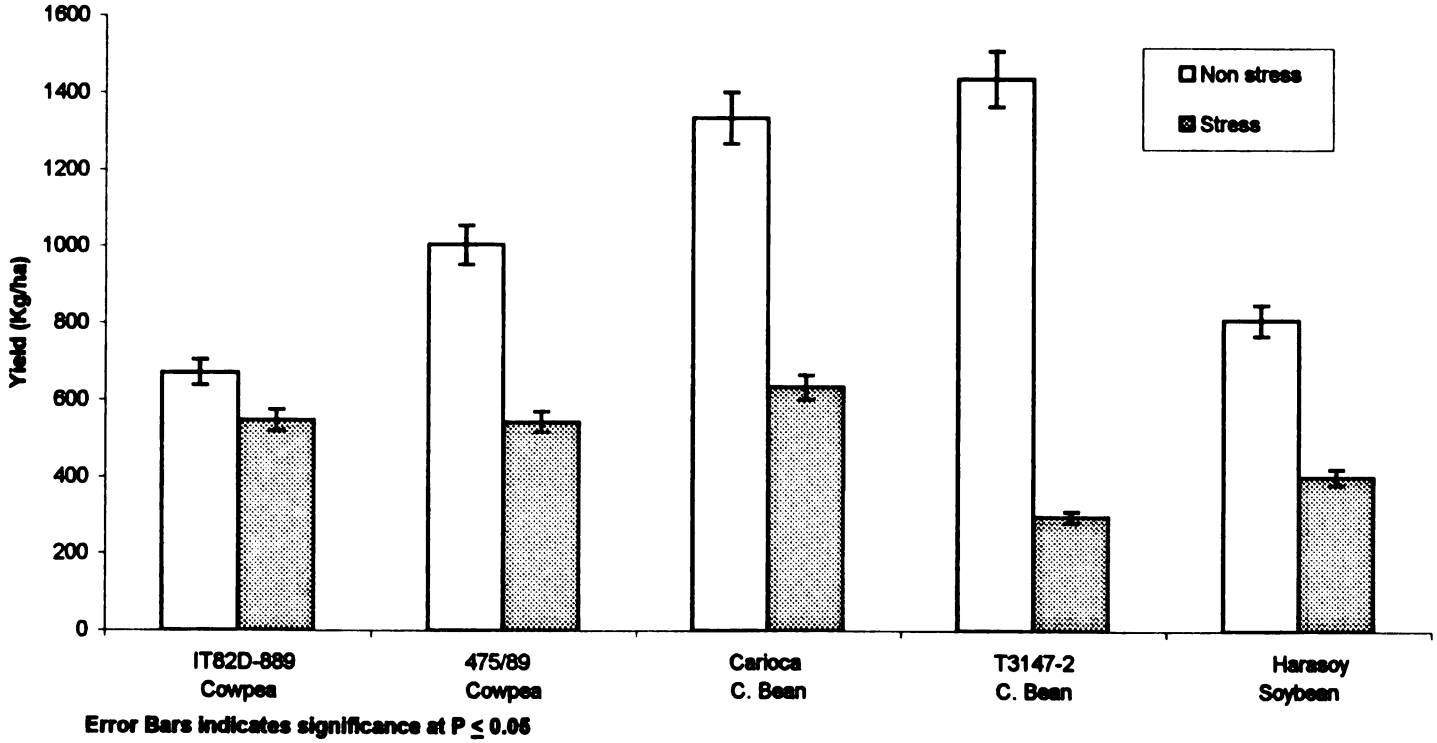
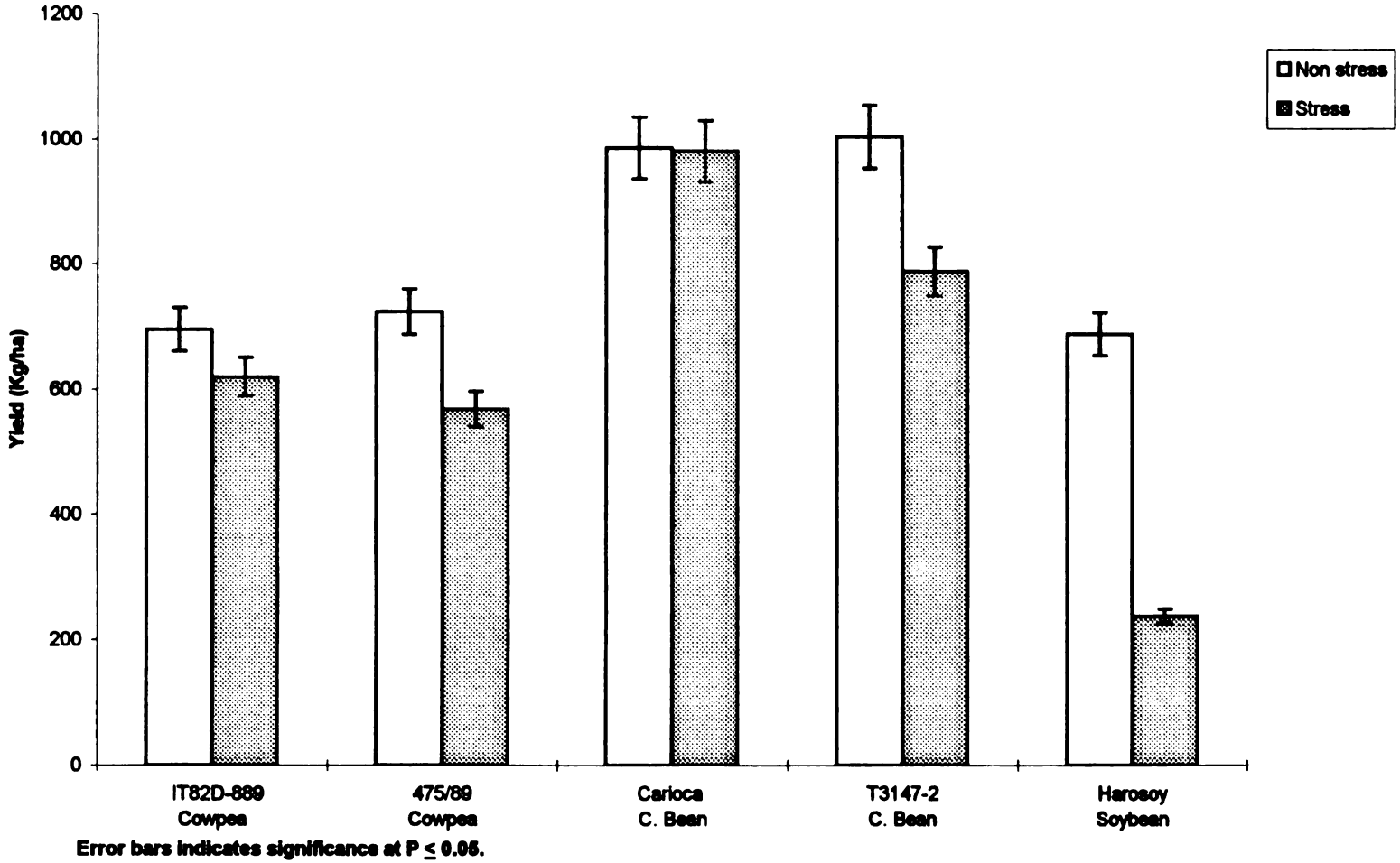


Figure 2. Yield of common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Station, MI. 1996.



yield than the cowpea IT82D-889 in 1995 but not in 1996, mainly due to reduced yield of 475/89 in 1996. Moisture stress reduced the yield of common bean, cowpea and soybean in both years (Figures 1 and 2), with the exception of Carioca in 1996. Yield reductions due to stress in 1995 were generally higher than in 1996 for all species except soybean (Tables 1 and 2), and the common bean cultivars had a higher yield reduction than the cowpea. The greater yield reduction in 1995 may be explained by the moderate (0.54) drought intensity in 1995 and the mild (0.22) drought intensity in 1996. Thus, the moisture stress was greater in 1995 than in 1996. The cultivar T3147-2 had the highest yield reduction in 1995 and one of the highest in 1996 (Figures 1 and 2). The cowpea genotype IT82D-889 had the lowest yield with adequate soil moisture; however, it had the least yield reduction due to moisture stress in 1995 and the second lowest in 1996 (Figures 1 and 2).

Drought Susceptibility Index (DSI), Stress Tolerance Index (STI), and Geometric Mean (GM)

The cowpea genotype IT82D-889 had a DSI of 0.97 and 0.50 in 1995 and 1996, respectively (Tables 1 and 2). T3147-2 had the highest DSI of all genotypes and species in 1995 and was higher than the other common bean (Carioca) in 1996. Carioca had the highest STI in 1995 and 1996. The DSI is reported to estimate drought tolerance. A DSI value of one is reported to equal average resistance (Fischer and Maurer, 1978). Values lower than one represent

Table 1. Arithmetic mean, percent yield reduction, geometric mean, drought susceptibility index (DSI), and stress tolerance index (STI) of two cowpea and two common bean genotypes grown under stress and non-stress soil moisture conditions at the Kellogg Biological Station in Hickory Corners, MI in 1995.

Genotype	Species	Arithmetic Mean	%Yield Reduction	Geometric mean	DSI	STI
		Kg ha^{-1}		Kg ha^{-1}		
IT82D-889	Cowpea (*Vigna unguiculata*)	608	18	604	0.97	0.33
475/89	Cowpea (*Vigna unguiculata*)	772	46	737	0.85	0.49
Carioca	C. Bean (*Phaseolus vulgaris*)	984	53	919	0.98	0.77
T3174-2	C. Bean (*Phaseolus vulgaris*)	868	79	652	1.47	0.39
Harosoy	Soybean (*Glycine max*)	605	51	570	0.94	0.29

Table 2. Arithmetic mean, percent yield reduction, geometric mean, drought susceptibility index (DSI), and stress tolerance index (STI) of two cowpea and two common bean genotypes grown under stress and non-stress soil moisture conditions at the Kellogg Biological Station in Hickory Corners, MI in 1996.

Genotype	Species	Arithmetic Mean	%Yield Reduction	Geometric Mean	DSI	STI
		Kg ha^{-1}		Kg ha^{-1}		
IT82D-889	Cowpea (*Vigna unguiculata*)	657	11	656	0.50	0.64
475/89	Cowpea (*Vigna unguiculata*)	645	22	640	0.98	0.61
Carioca	C. Bean (*Phaseolus vulgaris*)	984	0	983	0.02	1.44
T3147-2	C. Bean (*Phaseolus vulgaris*)	896	22	889	0.98	1.18
Harosoy	Soybean (*Glycine max*)	463	66	404	2.98	0.24

greater than average resistance, and values greater than one indicate susceptibility. The stress tolerance index (STI) has been developed as an alternative to DSI. STI is reported to measure both stress tolerance and yield potential. With STI, the higher the value, the greater the stress tolerance and the higher the yield potential. In 1995, both DSI and STI would have selected 475/89 as the more drought tolerant cowpea. In 1996, DSI would have selected IT82D-889 and the STI would have indicated that there was no difference between the two with regard to tolerance and yield potential. The greater yield of 475/89 in 1995 and the lack of differences in yield between the two cowpeas in 1996 indicate that 475/89 would have been the more desirable genotype. Thus STI was a more accurate indicator of cowpea field performance than was DSI. Both DSI and STI would have selected Carioca as a more drought tolerant line than T3147-2 in both years and this agrees with the field performance, although T3147 has exhibited drought tolerance in other studies (Schneider et al., 1997; Yabba, 1997).

Geometric mean is an indicator of yield potential (Schneider et al. 1997; Yabba, 1997). The larger the GM, the greater the yield potential. In both years, Carioca had the highest GM of all species and genotypes (Tables 1 and 2). Ozone damage and sun scald were observed on common bean, soybean, and cowpea during 1996, and the summer of 1996 was generally colder than the summer of 1995. This reduced the rate of maturity in common bean and cowpea and undoubtedly contributed to the lower yields in 1996 in comparison to 1995.

Yield components of common bean, cowpea, and soybean

A significant difference was observed in seed weight per 100 seeds among the species in both years (Figures 3 and 4). In both years, T3147-2 had a higher seed weight than Carioca, Harosoy and the two cowpea genotypes and Carioca had the second highest. In 1996, moisture stress only reduced seed weight of the non-nodulating Harosoy, but moisture stress reduced the seed weight of T3147-2 and Harosoy in 1995 (Figures 3 and 4). Singh (1995) observed that water stress reduced seed weight of common bean; however, Acosta-Gallegos and Shibata (1989) saw no significant differences in seed weight between water stressed and non-stressed common bean plants. Flores-Lui (1982) concluded that yield components are only reduced when stress is imposed during pod filling, the type of stress imposed in this study. There were highly significant differences in the number of seeds per pod among the different species (Figures 5 and 6), with cowpea having up to 14 seeds per pod and Harosoy as few as 2 (Figures 5 and 6). Moisture stress did not reduce the number of seeds per pod in either year (data not shown). The cowpea 475/89 produced more seeds per pod than IT82D-889 and the common bean Carioca produced more seeds per pod than T3147-2. A significant species difference was observed in the number of pods per plant. In 1996, the non-nodulating Harosoy had the highest number of pods per plant (Figure 7), followed by the cowpea IT82D-89. Moisture stress did not reduce pod number in Carioca or T3147-2, but it did in IT82D-889, 475/89, and Harosoy

Figure 3. Seed weight per 100 seeds of common bean (*Phaselous vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Research Station, MI. 1995.

