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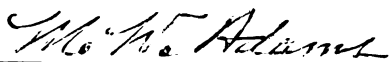
PRODUCTIVITY OF MALAWIAN LANDRACE DRY BEANS
UNDER INTERCROPPING AND DROUGHT CONDITIONS

presented by

Alexander B. C. Mkandawire

has been accepted towards fulfillment
of the requirements for

Ph.D. degree in Crop and Soil Sciences


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**PRODUCTIVITY OF MALAWIAN LANDRACE DRY BEANS
UNDER INTERCROPPING AND DROUGHT CONDITIONS**

By

Alexander B. C. Mkandawire

A DISSERTATION

**Submitted to
Michigan State University
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ABSTRACT

PRODUCTIVITY OF MALAWIAN LANDRACE DRY BEANS UNDER INTERCROPPING AND DROUGHT CONDITIONS

By

Alexander B. C. Mkandawire

Malawi is a country of great ecological diversity. The original bean (*Phaseolus vulgaris* L.) introductions, brought more than 300 years ago, have evolved with great morphological variation. The process of evolution is greatly influenced by two environmental parameters; namely: temperature and moisture. In Malawi, moisture seems to exert greater influence on net primary productivity than temperature. Studies were conducted to better understand the role of Malawian landrace bean components in bean crop productivity under conditions of limited soil moisture. In one set of experiments limited moisture conditions were imposed on the beans by intercropping them in the same row with a more aggressive species [maize (*Zea mays* L.)], which is a popular cropping system in Malawi. The other set of experiments involved controlled drought in field-simulated culture. The aim here was to observe any genotypic variability in both *Phaseolus* and *Vigna* species in water-use efficiency (WUE) under either well-watered or drought conditions.

Intercropping beans and maize resulted in significantly lower soil moisture than when beans were grown in monoculture stands. This resulted in significant reductions in bean seed yields of some landraces under the intercropping system. However, there was no evidence for reduction in seed yield of other landraces grown under the same system. This indicates that some of these landraces are adapted to such intercropping stresses. Criteria of estimating relative drought tolerance substantiated this observation. Most of those landraces that were adapted showed higher leaf diffusive resistances. Combined over all experiments, under stress conditions, economic yield was significantly and positively ($r=0.242$) associated with leaf diffusive resistance but significantly and negatively ($r=-0.472$; $r=-0.243$) associated with leaf transpiration and leaf temperature, respectively. However, from data combined from one intercropping and one WUE experiment, no significant relationship was obtained between total biological yield and either leaf moisture retention capacity (LMRC) or specific leaf weight (SLW) under stress conditions. And there was no significant relationship between LMRC and SLW.

Genetic variability exists among *Phaseolus* and *Vigna* species in their WUE and drought tolerance. *Vigna* species performed similarly to *Phaseolus* species agronomically although they were expected to show higher water-use efficiency and drought tolerance. In one of the two WUE

experiments the Malawian landraces significantly increased their WUR under drought such that they yielded equally well under drought as under well-watered conditions. The Malawian landrace component 5 (Katolika) proved to be a drought tolerant genotype in 3 years.

The genetic variability in the Malawian component landraces in drought tolerance suggests that the mixtures planted by farmers in Malawi are comprised of both higher yielding but probably susceptible and the lower yielding but drought tolerant components. This provides one explanation of why Malawian farmers grow bean mixtures. They may want to maximize seed yields during good years by planting landraces of higher yielding potential while at the same time minimizing yield losses, in the event of a drought, by including drought tolerant landrace components.

DEDICATION

**To my parents, Benard and Tamala Mkandawire
and my parents-in-law, Patson and Mirian Khonje.**

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I wish to express my sincere gratitude to Dr. M. Wayne Adams for serving as my major professor. He directed both my program of study and the research I conducted. I thank him for reading the manuscript and providing the necessary professional criticisms. I felt honored to have been one of his graduate students. I deeply appreciate the financial support from the Bean/Cowpea CRSP Project of which he is the U.S. Principal Investigator.

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More importantly, we enjoyed corresponding with parents, brothers, sisters, and a lot of friends back in Malawi. But God so loved my father-in-law that He called him before I completed my studies so that we could see each other again. May God bless them all.