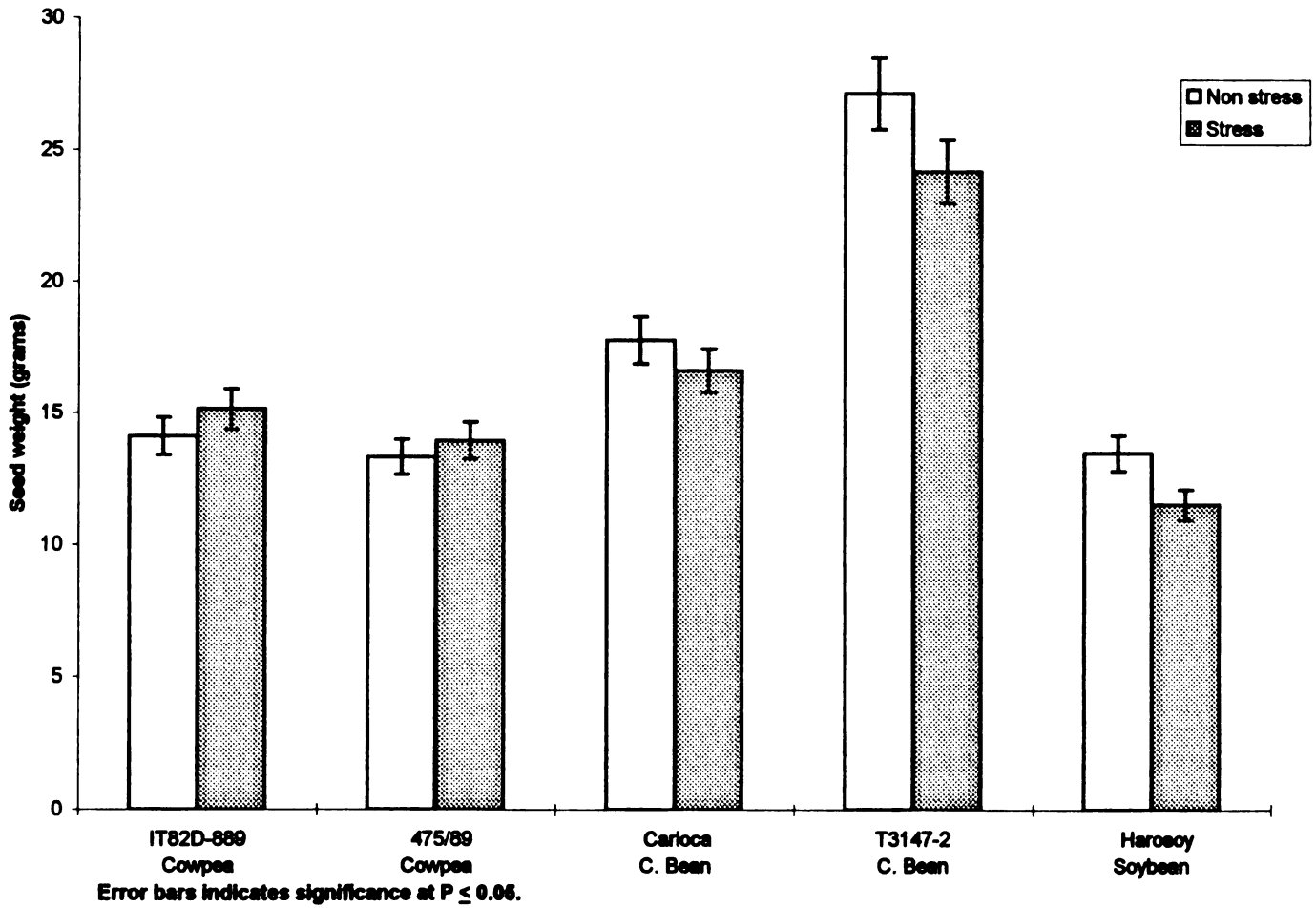
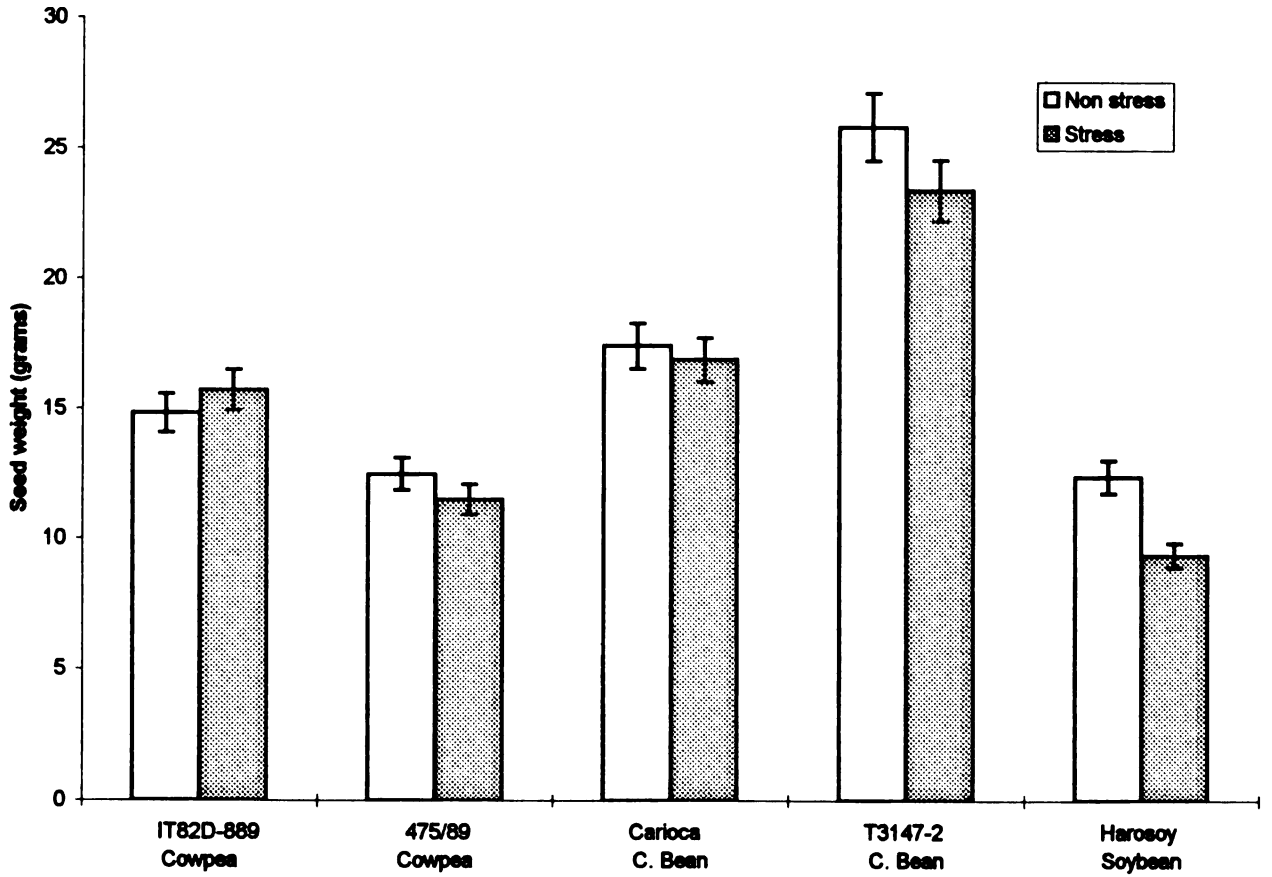
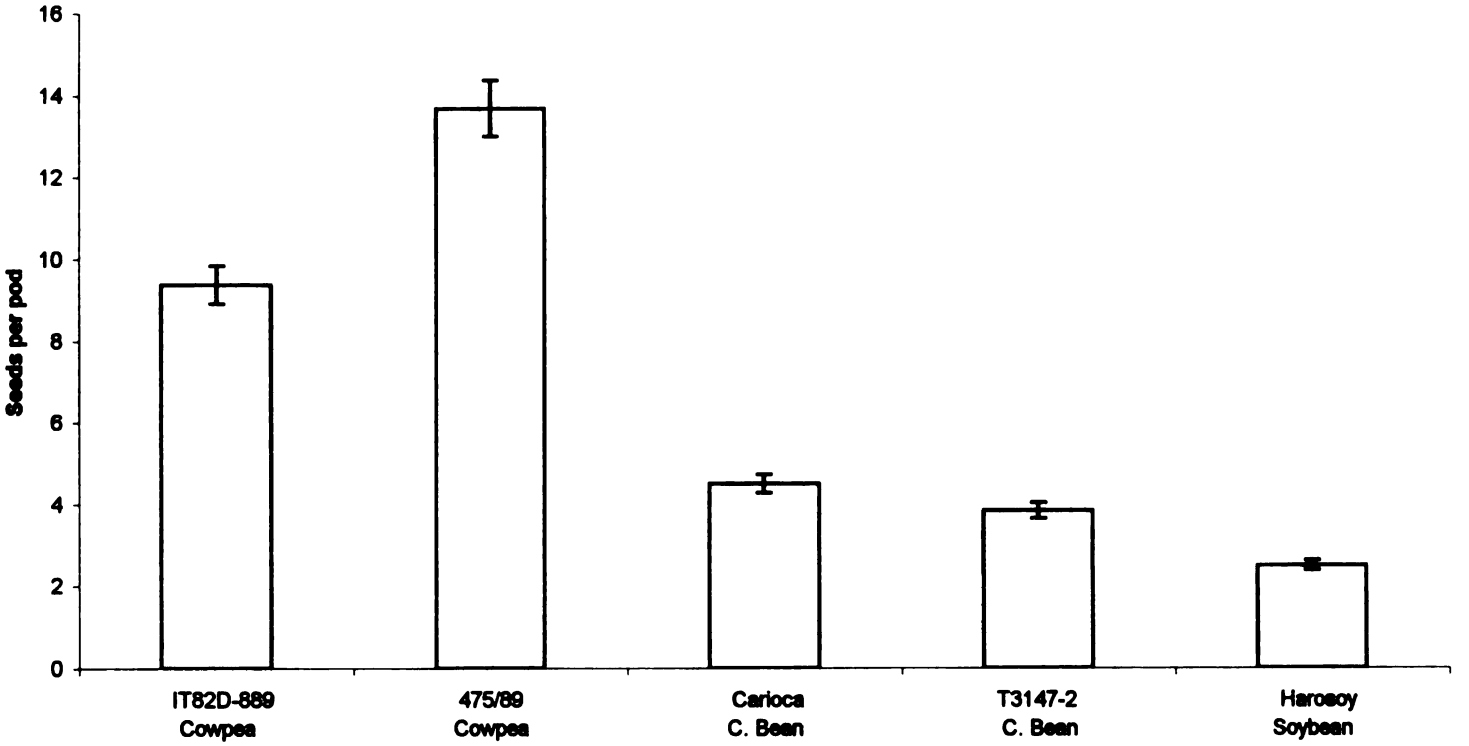


Figure 4. Seed weight per 100 seeds of common bean (*Phaselous vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Research Station, MI. 1996.



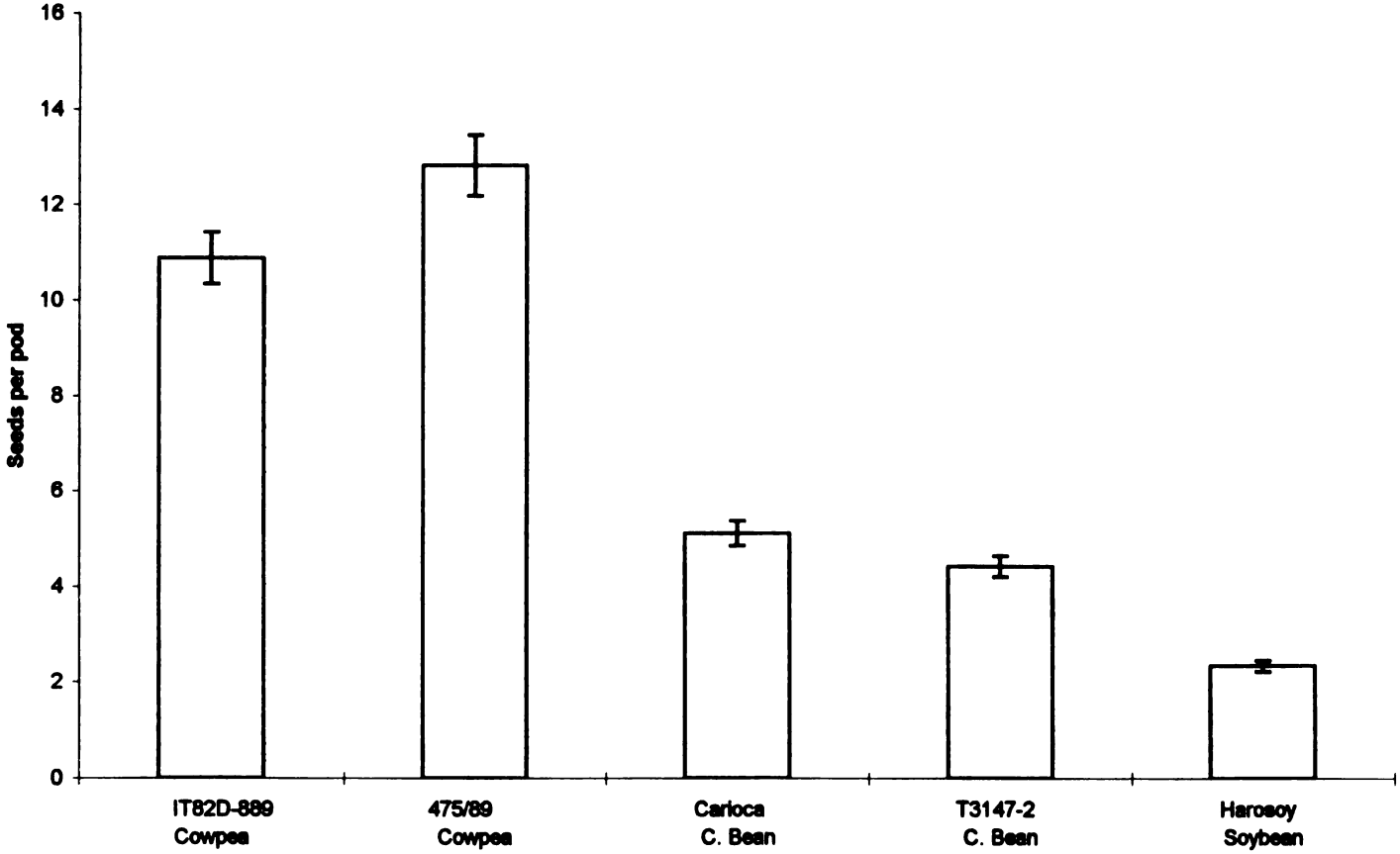
Error bars indicates significance at $P \leq 0.05$.

Figure 5. Seeds per pod of common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown in a rainshelter at the Kellogg Biological Station, MI. 1995. Data are combined for non-stress and stress soil moisture conditions.



Error bars indicates significance at $P \leq 0.05$.

Figure 6. Seeds per pod of common bean *Phaseolus vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological station in Hickory Corners, MI. 1996.



(Figure 7). The number of pods per plant was not determined in 1995. Acosta-Gallegos and Shibata (1989) concluded that the number of pods per plant is the yield component most reduced by moisture stress, however their finding may have been under a more severe stress than the one experienced in 1996.

Generally, cowpea aborted the most seeds under both stress and non-stress moisture conditions (Figures 8 and 9). This probably relates to the fact that cowpeas produced the greatest number of seeds per pod. The common bean genotype Carioca aborted the least number of seeds in 1995 (Figure 8). The soybean Harosoy and the common bean T3147-2 aborted the same number of seeds (Figures 8 and 9), although more seeds were aborted in 1995 than in 1996 in all species (Figures 8 and 9). Moisture stress did not increase the number of seeds aborted in 1995 or 1996 (data not shown). Similarly, Acosta-Gallegos and Shibata (1989) observed no differences between control plants and stressed plants in number of aborted seeds or in number of under-developed ovules and concluded that strong intra-ovary competition occurs under both stress and non-stress conditions. This may be a result of a small source relative to the sink during seed fill or inefficient remobilization.

Highly significant differences among species were observed in the shelling percentage in both years (Figures 10 and 11). Under adequate moisture conditions, T3147-2 had a significantly higher shelling percentage than non-nodulating Harosoy (soybean) and both cowpeas in 1996 (Figure 11). In 1995 and

Figure 7. Number of pods per plant of common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Research Station, MI. 1996.

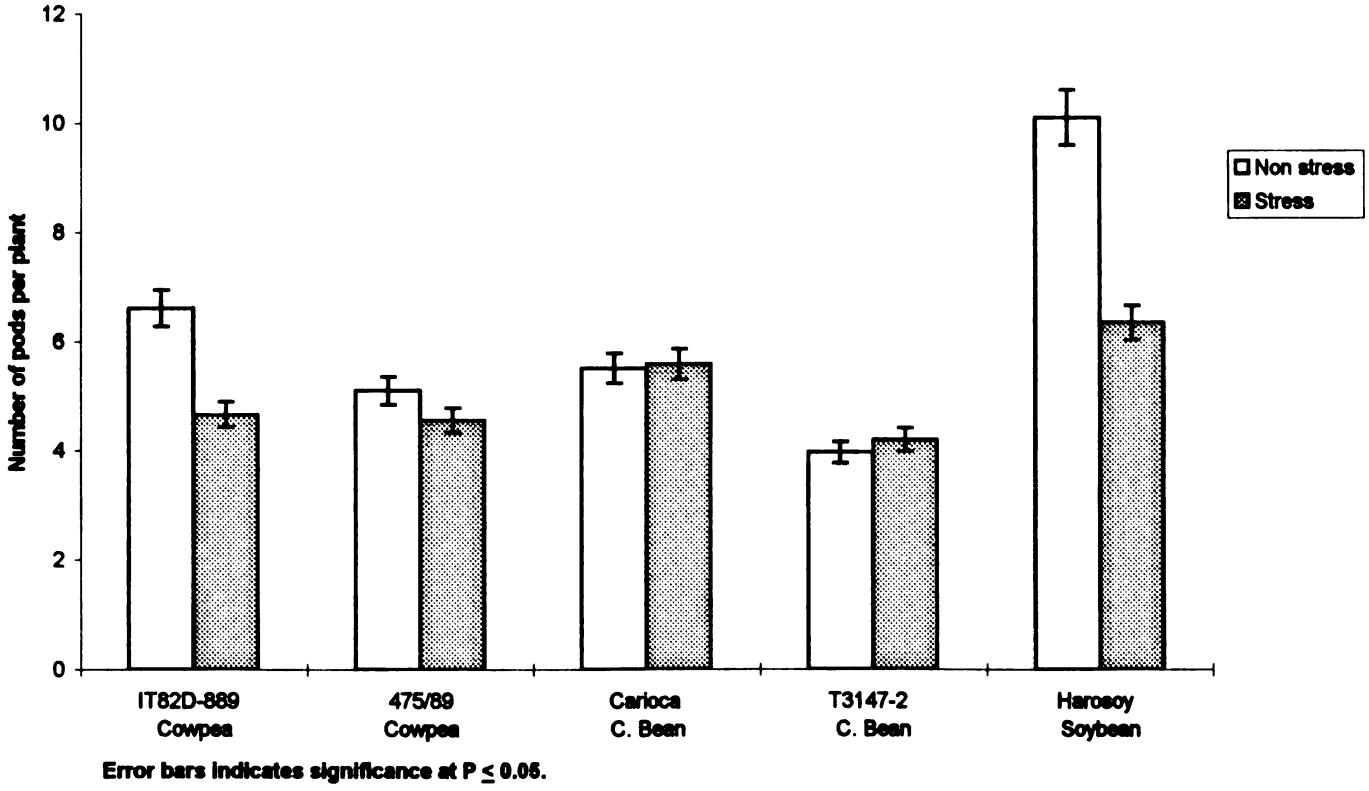
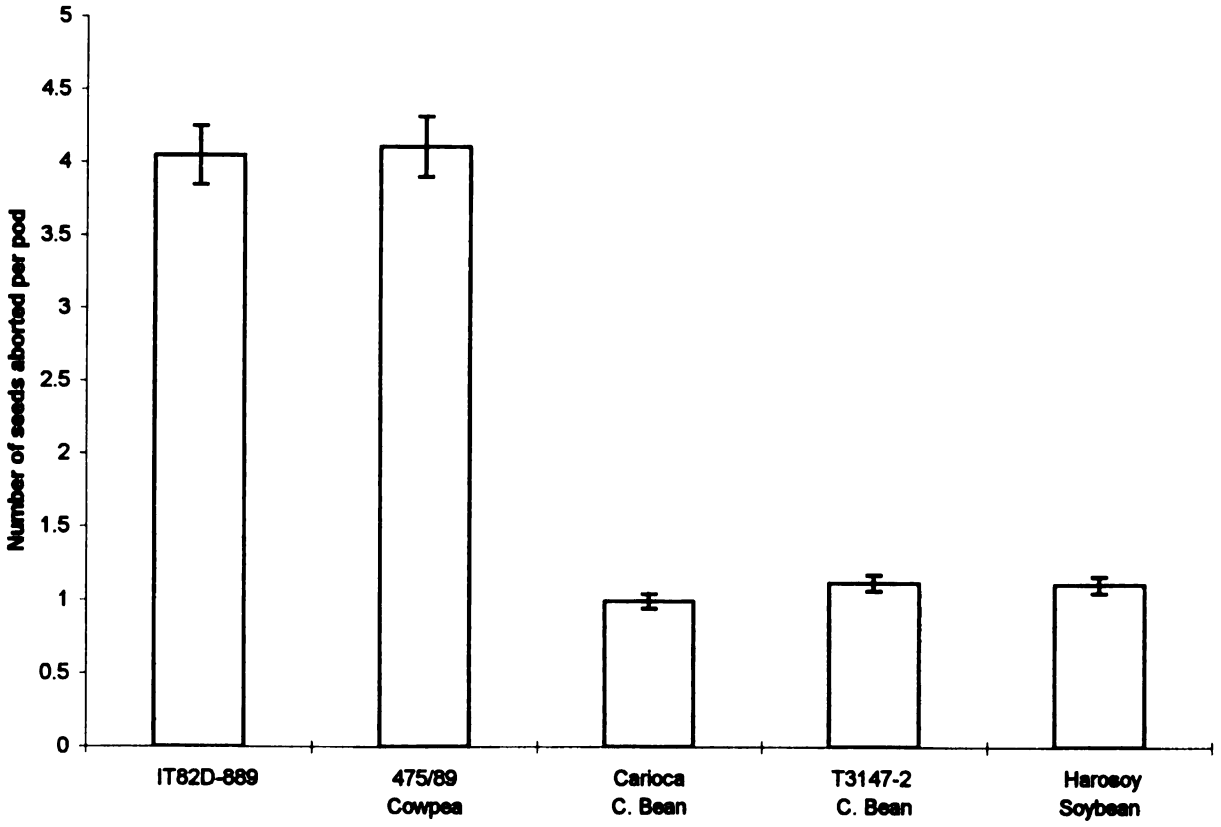
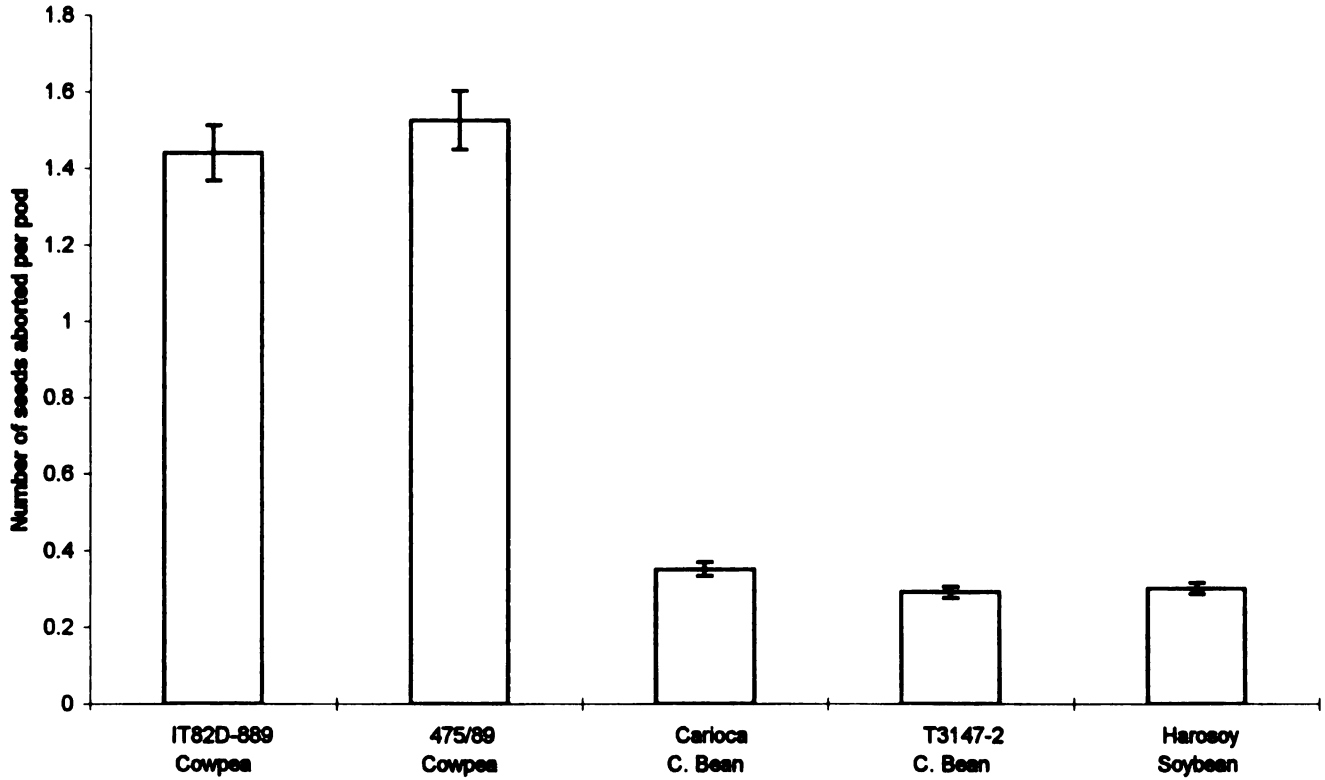