Lastly, but most important, I extend my love once again to my wife, Sheila Easter, our two daughters Maudie and Lusungu, and our son Alexander Jr., for making me realize the joy of going to graduate school while raising a family at the same time. May the Lord bless them too.

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INTRODUCTION

Malawi comprises a narrow stretch of land west and south of Lake Malawi. It spans from about 7 to 18 degrees latitude south of the Equator and 33 to 36 degrees east of Greenwich. The country is characterized by extraordinary ecological and cultural diversity. Its area ranges from hot, humid lowlands in the Shire valley at below 100 m to cool, rugged peaks at over 2700 m above sea level. Among legumes in Malawi, dry beans (*Phaseolus vulgaris* L.) rank second only to peanuts (*Arachis hypogaea* L.) as evidenced by grain sales at ADMARC, an agricultural marketing firm. However, peanuts are a cash crop whereas beans are generally regarded as a food crop. Therefore, much larger quantities of beans, than can be documented, are produced. Beans originated in the Andean region (Peru and Bolivia) in South America and in Meso-America (Mexico) (Kaplan, 1965). In general, the former center of origin comprises mostly the large-seeded types (mostly Types I and IV) and the latter center of origin comprises mostly the small-seeded types (mostly Types II and III) although medium- to large-seeded pintos, bayos, and canarios are also found. Malawians generally prefer the large-seeded kidney bean types. Apparently in the 16th century the Spaniards and the Portuguese took beans, most probably from the South American (Andean) center of origin, to Europe and then to

Africa (Purseglove, 1968). Beans probably reached Malawi from the eastern coast of Africa (Mozambique) about 300 years ago though the influence of traders (Mughogho et al., 1972). Eastern Africa is now generally considered a center of cultivation.

Probably as a consequence of Malawi's ecological and cultural diversity, these original bean introductions have evolved with gross morphological variation (Adams, 1982) and are grown as such in mixtures by Malawian farmers. They fit Harlan's (1975) description of 'landraces' and will be referred to by this name. These landraces manifest a rich diversity in growth habits, seed sizes, colors, and shapes, among many other intrinsic and extrinsic characteristics. Archaic as this system of production of bean mixtures may seem, it confers important advantages under the tropical subsistence cropping systems. The different components of a single mixture may germinate at different rates thereby extending the seedling establishment period. Pure seed types would cause serious repercussions in the event of drought occurring during germination. The same differential in germination may stagger the maturation times. It is very important for a subsistence farmer, with labor constraints, to harvest the entire field by hand and at the right time for each component line. Bean mixtures may have other advantages such as in disease and insect pest resistance. Also, since these landraces have basically evolved over many generations, the environment has played a major role in

their evolutionary process. Two environmental variables exercise major control over crop species evolution; namely, moisture and temperature. Usually moisture varies more than temperature both within and among cropping seasons. And so moisture is widely regarded as exerting the largest influence on evolution, and also the maintenance of the landraces. One is led to speculate that the diverse bean mixtures contain some drought tolerant components which provide a buffering capacity during drought years to maintain the yield stability that is so much treasured by subsistence farmers.

The objectives of this study were fourfold:

- a. To show that intercropping bean and maize (*Zea mays* L.) aggravates the drought beans encounter in the field in such cropping systems (and probably, to some extent, overcome by bean mixtures);
- b. To show variability in Malawian bean and other genotypes in response to the drought so caused (in a. above) or caused artificially under controlled conditions;
- c. To show variability in water-use efficiency (WUE) of different dry bean genotypes as a strategy used by some bean plants when grown under limited moisture conditions; and
- d. To show variability in simple characteristics that have been associated with drought resistance elsewhere. These characteristics are essential when

selecting for drought tolerant progeny among vast segregating populations in a breeding program where modern instruments are cumbersome, prohibitive in terms of cost, and time-consuming.

LITERATURE REVIEW

Definition of Drought

'Drought' is probably one of the most confusing, nebulous, and imprecise terms in agronomic plant science today. The confusion is portrayed through the perception of it by the different schools of thought. The Webster's English Dictionary describes the term as derived from the old english term 'drugoth,' which meant 'prolonged dry weather.' Meteorologists often define drought as a 'period of lack of precipitation,' usually with precipitation as a sole cause of drought. But lack of current precipitation is only one of the factors affecting the supply of moisture to crops. Initial amount of moisture contained in the soil at planting time is another source of moisture that needs to be incorporated in the definition.

However, such a definition would still fall short in relation to crop productivity. Crop scientists generally regard a drought as a 'lack of both soil moisture and precipitation from planting up until physiological maturity of crops.' Lack of both factors outside the crop season can not, therefore, qualify as a 'drought.' It is still confusing, however, because during the same crop season a crop of one species in one field may experience drought whereas another crop of a different species in an adjacent field may not experience any drought. And drought is also

caused by a high demand for moisture by the atmosphere just as much as the shortage of moisture on the supply side (initial soil moisture and precipitation). As a result, crop physiologists define drought as 'the period of moisture deficit that adversely affects a specific crop's growth and development or any of its related physiological processes.'

Henckel (1964) has defined drought resistant plants as 'those plants which, in the process of ontogenesis, are able to adapt to the effect of drought and which can normally grow, develop and reproduce under drought conditions because of a number of properties acquired in the process of evolution, under the influence of environmental conditions and natural selection.' Suffice it to say that this same process can be directed carefully through crossing and artificial selection in plant breeding procedures. Under such circumstances the span of time for obtaining drought resistant plants should be much abridged in comparison to evolution by natural selection.

Measuring Plant Water Status

Stomatal conductance

Plants have to exist in an environment of continual dilemma of absorbing carbon dioxide for photosynthesis with consequential dehydration of tissue due to exposure to dry atmosphere. They have overcome this dilemma by evolving leaves with an epidermis composed of a relatively

impermeable cuticle and turgor-operated valves called 'stomata.' The epidermis, therefore, not only reduces rates of carbon dioxide and water vapor exchange but it also provides a means of controlling the balance between water loss and dry matter production. Therefore, measuring the resistance to carbon dioxide and water vapor transfer between the atmosphere and the internal tissues of the leaf imposed by the stomata (stomatal resistance) is important in many studies of biomass production. If the limitation (resistance) offered by stomata is being compared with the flux of carbon dioxide or moisture, or even being correlated with some biological or environmental variable such as leaf water status, it is more meaningful and less prone to misinterpretation to express it as a conductance (reciprocal of resistance) rather than as a resistance (Burrows and Milthorpe, 1976). Fluxes are proportional to conductances but inversely proportional to resistances. But most instruments are calibrated against physical resistances. Therefore, measurements are made as resistances and then conductances are calculated.

Stomatal conductance can be obtained by measuring the rate of gaseous loss by porometry. The mass-flow porometer measures the rate at which air is forced through leaves under pressure (Hsiao and Fischer, 1975). The diffusion porometer measures the rate at which water vapor diffuses out of leaves. Mass-flow porometers are simple, cheap, and usually do not involve electronic circuitry. They, however,

have the following disadvantages: i. They are best used for comparative rather than absolute measurement because of errors; ii. Their use is restricted mainly to leaves with stomata on both surfaces; iii. Leakage of air from the apparatus can cause errors. Diffusion porometry, on the other hand, is based on measurement of the rate of water vapor loss from a leaf or portion of a leaf enclosed in a porometer chamber (Kanemasu, 1975). The rate of loss is determined from the rate of increase in humidity. Water loss is from both the stomata and the cuticle. It is generally understood that most of the loss occurs from the stomata, but the cuticular component becomes increasingly important as stomata close.

Water Potential

By definition, water potential (U) is the potential energy per unit mass of water with reference to pure water at zero potential. It is empirically calculated as:

$$U = RT/V_w \ln a_w \dots\dots(1)$$

where R = the gas constant, T = absolute temperature (K), V_w = partial molal volume of water, and a_w = activity of water. As a result, water in most biological systems has less potential energy than pure water hence water potential is given in negative values. There are two main ways of measuring water potential, namely; i. The pressure chamber

technique (Scholander et al., 1965) and ii. Thermocouple hygrometry.