Figure 8. Number of seeds aborted per pod in common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and soybean (*Glycine max*) grown in a rainshelter at the Kellogg Biological Research Station, MI. 1995. Non-stress and stress data combined.



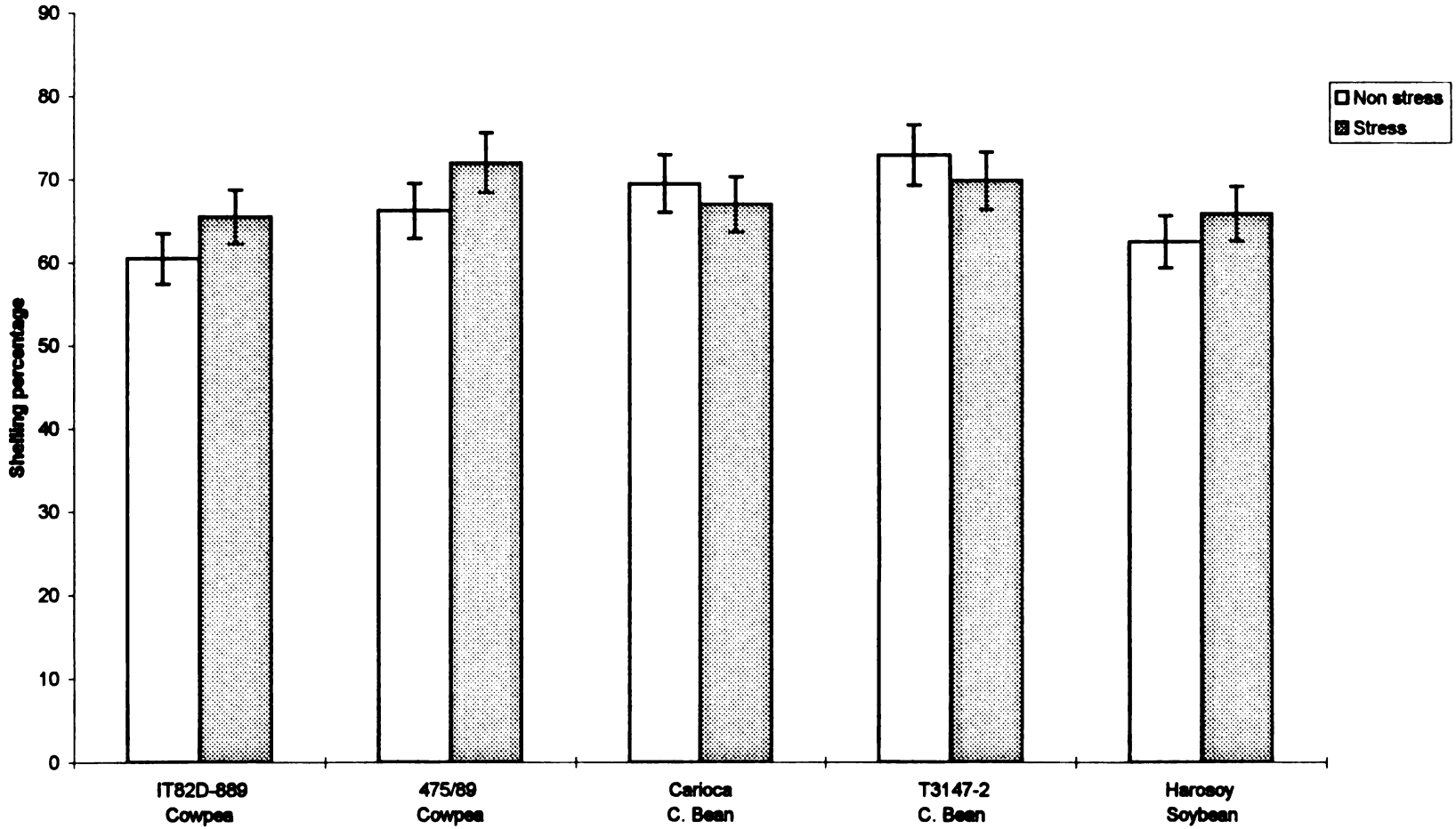
Error bars indicates significance at $P \leq 0.05$.

Figure 9. Number of seeds aborted per pod in common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Station, MI. 1996.



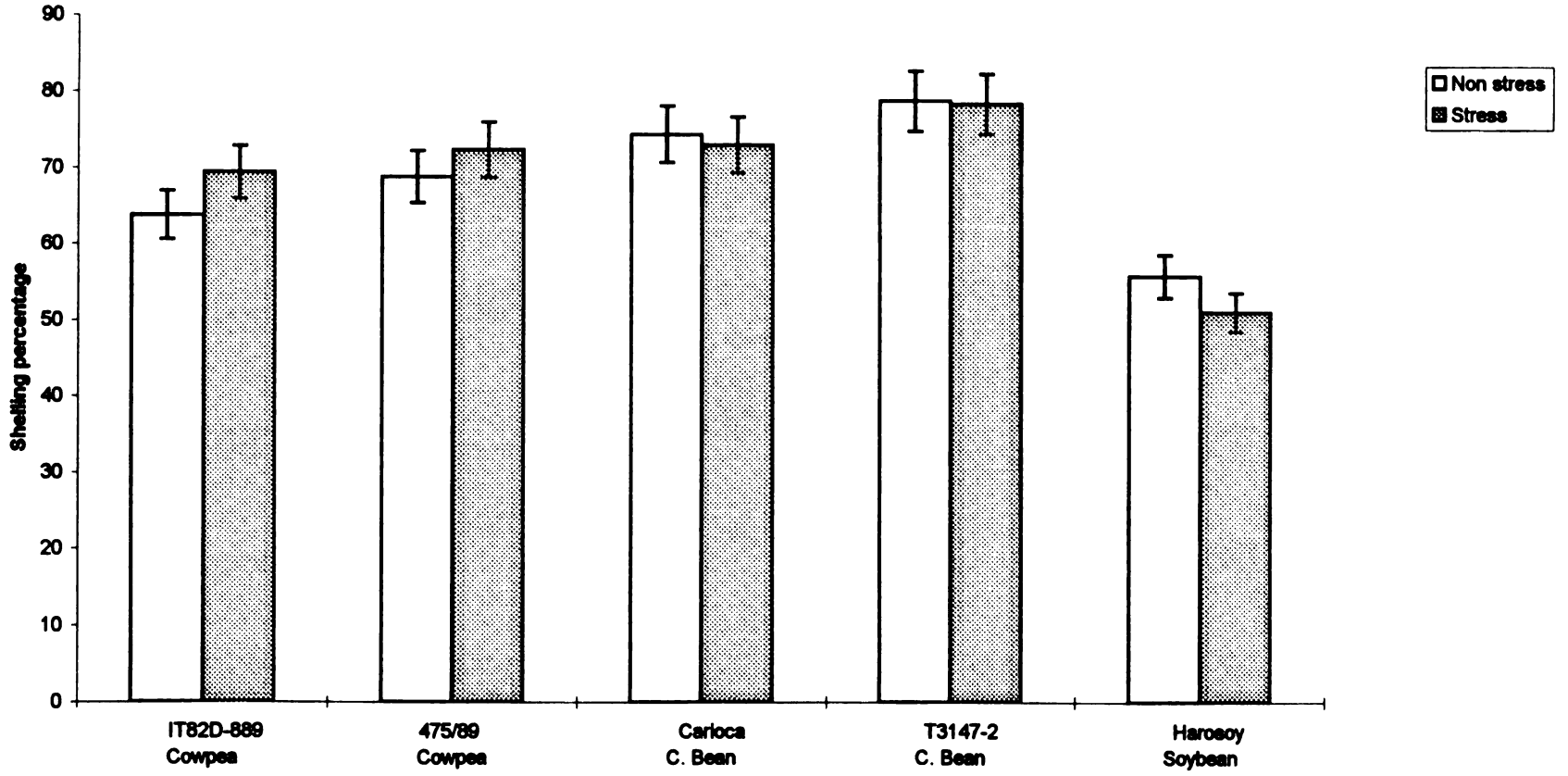
Error bars indicates significance at $P \leq 0.05$.

Figure 10. Shelling percentage of common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Station, MI. 1995.



Error bars indicates significance at $P \leq 0.05$.

Figure 11. Shelling percentage of common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*) and soybean (*Glycine max*) grown under non-stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Station, MI. 1996.



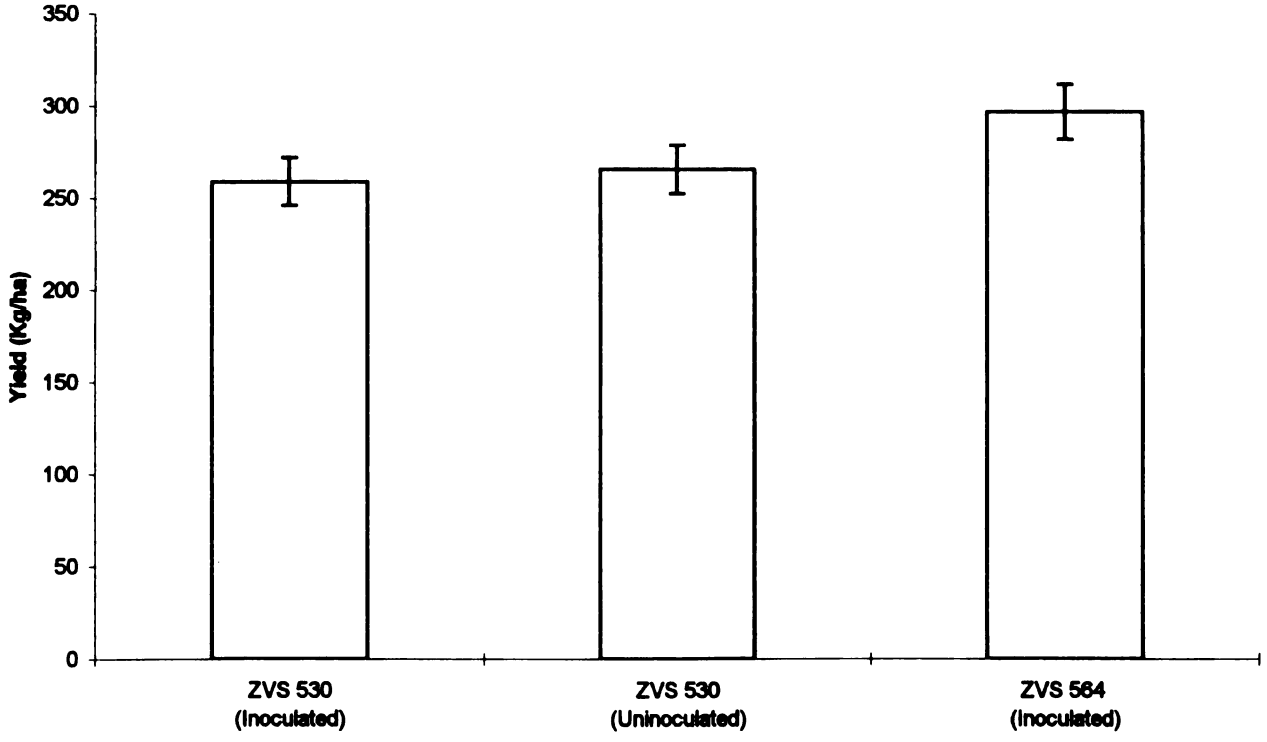
Error bars indicates significance at $P \leq 0.05$.