The pressure chamber is simple, cheap, rugged, and ideally suited for field studies (Ritchie and Hinckley, 1975). A leaf cut from the plant is placed in the chamber with the cut-end projecting through the hole in a rubber gromet assembly. The pressure applied to the leaf to return the water interface to where it was before detachment is equal and opposite to the tension in the xylem of the intact plant. The osmotic potential of xylem sap is usually extremely low (about 0.2 kPa) and as a result the hydrostatic pressure in the xylem is approximately equal to the water potential. The pressure chamber technique is now the most widely used method for characterizing plant water status.

Plant Water Content

Cell elongation is very sensitive to cell turgor. As a result plant water status strongly influences plant growth and dry matter production through its effect on leaf and root expansion and on photosynthesis. The amount of water in plants could be expressed in different ways (Slavik, 1974):

$$\text{Water content} = [\text{fresh wt} - \text{dry wt} / \text{dry wt}] \times 100\% \quad \dots(2)$$

$$\text{Relative water content} = \frac{[\text{fresh weight} - \text{dry weight}] \times 100\%}{[\text{turgid weight} - \text{dry weight}]} \quad \dots(3)$$

$$\text{Water saturation deficit} = [100 - \text{Relative water content}] \dots(4)$$

Turgid weight is obtained by floating leaves or leaf discs on water at the light-compensation point until constant weight is obtained. Determining water content requires relatively simple and cheap equipment and many samples can be taken as replicates or across a large number of treatments. However, the technique for determining relative water content requires considerable skill and precision to obtain accurate results.

Leaf Water Retention Capacity

This is a fairly new technique. Leaves are removed from the plants and weighed as soon as possible. They are then hung on a wire in a room kept at a constant room temperature for about 48h. After that they are weighed and oven-dried at 80C for 48h. The amount of water retained during air drying is obtained by subtraction and expressed on total water content as per cent. This method was found to show cultivar differences in wheat (*Triticum aestivum* L.); it was thought better than other methods such as

stomatal conductance and leaf temperature (Clarke et al., 1982). It seems to be more consistent than other methods, and cultivar differences in the capacity to retain water have been indicated in beans (Tesda, 1984).

Drought Resistance Mechanisms

Plant mechanisms involved in adaptation to drought have recently been classified by three systems, namely; a. Drought escape, drought avoidance, and drought tolerance (Turner, 1979; Levitt, 1982); b. Phenological, morphological, and physiological mechanisms (Turner and Begg, 1981; Turner, 1982) and c. Adaptations i. leading to the acquisition of the maximum amount of water; ii. to ensure the conservation and efficient use of water; and iii. protecting cells and tissues from damage and death during severe desiccation (Fitter and Hay, 1981). It should be emphasized, however, that although the systems of classification are different, they all aim at describing the same plant response to both increasing soil and plant moisture deficits. I will review the mechanisms enabling plants to adapt under drought conditions based on the second system of classification.

Phenological Mechanisms

Phenology refers to the timing of major developmental events such as germination, flowering, senescence, and so forth. Phenological changes in timing of crop developmental changes that the plants go through from germination up to and including maturity play a role in plants subjected to drought. Two aspects of phenological mechanisms are; a. changes in phenological development and, b. developmental plasticity (Turner, 1982). A plant growing on an increasing soil moisture deficit, without the probability of relief of drought stress, may use the strategy of going into the reproductive stage sooner and maturing earlier (Hall and Grantz, 1981). And actually, this particular strategy seems to be of major importance in some mediterranean zones characterized by terminal drought. Breeding for earliness under such conditions has been suggested (Turner, 1982; Quizenberry, 1982). The problem is that although such genotypes yield better under terminal drought they generally yield poorly when grown in zones with unpredictable droughts. This is because their capacity is limited by a shorter duration of crop growth whether adequate soil moisture is available or not. But effects of water deficits on phenological development are usually small. Mild droughts seem to hasten flowering and maturity in wheat (Turner, 1966) but not in sunflower (*Helianthus annuus* L.) (Takami et al., 1981). It would seem that other variables of the environment such as high temperature during severe

droughts and photoperiods have a much more marked influence on phenological development (Turner, 1982). Muhammad (1983), working with 16 cultivars of beans, five day temperatures, five night temperatures, and a 12h daylength, found that the time to flowering decreased as the temperature was raised and vice versa.