1996, the cowpeas 475/89 and IT82D-889 tended to have a higher shelling percentage under stress conditions than under non-stress conditions, while the reverse was true for common bean in 1995. The soybean had a significantly lower shelling percentage than all the other species under both stress and non-stress conditions in 1996 (Figure 11).

Bambara Groundnut

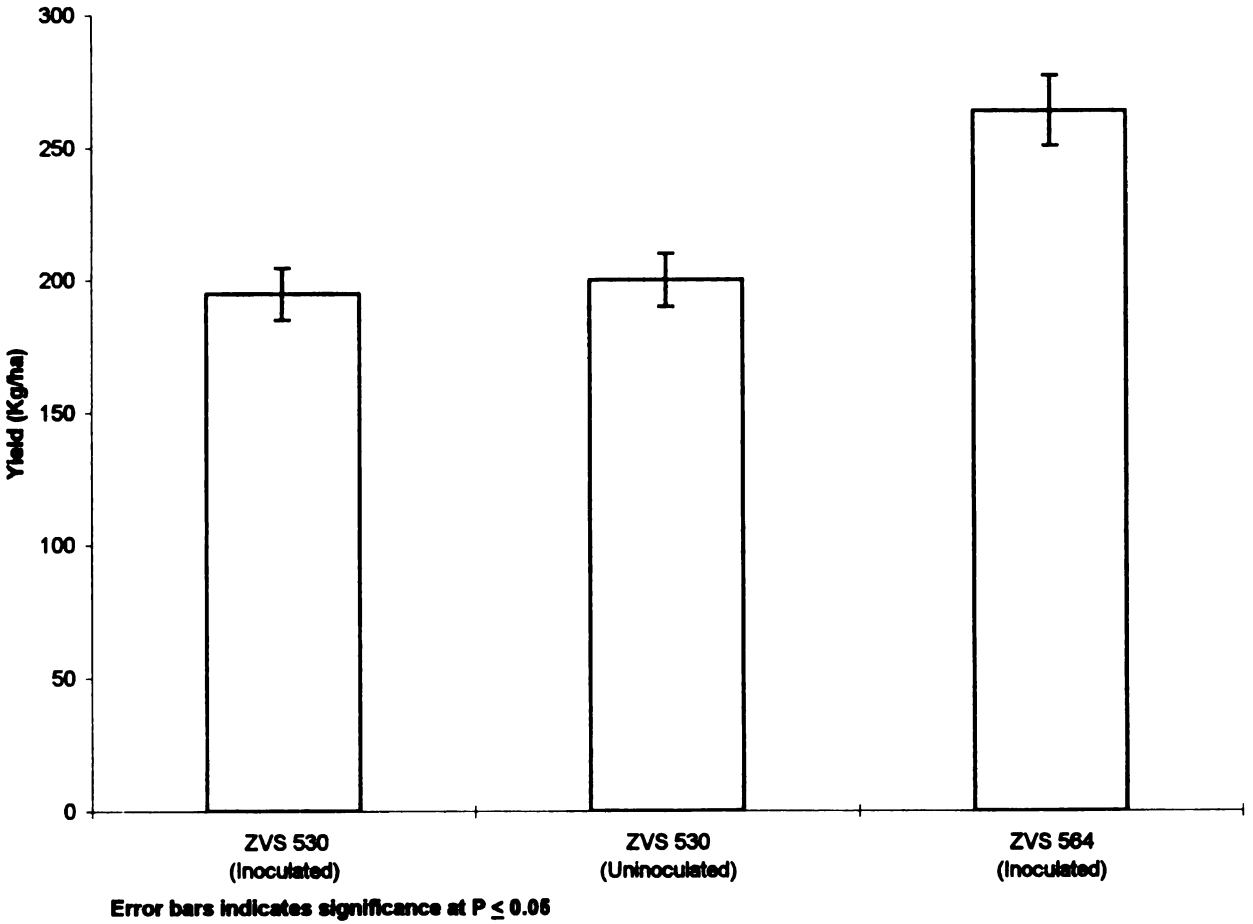
Bambara groundnut flowered well, but tended to stay in the flowering stage for a relatively long time. Less than half the plants produced pods in both years and frost came before they had completed the seed fill stage. Consequently, yields were low (Figures 12 and 13), less than 300 kg/ha each year. Moisture stress did not affect Bambara groundnut and there were no visible signs of wilting (data not shown). The genotype ZVS 564 had the highest yield in both years (Figures 12 and 13), while the inoculated and non-inoculated Bambara groundnut showed no yield differences in either year (Figures 12 and 13). All legumes were fertilized at a rate of 40 kg N ha^{-1}, the recommended rate for common bean. This level of fertility was probably excessive for Bambara groundnut and may have helped produce lower yields as indicated by previous researchers (Anonymous, 1979; Chomchalow, 1993). It is highly possible that Bambara groundnut yield was inhibited by the Michigan photoperiod. Day length is almost 16 hours in July and August in Michigan, and Bambara groundnut is normally grown in regions of the world that have much shorter photoperiods than Michigan (Heller et al., 1997).

Figure 12. Yield of Bambara groundnut (*Vigna subterranea*) grown in a rainshelter at the Kellogg Biological Research Station, MI. 1995. Data are combined for non-stress and stress soil moisture conditions.



Error bars indicate significance at $P \leq 0.05$

Figure 13. Yield of Bambara groundnut (*Vigna subterranea*) grown at the Kellogg Biological Research Station, MI. 1996. Data are combined for non-stress and stress soil moisture conditions.



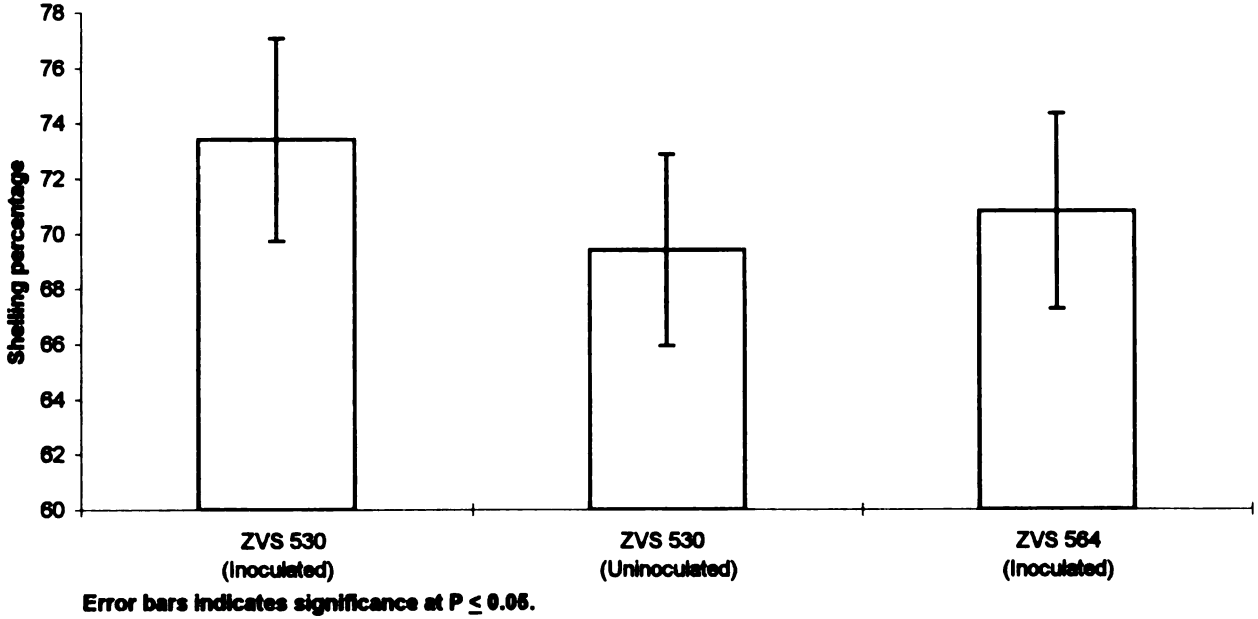
Improper photoperiod is known to reduce Bambara groundnut yield (Begemann 1988). Bambara groundnut yields have been reported to range from 150 to 6000 kg ha^{-1} (Chomchalow, 1993). Earthing is crucial in Bambara groundnut (Nleya Unpublished data) In 1995, all the treatments were not earthed and all earthing occurred beyond the optimum time. In both years, weed pressure was higher than desirable and could have reduced yield. Bambara groundnut is a small plant and cannot compete with weeds as effectively as other legumes like cowpea, soybean and common bean. No herbicides were used because there was uncertainty about which herbicides were safe to use with Bambara groundnut. Consequently, all weeding was done by hand.

Bambara groundnut treatments did not differ in shelling percentage (Figures 14 and 15). In 1995 the un-inoculated Bambara groundnut genotype ZVS530 had the highest seed weight of the Bambara groundnut treatments (Figure 16), while ZVS 564 had the highest in 1996 (Figure 17). In both years, Bambara groundnut had very low seed weight, suggesting the growing season was not long enough. The original seeds from Zimbabwe had 100 seed weight of 148.7g, while these data show a 100 seed weight of less than 30 g.

Greenhouse Study

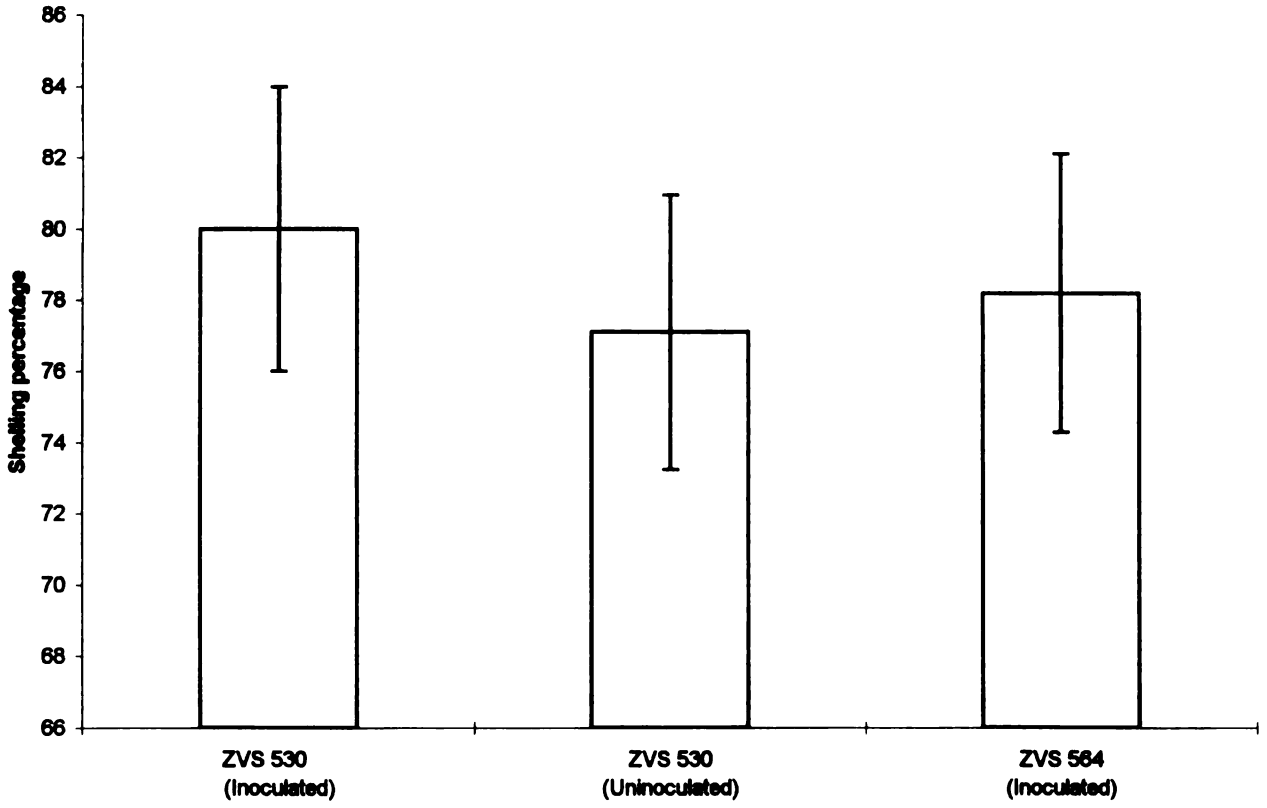
The greenhouse temperatures in July when watering was terminated for the first experiment were generally much higher than in September when watering was terminated for the second experiment. As a result all cultivars survived for a

Figure 14. Shelling percentage of Bambara groundnut (*Vigna subterranea*) grown in a rainshelter at the Kellogg Biological Station, Mi 1995. Data are combined for non-stress and stress soil moisture conditions.



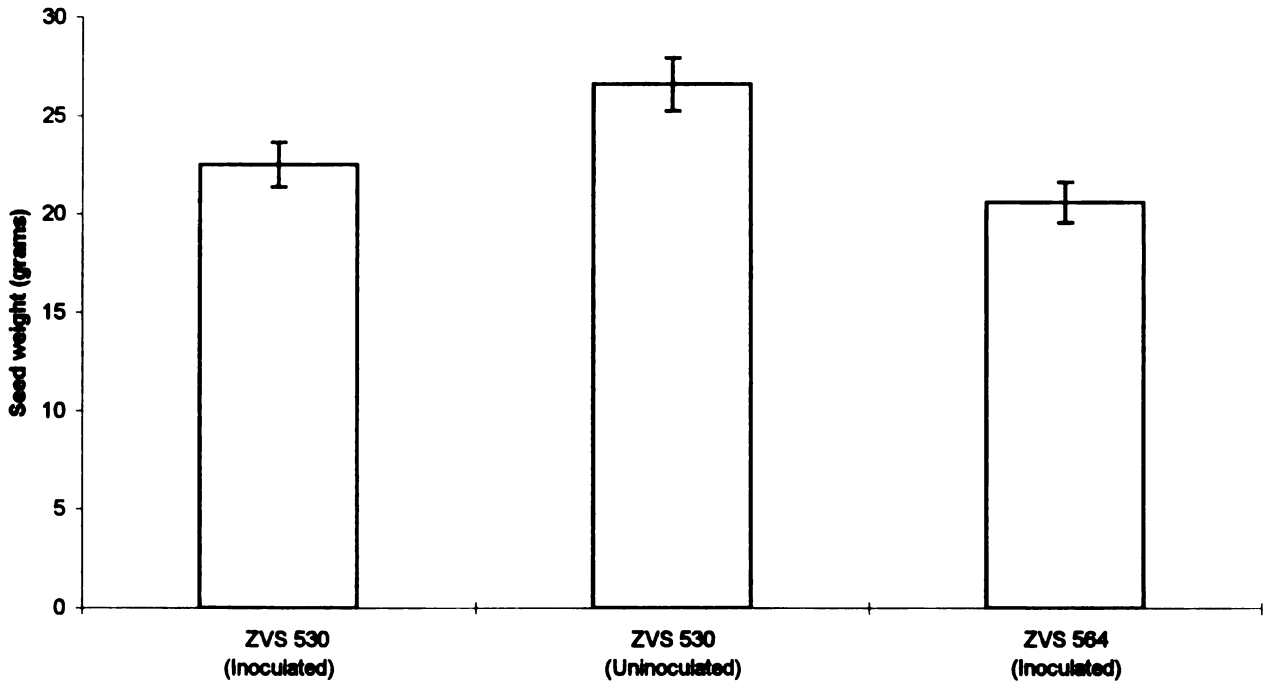
Error bars indicates significance at $P \leq 0.05$.

Figure 15. Shelling percentage of Bambara groundnut (*Vigna subterranea*) grown in a rainshelter at the Kellogg Biological Research Station, MI. 1996. Data shown combined non-stress and stress soil moisture conditions.



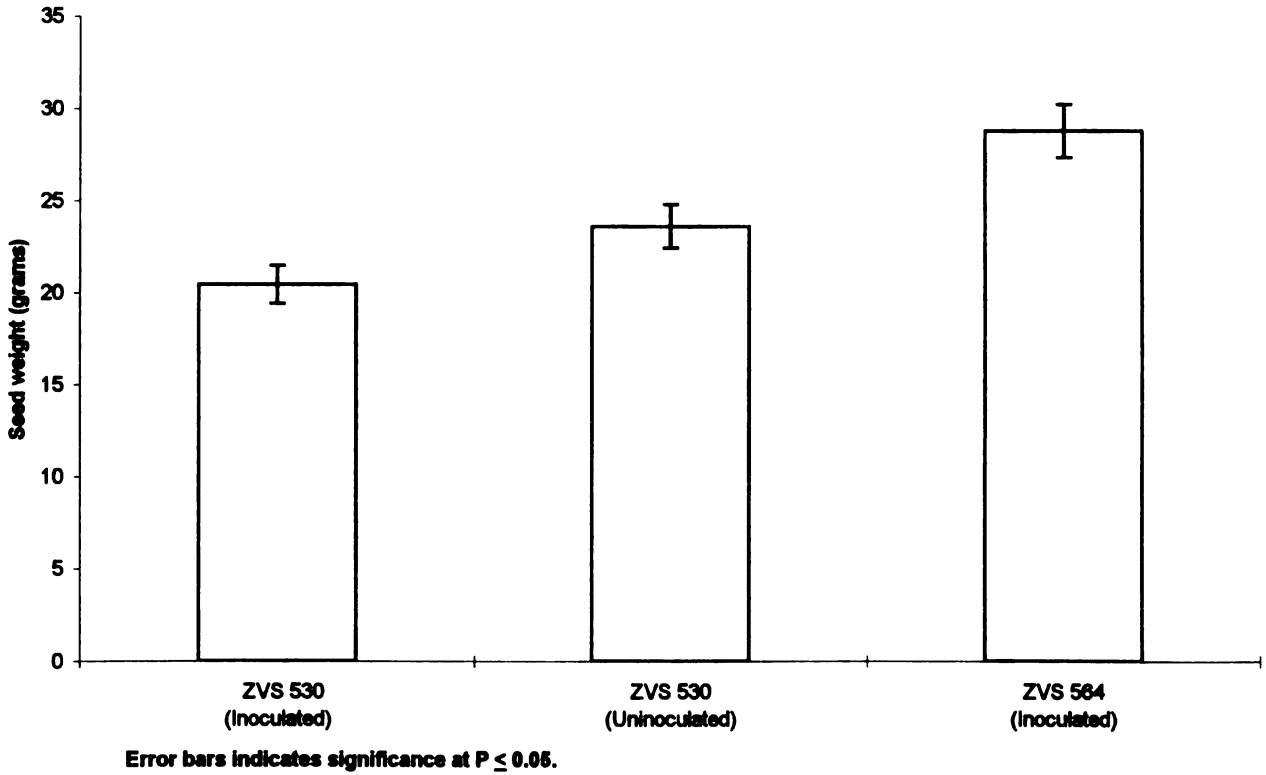
Error bars indicates significance at $P \leq 0.05$.

Figure 16. Seed weight per 100 seeds of Bambara groundnut (*Vigna subterranea*) grown in a rainshelter at the Kellogg Biological Research Station, MI. 1995. Data are combined for non-stress and stress soil moisture conditions.



Error bars indicate significance at $P \leq 0.05$.

Figure 17. Seed weight per 100 seeds of Bambara groundnut (*Vigna subterranea*) grown in a rainshelter at the Kellogg Biological Research Station, MI. 1996. Data are combined for non-stress and stress soil moisture conditions.



Error bars indicates significance at $P \leq 0.05$.

longer length of time after watering was terminated in September, since moisture stress under low temperature is less devastating to the plants than moisture stress under high temperatures (Tables 3 and 4). In both experiments, common bean cultivars were the most susceptible to moisture stress (Tables 3 and 4). The cowpea cultivars were the most tolerant to moisture stress in the June planting, but cowpea and Bambara groundnut did not differ in the August planting. In the June planting, cowpea had terminal green leaves well after the common bean and Bambara groundnut were dead. The cowpea cultivars showed a tendency to shed lower leaves once water was stopped. This agrees with the field data which showed that cowpea cultivars had the least yield reductions under moisture stress conditions. In the June planting, the box depth affected the time it took the plants to die (Table 3), undoubtedly due to the greater soil moisture reserves in the box with the 20 cm depth and the higher temperatures that plants were exposed to during the summer months. Plants dried out more rapidly in the 12-cm than 20-cm box.

CONCLUSIONS

Moisture stress reduced the number of pods per plant in cowpea and soybean, but not in common bean. Moisture stress reduced seed weight of T 3147. It reduced the number of seeds per pod in cowpea in 1996. Cowpea was more drought tolerant than common bean, although common bean produced a higher

Table 3. Potential drought tolerance screening method measuring days to permanent wilting for Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), and cowpea (*Vigna unguiculata*) grown in a 1:1 sand:soil media in growth boxes (1.5 x 1.5 x 12 and 1.5 x 1.5 x 20 cm) in a greenhouse, at the Michigan State University from June 18, 1996 to July 26, 1996.

Genus and species	Genotype	Days to permanent wilting	
		Box depth	Box depth
		12 cm	20 cm
Bambara groundnut (*Vigna subterranea*)	ZVS 530	12 c*	12 c
Bambara groundnut (*Vigna subterranea*)	ZVS 564	15 b	15 b
C. Bean (*Phaseolus vulgaris*)	Carioca	12 c	14 b
C. Bean (*Phaseolus vulgaris*)	Natal Sugar	12 c	14 b
C. Bean (*Phaseolus vulgaris*)	T 3147-2	12 c	14 b
Cowpea (*Vigna unguiculata*)	475/89	20 a	20 a
Cowpea (*Vigna unguiculata*)	ITD-889	21 a	21 a
Coefficient of variation		48	48

*Letters indicate significant difference at $P \leq 0.05$.

Table 4. Potential drought tolerance screening method measuring days to permanent wilting for Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), and cowpea (*Vigna unguiculata*) grown in a 1:1 sand:soil media in growth boxes (1.5 x 1.5 x 12 and 1.5 x 1.5 x 20 cm) in a greenhouse, at the Michigan State University from August 20, 1996 to October 26, 1996.

Genus and species	Genotype	Days to Permanent Wilting
		Combined Box Depth
Bambara groundnut (*Vigna subterranea*)	ZVS 530	34 ab*
Bambara groundnut (*Vigna subterranea*)	ZVS 564	35 a
C. Bean (*Phaseolus vulgaris*)	Carioca	24 cd
C. Bean (*Phaseolus vulgaris*)	Natal Sugar	20 d
C. Bean (*Phaseolus vulgaris*)	T 3147-2	28 bc
Cowpea (*Vigna unguiculata*)	475/89	38 a
Cowpea (*Vigna unguiculata*)	IT82D-889	40 a
Coefficient of variation		16

*Letters indicate significant difference at $P \leq 0.05$

yield than cowpea. STI was a better predictor of yield performance than DSI. Natal sugar did not mature in Michigan, but T3147 produced a smaller number of pods than Carioca and had a higher yield reduction under stress. The cowpea genotype 475/89 produced a higher yield and greater number of seeds per pod than IT82D-889. Cowpea produced more seeds per pod than bean or Bambara groundnut and had the highest percentage of seed abortion under both stress and non-stress conditions. Unfortunately, field performance of Bambara groundnut could not be compared to the other three species. Results of both the 12- and 20-cm box depths indicated that cowpea was more drought tolerant than Bambara groundnut and that Bambara groundnut was more drought tolerant than common bean

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CHAPTER 2

EFFECT OF MOISTURE STRESS ON NITROGEN PARTITIONING AND REMOBILIZATION IN BAMBARA GROUNDNUT, COWPEA, AND COMMON BEAN

ABSTRACT

Improvements in N partitioning and remobilization may lead to yield increases. This study was undertaken to study the effects of moisture stress on nitrogen partitioning in Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and a non-nodulating isoline of the soybean (*Glycine max*) Harosoy. The study included three common bean lines (Carioca, Natal Sugar and T 3147), two cowpea lines (IT82D-889 and 475/89), three Bambara groundnut treatments (inoculated and uninoculated ZVS 530 and inoculated ZVS 564), and Harosoy grown under stress and non-stress moisture conditions in a rainshelter at the Kellogg Biological Station in Hickory Corners, MI in 1995 and 1996. Cowpea contained the highest leaf- and stem-N concentration at all stages of development and had the highest reproductive-N concentration at flowering and podfill, with the exception of Bambara groundnut at podfill. Soybean remobilized more N from the leaves than common bean and common bean remobilized more than cowpea and Bambara groundnut. There was

a tendency for moisture stress to increase N concentration in common bean. Leaf-N concentration was lower in 1996 than in 1995 in all species and at all growth stages.