Morphological Mechanisms

Water is absorbed from the soil by the roots. Increasing soil water deficits near the soil surface seem to induce compensatory extension of the roots to deeper, unexploited soil layers. The deep rooting systems characterize plants that are drought avoiders because they are able to exploit soil moisture in the lower soil profiles. This is more so in regions dependent on reserves of soil moisture where incomplete extraction of stored water may pose a limitation to high productivity (Jordan and Miller, 1980). Malawi lies in the arid region and is exposed to mainly unpredictable droughts. Usually the crops depend on current rainfall. Under such conditions, developing a deep rooting system may not necessarily be a good enough strategy since the crop virtually depends on current rainfall. However, some areas in Malawi experience a bimodal type of rainfall pattern. In such areas, e.g. Mulanje and Thyolo, beans are planted twice in a year. Usually, the first crop is intercropped with maize (H. Mloza-Banda, personal communication) and faces unpredictable

droughts. The second and primary crop is grown during the second rains in monocultures facing terminal droughts and depends largely on stored moisture during seed filling. Deep rooting systems would be beneficial under these conditions of terminal drought. However, under conditions of abundant soil moisture supply throughout the root zone, extensive root branching, as opposed to deep rooting systems, and eventual size of the root system assume utmost importance. Passioura (1972, 1976, 1982) has extensively studied the role of roots in the uptake of water and how water is translocated in the vascular systems of crop plants, especially wheat. He has worked in a mediterranean environment of Australia, where the wheat is largely grown on moisture reserves and experiences terminal drought. From his work two observations have been: a, the ability of a crop to produce a large rooting density at depth if deep subsoil water exists; and b, a longitudinal resistance to flow which may influence the rate at which water collected in the subsoil is transported to the shoots.

He concluded that depending on the environment, it may be worthwhile to decrease the resistance, if there is evidence that roots are leaving available water in the soil at maturity. On the other hand, it may be worthwhile to increase the resistance if there is evidence that roots are leaving an inadequate supply of water in the soil at flowering. Modifying resistance to water flow is

accomplished by breeding for narrow or broad cross-sectional area of xylem vessels.

Physiological Mechanisms

Leaf expansion

Leaf expansion is probably the first indicator of the plants' response to drought stress (J. T. Ritchie, personal communication) and as a result irrigation managers have used it to decide when to irrigate their crops. This is because cell enlargement, which is responsible for growth apart from cell division, is the most sensitive process to droughts (Slatyer, 1967; Hsiao, 1973). In maize, Boyer (1970a) showed a rapid decline in leaf enlargement at leaf water potentials below -0.2 MPa, ceasing altogether at -0.7 to -0.9 MPa. Photosynthesis begins to be affected at leaf water potentials below -0.8 MPa, i.e. only after cessation of leaf expansion. Cell enlargement occurs only when turgor pressure is positive, which can be as high as 0.6 to 0.8 MPa in sunflower (Boyer, 1970a). Usually, some species of crops will reduce their osmotic potentials to increase turgor pressure so that cell enlargement and leaf expansion can continue. This is called 'osmotic adjustment' or 'osmoregulation' and has been elaborated elsewhere in this review of literature. The relationship, however, between cell enlargement and turgor pressure has been described by

the following equation (Greacen and Oh, 1972; Green et al., 1971).

$$G = E(P - P_{min}) \dots\dots\dots(5)$$

where G is the growth rate, E is a coefficient for the gross extensibility of the cell walls, P is the pressure potential, and P_{min} is the minimum pressure below which growth will not occur. Gross extensibility and threshold turgor are not constants and can change under water deficit so as to permit resumption of growth at reduced turgor. This adaptation to stress may occur as a result of an increase in extensibility and/or a decrease in the threshold turgor. However, if under severe water stress turgor pressure fell to zero, then no amount of adjustment of these two parameters would permit a resumption of growth. In situations where turgor pressure is approaching zero, the plant can only maintain growth through osmotic adjustment.

Photosynthesis

Stomata act as regulators for both carbon dioxide exchange and water loss in plants. Water deficits sufficient to close stomata should also depress photosynthesis through increased resistance to carbon dioxide uptake. And so the conventional explanation for reduced photosynthesis under drought conditions has been stomatal closure (Boyer, 1970a). The change in net

photosynthesis with leaf water potential follows that of stomatal conductance (Boyer, 1970b). And these changes are reflected in rates of transpiration measured concurrently. Troughton (1969) concluded that stomatal closure was the primary event in depression of photosynthesis under drought conditions. Using cotton (*Gossypium hirsutum* L.), he showed that leaf conductance decreased at relative water content of 80%, whereas mesophyll conductance was only reduced at 75%.