INTRODUCTION

Future improvements in yield may come from improvements in N partitioning and remobilization of assimilates into harvested components (Loomis et al., 1979). Remobilization may be defined as the movement of nutrients from living plant parts to other parts, mostly though not exclusively, to the reproductive parts (Loberg et al., 1984). Different legume species have different abilities to remobilize nutrients during the reproductive stages. Zeiher et al. (1982) estimated that remobilized nitrogen contributes 20 to 100% of total nitrogen at maturity in soybean.

Moisture stress affected the total accumulation of nitrogen in cowpea, soybean, and lablab bean (Chapman and Muchow, 1985). Cure et al. (1985) showed a relatively rapid decline in leaf nitrogen concentration when moisture stress was induced during the mid seed-fill stage of soybean. In Nigeria, Wien et al. (1979) observed that water-stressed cowpea translocated more nitrogen to the pods than plants supplied with adequate moisture. Foster et al. (1995) observed that a greater proportion of seed nitrogen was obtained from remobilized nitrogen under moderate moisture stress conditions in common bean, but less N remobilization occurred under severe moisture stress. They suggested that nitrogen remobilization might aid yield stability during conditions of moderate moisture stress, but becomes less important under severe or prolonged moisture stress. Selemat and Gardner (1985) inferred that nitrogen was remobilized from

leaves to pods during periods of nitrogen stress in non-nodulating peanut (*Arachis hypogaea*) cultivars, but no remobilization occurred in the nodulated plants. Likewise, DeVries et al. (1989) showed that moisture stress had no effect on nitrogen concentration of leaves and stems of peanuts. This study was undertaken to study the effects of moisture stress on nitrogen partitioning in Bambara groundnut, common bean, cowpea, and non-nodulating soybean.

MATERIALS AND METHODS

The experiments were planted in a modified split plot design on a Spinks sandy soil (Psammentic Hapludalfs, sandy, mixed, mesic) in a rainshelter at the Kellogg Biological Research Station in Hickory Corners Michigan in 1995 and 1996. The experimental design was a modified split-plot in a randomized complete block with two moisture treatments (stress and non stress) as the main plots and genotypes as sub-plots. There were four replications and treatments consisted of two cowpea genotypes (IT82D-889, 475/89), two Bambara groundnut genotypes (ZVS 530 inoculated, ZVS uninoculated, and ZVS 564), three common bean genotypes (Carioca, T3147-2, Natal Sugar) and a non-nodulating soybean isoline (Harosoy). All the genotypes were obtained from the Department of Research and Specialist Services in Zimbabwe except T3147-2 and Harosoy which were obtained from the breeding programs of Dr. James Kelly at Michigan State University and Dr. J. E. Harper at USDA-ARS in Urbana, IL., respectively.

Neutron probe access tubes were installed in each plot to a depth of 1m prior to planting. Forty kg N ha^{-1} was broadcast using 19-19-19 fertilizer, the normal fertilizer rate for common bean. Common bean was inoculated with a granular form of *Rhizobium phaseoli*, the cowpeas with *Rhizobium* cowpea miscellany nitrogen EL, and Bambara groundnuts with *Voandzeia* Special 1. The cowpea and Bambara groundnut inoculum were obtained from Nitragin ™ Inoculants and were manufactured by Liphatech, Inc. The non-nodulating soybean (Harosoy) and a non-inoculated Bambara groundnut (ZVS 530) treatment were used as controls. It was assumed that the Bambara groundnut rhizobium was not present in the soil since Bambara groundnut had never been grown on that soil. An inoculated ZVS 530 was also grown. The four-row plots were each 2 m. long and 0.5 m wide. The intra-row spacings were 8 cm, 15 cm and 25 cm for the common bean, Bambara groundnut and cowpea respectively. Three applications of fungicide (Benlate for anthracnose and Sevin for Japanese beetles) of 1.12 kg ha^{-1} were made in 1995 at two week intervals starting on July 14. Two applications of Benlate were made in 1996.

Terminal moisture stress was initiated on July 29 in 1995 and July 21 in 1996. Sampling for nitrogen partitioning was done at three stages -- vegetative, flowering, and podfill. Planting was done on June 20 and June 6 in 1995 and 1996, respectively. Sampling for the vegetative stage was done on August 4, 1995 at 44 days after planting (DAP) and on July 19, 1996 (45 DAP) for all treatments.

In 1995, sampling during the flowering stage was done on August 25, (66 DAP) for all treatments. The flowering stage of common bean was used as the reproductive sampling date. In 1996, the treatments were sampled at different dates as each species and genotype reached the flowering stage. Common bean was sampled on August 8 (64 DAP), soybean on August 16, (72 DAP), cowpea on August 23 (79 DAP), and Bambara groundnut on September 15 (102 DAP). In 1995, sampling for the podfill stage was done on September 9 for common bean and cowpea (81 DAP), October 1 for soybean (103 DAP), and October 8 for Bambara groundnut (110 DAP). In 1996, sampling for the podfill stage was done on August 23 (79 DAP) for common bean, September 15 (102 DAP) for cowpea, and October 3 (120 DAP) for soybean and Bambara groundnut. At sampling, three plants per plot were cut at the base of the stem, dipped in water to remove all soil, and separated into leaves, stems and reproductive parts (flowers and/or pods) for subsequent determination of dry weight and total nitrogen. Nitrogen was determined by Kjeldahl digestion and total nitrogen was analyzed using the Latchet procedure. The Fischer and Maurer (1978) drought intensity index (DII) was used to determine the degree of moisture stress that had been induced. This method uses the average yield of all genotypes under stress and non-stress (Y_s and Y_p), respectively to determine drought intensity according to the following equation: $DII = 1 - Y_s/Y_p$.

RESULTS AND DISCUSSION

Nitrogen Partitioning

Leaves

In 1995, leaf-N concentration for the two cowpea genotypes (IT8d-889 and 475/89) did not differ during the vegetative, flowering or podfill stages (Tables 1 and 2). During the vegetative stage cowpea had a significantly higher leaf-N concentration than Bambara groundnut ($\alpha \leq 0.0001$), common bean ($\alpha \leq 0.01$), and soybean ($\alpha \leq 0.10$) (Tables 1 and 2). Leaf-N concentration remained significantly higher ($\alpha \leq 0.001$) in cowpea leaves than in Bambara groundnut, common bean, and soybean leaves during flowering. By podfill, cowpea had a significantly higher leaf-N concentration than common bean ($\alpha \leq 0.10$) and soybean ($\alpha \leq 0.01$), but did not differ from Bambara groundnut (Tables 1 and 2).

In 1995, common bean had a higher ($\alpha \leq 0.0001$) leaf-N concentration than Bambara groundnut during the vegetative stage, but did not differ from soybean (Tables 1 and 2). During flowering, common bean had a higher leaf-N concentration than Bambara groundnut ($\alpha \leq 0.01$) and soybean ($\alpha \leq 0.05$). By podfill, common bean and Bambara groundnut did not differ, and common bean had a higher leaf-N concentration than soybean ($\alpha \leq 0.001$) (Tables 1 and 2). T3147-2 had a lower leaf-N concentration than the Zimbabwean common bean genotypes (Carioca and Natal Sugar) at flowering and podfill.

Leaf-N concentration values were lower in 1996 than in 1995 (Table 1),

Table 1 Leaf-N concentration (%) at the vegetative, flowering, and podfill stages in Bambara groundnut (*Vigna subterranea*), bean (*Phaseolus vulgaris*), soybean (*Glycine max*) and cowpea (*Vigna unguiculata*) grown under non stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Research Station, MI. in 1995 and 1996.

		1995				1996		
Species	Genotype	Vegetative Combined NS & S	Flowering		P.F.[§] Combined NS & S	Vegetative Combined NS & S	Flowering Combined NS & S	P.F. Combined NS & S
			%					
			NS	S				
Cowpea	IT82-889	5.0 a[•]	4.3 a	4.0 a	2.8 b	3.2 a	2.3 a	2.5 a
Cowpea	475/89	4.7 ab	4.2 a	4.0 a	2.7 b	3.5 a	2.2 a	2.2 a
C. Bean	Natal Sugar	4.2 bc	3.8 b	4.0 a	3.4 a	---[£]	---	---
C. Bean	Carioca	4.6 ab	4.2 a	3.1 b	2.8 b	2.6 bc	1.6 a	1.4 bc
C. Bean	T3147-2	4.2 bc	3.7 b	3.2 b	2.1 c	2.1 c	2.0 a	1.6 b
Bambara[†]	ZVS 530(I[‡])	3.6 de	3.5 bc	3.4 b	2.8 b	2.4 bc	1.9 a	2.3 a
Bambara	ZVS 530	3.9 de	3.4 bc	3.4 b	2.0 c	2.7 b	1.7 a	2.4 a
Bambara	ZVS 564	3.3 e	3.3 c	3.4 b	2.9 ab	2.3 bc	1.8 a	2.3 a
Soybean	Harosoy	4.5 b	3.2 c	3.9 a	2.1 c	2.7 b	1.8 a	1.1 c

[•]Different letters within a column represent significant difference at $\alpha \leq 0.05$ according to Tukey's least significant difference.
[§] P.F. NS and S represent pod fill, Non stressed, and Non stressed, respectively.

[£, †, ‡] Represent missing data, Bambara groundnut and inoculated Bambara groundnut, respectively.

Table 2. Species contrasts for leaf-N concentration of Bambara groundnut (*Vigna subterranea*), bean (*Phaseolus vulgaris*), cowpea (*Vigna subterranea*), and soybean (*Glycine max*) grown in a rainshelter at the Kellogg Biological Station, MI. in 1995 and 1996.

	1995			1996		
	Leaf-N Concentration (%)					
Growth Stage	Vegetative	Flowering	Podfill	Vegetative	Flowering	Podfill
Contrast						
Cowpea vs. Bambara[†]	****[‡]	***	ns	****	*	ns
Cowpea vs. C. Bean	**	***	+	****	*	****
Cowpea vs. Soybean	+	***	**	**	+	****
C. Bean vs. Bambara	****	**	ns	ns	ns	****
C. Bean vs. Soybean	ns	*	***	**	+	****
IT8D-889 vs 457/89	ns	ns	ns	ns	ns	+
Carioca vs. T3147-2	ns	**	**	+	ns	ns
Carioca vs. Natal Sugar	ns	ns	*	---[§]	---	---
T3147-2 vs. Zim var.	ns	*	*	---	---	---
ZVS530(I) vs ZVS 530	ns	ns	ns	ns	ns	ns
ZVS530(I) vs ZVS 564	ns	ns	ns	ns	ns	ns

[†,§] Represent Bambara groundnut and missing data, respectively.
[‡]The symbols +, *,**,***,**** represent significant difference at $\alpha \leq 0.10, 0.05, 0.01, 0.001$, and 0.0001, respectively.

probably due to leaf bronzing and chlorosis resulting from ozone and sunscald, respectively, in 1996. Nevertheless, patterns of leaf-N concentration in 1996 were very similar to those of 1995 (Tables 1 and 2). Cowpea retained a higher leaf-N concentration than common bean from the vegetative stage through podfill in 1996, while common bean had a higher leaf-N concentration than soybean at podfill. Leaf-N concentration of Bambara groundnut at podfill equaled that of cowpea in 1996. This research utilized a non-nodulating soybean, but the results are similar to that of DeVries et al. (1986) which found that soybean leaves at harvest contained less N than peanut and pigeonpea leaves at harvest. Results indicated that soybean partitioned the least amount of N to the leaves, followed by common bean, with cowpea and Bambara groundnut partitioning the most. It suggests that soybean remobilized more N from the leaves than common bean and that common bean remobilized more than cowpea and Bambara groundnut. The soybean was non-nodulating and the 40 kg N ha^{-1} is the recommended N fertilizer rate for common bean, but was insufficient to meet the needs of the non-nodulating soybean as indicated by the light green color of the soybean leaf tissue during the growing season. Bambara groundnut did not mature within the Michigan environment and the higher leaf-N concentration may simply reflect that the plant had not completed the process of remobilizing N from leaves to developing seeds. Cowpea reached physiological maturity approximately three weeks after common bean and the higher leaf-N concentration may again simply

reflect that N remobilization from cowpea leaves was less advanced than in common bean and soybean by the sampling date in 1995. However, species comparisons produced the same results in 1996 when each species was sampled when it reached each specific stage of development. The relatively higher N concentration in cowpea is compatible with the statement by Summerfield et al. (1985) indicating that cowpea yields appear to be limited by the crop's ability to assimilate carbon and N during the reproductive period and its ability to partition large amounts of C and N into fruit production. By podfill, the cowpea 475/89 had a lower ($\alpha \leq 0.10$) leaf-N concentration than the cowpea IT82D-889. Values for the nitrogen concentration in the leaves by podfill ranged from a low of 2.0% to a high of 3.4 % in 1995 and a low of 1.1% to a high of 2.5% in 1996 (Tables 1 and 2). These values are consistent with values reported by Dubois and Burris (1986).