However, as early as 1967, Nir and Poljakoff-Mayber reported that isolated chloroplasts from desiccated swiss chard (*Beta vulgaris* L.) showed less Hill activity and cyclic photophosphorylation. Photosynthesis of water stressed (below -1.1 to -1.2 MPa) sunflower leaves failed to respond to elevated carbon dioxide under high (or low) photosynthetically active radiation (PAR). But at low PAR where photochemical activity limits photosynthesis, a decline from -0.4 to -1.8 MPa resulted in a 70% drop in photosynthesis (Boyer, 1971b). The activity of isolated chloroplasts from stressed leaves shows that electron transport and photophosphorylation drop rapidly at leaf water potentials of less than -1.0 to -1.2 MPa, and it has been suggested that these activities limit photosynthesis below -1.1 MPa (Boyer, 1971b; Keck and Boyer, 1974). Since photosynthesis begins to decline at about -0.8 MPa, the contention is that stomatal resistance prevails as the primary factor at mild stresses, -0.8 to -1.1 MPa, but that chloroplast activities predominate at more severe stresses.

Recent evidence suggests that the reduction in photosynthesis is not as much a function of stomatal closure and/or light reactions as it is of adverse effects on the carbon fixation capacity. Johnson et al. (1985) determined the stomatal limitation to photosynthesis under drought in wheat. Their analysis of photosynthesis versus internal carbon dioxide concentration response curves indicated that, although stomata closed in response to stress, the stomatal limitation was less than 40% of the total limitation to photosynthesis. They suggested that internal leaf capacity for photosynthesis ('dark' reactions) was largely responsible for the limitation to photosynthesis and that stomatal control may be in part mediated by the internal capacity of leaves to photosynthesize.

Nitrogen Fixation

Spent (1976) has performed experiments in this area and has critically reviewed the subject. The consensus of her review is that depending on the stage when it occurs, drought may depress nodulation or nitrogen fixation by the existing nodules. Finn and Brun (1980) have plotted specific nodule activity (SNA) as a function of nodule water potential, and for comparison the stomatal resistance of soybean (*Glycine max* (L.) Merr.) plants pretreated for 20h with polyethylene glycol (PEG). As nodule water potential decreased from about -0.5 to -1.5 MPa stomatal resistance increased from 8 to 38 sec/cm whereas SNA decreased from 36

to 15 umoles acetylene/g nodule fresh weight/h. A question arises as to whether nodule function is diminished because photosynthesis (source of ferredoxin, ATP, and NADPH for reduction of dinitrogen) is depressed or whether there is a direct effect of drought on the nitrogen fixation process. Using subterranean clover (*Trifolium subterraneum* L.) Dejong and Phillips (1982) found that acetylene reduction (AR) was depressed earlier and to a greater extent than carbon exchange rate (CER) when drought was imposed. Over three dry-down cycles CER was decreased less than 50% whereas there was a 90% inhibition of AR.

Using soybean, Pankhurst and Sprent (1975b) determined that increasing the oxygen partial pressure reversed the water-stress induced depression in AR activity (by 75% at atmospheric levels of carbon dioxide) in moderately stressed (-0.75 MPa) nodules. Moreover, AR of nodule slices, nodule breis, and bacteroids from moderately stressed nodules was similar to turgid nodules. These results suggest that drought induces a barrier to oxygen diffusion into nodules, thereby reducing their activity by limiting energy production. With a scanning electron microscope Pankhurst and Sprent (1975a) further showed that soybean nodules have lenticels and that these collapse under drought. Oxygen limitation, therefore, seems to be the direct cause of reduced nitrogen fixation in moderately stressed nodules. With severe droughts other factors associated with tissue and enzyme alteration come into play. Recovery from such

stress involves regrowth of existing nodules in those species with a nodule meristem (most grain legumes), whereas species with non-meristematic nodules (spherical nodules) recover by growth of new nodules.