Stems

In 1995, cowpea had a higher stem-N concentration than Bambara groundnut during the vegetative and reproductive stages (Tables 3 and 4). Bambara groundnut had a higher stem-N concentration than common bean at the vegetative ($\alpha \leq 0.0001$), flowering ($\alpha \leq 0.05$), and reproductive ($\alpha \leq 0.0001$) stages in 1996, but was only higher at flowering in 1995. (Tables 3 and 4). As with leaf-N concentration, no differences were observed between the Bambara groundnut genotypes in stem-N concentration at any stage of development in the

Table 3. Stem-N concentration (%) at the vegetative stage, flowering, and podfill in Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), soybean (*Glycine max*) and cowpea (*Vigna unguiculata*) grown under non stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Research Station, MI. in 1995 and 1996.

		1995			1996		
Species	Genotype	Vegetative Combined Stressed & Non stressed	Flowering Combined Stressed & Non stressed	Podfill Combined Stressed & Non stressed	Vegetative Combined Stressed & Non stressed	Flowering Combined Stressed & Non stressed	Podfill Combined Stressed & Non stressed
				%			
Cowpea	IT82D-889	2.6 a*	1.6 ab	1.0 ab	0.6 bcd	1.4 a	0.9 b
Cowpea	475/89	2.6 a	1.5 b	0.9 ab	0.8 ab	1.2 ab	1.0 b
C. Bean	Natal Sugar	2.4 b	1.6 ab	1.1 a	-----£	-----	----
C. Bean	Carioca	2.7 b	1.5 b	0.9 ab	0.3 d	0.5 c	0.7 bc
C. Bean	T3147-2	1.8 c	1.1 c	1.1 a	0.4 d	0.9 bc	0.5 c
Bambara†	ZVS 530(I‡)	2.1 b	1.8 a	1.1 a	0.7 bcd	1.2 ab	1.5 a
Bambara	ZVS 530	2.2 b	1.8 a	1.0 ab	0.8 bc	1.4 a	1.4 a
Bambara	ZVS 564	2.2 b	1.8 a	1.2 a	1.2 a	1.2 ab	1.6 a
Soybean	Harosoy	1.5 d	1.0 c	0.4 b	0.5 cd	0.6 c	0.4 c
CV		12	14	74	56	43	36

*Different letters represent significant difference at $\alpha \leq 0.05$ according to Tukey's least significant difference.
£, †, ‡ Represent missing data, Bambara groundnut and inoculated Bambara groundnut, respectively.

Table 4. Species contrasts for stem-N concentration of Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and soybean (*Glycine max*) grown under non stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Station, MI. in 1995 and 1996.

	1995			1996		
	Stem-N Concentration (%)					
Growth Stage	Vegetative	Flowering	Podfill	Vegetative	Flowering	Podfill
Contrast						
Cowpea vs. Bambara[†]	****[‡]	**	ns	ns	ns	****
Cowpea vs. C. Bean	****	*	ns	**	****	**
Cowpea vs. Soybean	****	****	+	ns	**	***
C. Bean vs. Bambara	ns	****	ns	****	***	****
C. Bean vs. Soybean	****	***	*	ns	ns	ns
IT8D-889 vs 457/89	ns	ns	ns	ns	ns	ns
Carioca vs. T3147-2	***	****	ns	ns	ns	ns
Carioca vs. Natal Sugar	ns	ns	ns	---[§]	---	—
T3147-2 vs. Zim var.	****	****	ns	---	---	---
ZVS530(I) vs ZVS530	ns	ns	ns	ns	ns	ns
ZVS530(I) vs ZVS564	ns	ns	ns	*	ns	ns

[†,§] Represent Bambara groundnut and missing data, respectively..

[‡] The symbols +, *,**,***,**** represent significant difference at $\alpha \leq 0.10, 0.05, 0.01, 0.001$, and 0.0001, respectively.

two years, with the exception of the vegetative stage in 1996 (Table 4). Inoculation or lack of inoculation made no difference in ZVS 530, presumably because the 40 kg N ha^{-1} was sufficient to meet the needs of the crop. Soybean had a significantly lower stem-N than common bean genotypes at all stages of growth in 1995, but the two did not differ in 1996 (Table 4).

Cowpea had the highest stem-N concentration followed by Bambara groundnut, although the data for Bambara groundnut must be viewed with suspicion since Bambara groundnut did not reach physiological maturity (Table 3). Chapman and Muchow (1985) observed increased nitrogen partitioning in stems and leaves of cowpea, lablab, black gram and pigeon pea under moisture stress conditions. In the current research, moisture stress did not affect stem-N concentration and only affected leaf-N during flowering in 1995.

Foster et al. (1995) reported higher stem-N under stressed conditions. They concluded that high stem-N concentration could imply inefficient remobilization of stem-N under severe moisture stress. Considering their observation, the lack of increased stem-N under stress in this study may simply be due to the mild moisture deficit, especially in 1996.

Reproductive Structures

Cowpea had a significantly higher ($\alpha \leq 0.0001$) reproductive-N concentration at the flowering stage than did common bean in 1995 and at podfill in 1996 (Tables 5 and 6). Reproductive-N concentration in cowpea was

Table 5. Reproductive-N concentration (%) at the vegetative, flowering, and physiological maturity in stages Bambara groundnut (*Vigna subterranea*), common bean (*P. vulgaris*), soybean (Glycine max) and cowpea (*Vigna unguiculata*) grown under non stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Research Station, MI. in 1995 and 1996.

		1995			1996	
Species	Genotype	Flowering		P.F.[§] Combined NS[§] & S	Flowering Combined NS & S	P.F. Combined NS & S
		%				
		NS	S			
Cowpea	IT82D-889	4.0 a	3.8 a	1.3 ab	2.1 a*	2.2 a
Cowpea	475/89	3.7 ab	3.6 a	1.7 a	0.9 bc	2.1 a
C. Bean	Natal Sugar	---[£]	1.7 c	1.8 a	---	---
C. Bean	Carioca	3.3 bc	3.0 b	1.4 ab	1.6 ab	1.8 b
C. Bean	T3147-2	3.1 bc	2.8 b	1.7 a	1.8 ab	2.0 ab
Bambara[†]	ZVS 530(I)	---	---	1.1 ab	0.4 c	2.2 a
Bambara	ZVS 530	---	---	0.7 b	0.5 c	1.8 b
Bambara	ZVS 564	---	---	0.7 b	0.6 c	1.7 b
Soybean	Harosoy	2.8 c	2.8 b	1.9 a	1.9 a	2.2 a

*Different letters within a column represent significant difference at $\alpha \leq 0.05$ according to Tukey's least significant difference.
[§] P.F., NS and S represent pod fill, Non stress, and stressed, respectively.
[£, †, ‡] Represent missing data, Bambara groundnut and inoculated Bambara groundnut, respectively.

Table 6. Species contrasts for reproductive-N concentration of Bambara groundnut (*Vigna subterranea*), common bean (*Phaseolus vulgaris*), cowpea (*Vigna unguiculata*), and soybean (*Glycine max*) grown under non stress and stress soil moisture conditions in a rainshelter at the Kellogg Biological Station, MI. in 1995 and 1996.

	----------1995----------		----------1996----------	
	Reproductive-N Concentration (%)			
Growth Stage	Flowering	Podfill	Flowering	Podfill
Contrast				
Cowpea vs. Bambara[†]	---[§]	*	**	*
Cowpea vs. C. Bean	****	ns	ns	*
Cowpea vs. Soybean	***	ns	ns	ns
C. Bean vs. Bambara	---	**	***	*
C. Bean vs. Soybean	0	ns	ns	+
IT8D-889 vs 457/89	ns	ns	*	ns
Carioca vs. T3147-2	****	ns	---	---
Carioca vs. Natal Sugar	****	ns	---	---
T3147-2 vs. Zim var.	***	ns	---	---
ZVS530(I) vs ZVS530	---	ns	ns	ns
ZVS530(I) vs ZVS564	---	ns	ns	**

[†,§]Represent Bambara groundnut and missing data, respectively.
[‡]The symbols +, *,**,***,**** represent significant difference at $\alpha \leq 0.10, 0.05, 0.01, 0.001$, and 0.0001, respectively.

significantly ($\alpha \leq 0.0001$) higher than in soybean at the flowering stage in 1995 (Table 6), however no differences were observed in 1996 between cowpea and soybeans at flowering or podfill. Between the cowpea genotypes, IT82D-889 had a higher ($\alpha \leq 0.1$) reproductive-N concentration than 475/89 in 1996 but not in 1995 (Table 6). The common bean genotype Carioca had a higher reproductive-N concentration than T3147-2 (Tables 5 and 6), in 1995 but not in 1996. The inoculated treatment of ZVS 530 had a higher reproductive-N concentration at podfill than the inoculated ZVS 564 in 1996 (Table 6). The non-nodulating soybean had a surprisingly high reproductive-N concentration in both years (Table 5). When considered along with the low N concentration in soybean leaves and stems, this supports the interpretation that soybean is very efficient in remobilizing N from vegetative to reproductive structures.

While not significant, there was a tendency in common bean for increased N concentration in leaves, stems, and reproductive structures of stressed plants at podfill in 1995 (Table 7) and in leaves and reproductive structures in 1996 (Table 8). In 1995, plants experienced a moderate moisture deficit (0..54) and a mild moisture deficit in 1996 (0.22). The tendency for increased N is consistent with the findings of Foster et al.(1995) which reported a tendency for higher nitrogen concentration in plants under severe moisture stress Foster et al. (1995) suggested that nitrogen remobilization may be severely impaired by greater moisture deficit, while N redistribution during a moderate moisture stress may contribute to yield

Table 7. N concentration of leaves, stems, and reproductive structures of common bean (*Phaseolus vulgaris* L.) grown under non-stress (NS) and stress (S) soil moisture conditions in a rainshelter at the Kellogg Biological Station in Hickory Corners, MI. in 1995.

Genotype	Leaves		Reproductive parts		Stems	
	N.S	S	N.S	S	N.S	S
Natal Sugar	3.21	3.55	1.47	2.07	0.80	1.39
Carioca	2.75	2.93	1.18	1.55	0.47	1.39
T3147-2	2.59	2.78	1.63	1.69	0.84	1.27

Table 8. N concentration of leaves, stems, and reproductive structures of common bean (*Phaseolus vulgaris* L.) grown under non-stress (NS) and stress (S) soil moisture conditions in a rainshelter at the Kellogg Biological Station in Hickory Corners, MI in 1996.

Genotype	Leaves		Reproductive parts		Stems	
	N.S	S	N.S	S	N.S	S
Carioca	1.40	1.82	1.89	2.05	0.58	0.50
T3147-2	1.33	1.51	1.66	1.90	0.69	0.61

stability.

CONCLUSIONS

Soybean remobilized more N from the leaves than common bean and common bean remobilized more than cowpea and Bambara groundnut. Similarly, cowpea contained the highest leaf- and stem-N concentration at all stages of development and had the highest reproductive-N concentration at flowering and podfill, with the exception of Bambara groundnut at podfill. There was a tendency for moisture stress to increase N concentration in common bean. Leaf-N concentration was lower in 1996 than in 1995 in all species and at all growth stages.

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CONCLUSIONS

Moisture stress reduced the number of pods per plant in cowpea and soybean, but not in common bean. Moisture stress reduced seed weight of T 3147, a common bean, and reduced the number of seeds per pod in cowpea in 1996. Cowpea was more drought tolerant than common bean, although common bean produced a higher yield than cowpea. Among common bean genotypes, Natal Sugar did not mature in Michigan, but T3147 produced a smaller number of pods than Carioca and had a higher yield reduction under stress. Between cowpea genotypes, 475/89 produced a higher yield and greater number of seeds per pod than IT82D-889. Cowpea produced more seeds per pod than bean or Bambara groundnut and had the highest percentage of seed abortion under both stress and non-stress conditions. Species and genotypes differed in yield, seed weight, pod and seed number, and the effect of moisture deficit on each yield component. STI was a better predictor than DSI of yield performance under moisture stress.

Results of both the 12- and 20-cm depth screening boxes indicated that cowpea was more drought tolerant than Bambara groundnut and that Bambara groundnut was more drought tolerant than common bean. Unfortunately, field performance of Bambara groundnut could not be compared to the other two species.

The non-nodulating soybean partitioned the least amount of N to the leaves, followed by common bean, with cowpea and Bambara groundnut partitioning the

most. This suggests that the non-nodulating soybean isoline remobilized more N from the leaves than common bean and that common bean remobilized more than cowpea and Bambara groundnut. Cowpea contained the highest leaf-, stem-, and reproductive-N values. There was variation for N concentration of leaves, stems, and reproductive structures among genotypes within each species. The relatively mild moisture stress in this study did not affect N concentration, although there was a tendency for moisture stress to increase N concentration in common bean.