Assimilate Remobilization

In dry beans, much like other crop plants, reproductive development depends on vegetative organs as sources of carbohydrates, nitrogen, and other materials. During early stages of reproductive growth, allocation of newly assimilated carbon from the leaves is shifted from vegetative tissues to the developing reproductive sinks. As the reproductive demands become greater, and/or aggravated by severe soil moisture deficits, concurrent assimilation of carbohydrates is not sufficient and they must be remobilized from pools of nonstructural compounds accumulated in vegetative tissues during earlier growth stages.

Adams et al. (1978) have indicated undetectable to large levels of starch in roots and stems of 23 dry bean cultivars. One may question the role of such large amounts of nonstructural carbohydrates in non-economic vegetative tissues. The case in point is that of attainment of high starch levels in some genotypes and not others. As it turns out, the root and stem may act as temporary storage organs to partially correct for an apparent imbalance. Sebasigari (1981) observed this concept among grain legumes grown at East Lansing, Michigan. Loss of reserve assimilates was

well correlated with grain growth. This concept closely associates with that of selecting for higher harvest indices especially under drought conditions (Sinclair et al., 1984).

In late August of 1965 a killing frost occurred in Guelph, Canada. However, grain yield of maize doubled by early October (Daynard et al., 1969). This suggests that assimilates manufactured before the frost and stored in the maize stalks may have contributed to grain yield. Maize stalks accumulate carbohydrates, primarily as sucrose, glucose, and fructose (Loomis, 1935). In this crop, maximum amounts of soluble solids usually have accumulated 3-4 weeks after anthesis (Campbell and Hume, 1970) and rapid declines in stalk soluble solids often occur during grain filling (Daynard et al., 1969). Hume and Campbell (1972) found that most of the soluble solids that accumulated and disappeared were in internodes below the ear. When pollination and grain development were prevented, total soluble solids in stalks increased until the end of the growing season, indicating that the decline in stalk soluble solids during grain filling was caused primarily by translocation of metabolites from the stalk to the grain.

Using wheat, during the droughts of 1975 and 1976 in England, Gallagher et al. (1976) assessed the importance of photosynthesis after anthesis and the translocation of materials assimilated before anthesis in supporting grain growth, using a simplistic method. They expressed the

increase in grain weight from anthesis to final harvest (dWg) by the following equation:

$$dWg = dWt - dWs \quad \text{.....(6)}$$

where dWt is the increase in total crop weight, and dWs is the increase in weight of plant parts other than the grain between anthesis and harvest. The largest portion of dWs consists of the stem and for brevity this term is referred to as stem weight. In a determinate plant dWs/dWg is the fraction of final grain weight apparently derived from translocation of materials assimilated before anthesis. In 1975 and 1976, when production of dry matter after anthesis was smaller in relation to requirements for wheat grain growth, the contribution of translocated materials to grain yield was much greater. These measurements showed that pre-anthesis assimilate contribution to grain yield in wheat was 35% in non-stressed plants and 56% in stressed plants.

Thorne (1966) indicated that in cereals the pre-anthesis assimilate contribution is small, being no more than 20% under non-stressed conditions. The 35% contribution indicated by Gallagher et al., (1976) probably was an overestimation. Using in situ labeling, with radioactive carbon, of the whole crop canopy at frequent intervals before and after anthesis, Bidinger et al. (1977) reported lower contributions, viz: 13% and 27% for wheat plants under non-stressed and drought-stressed conditions,

respectively. They also reported 12% and 17% assimilate contribution for barley (*Hordeum vulgare* L.) plants under similar respective conditions.

McCaig and Clarke (1982) have shown that carbohydrates accumulate in wheat stems to a maximum (25% to 48% of total biomass) about the time of anthesis and then decline as maturity is approached. They reported significant differences in stem carbohydrate levels between wheat and oats (*Avena sativa* L.) and between cultivars in either species. A controlled method is required to reveal genotypes that can sustain translocation-based kernel growth in the absence of photosynthesis. Leaf removal after anthesis was found to affect kernel growth differentially among various genetic materials (Bremner, 1972). Blum et al. (1983) destroyed all the spring wheat's important photosynthetic tissues, i.e. awns, glumes, leaf laminae and parts of the spike-peduncle, and leaf sheaths with a chemical desiccant. They grew four spring wheat cultivars (Lakhish, Cajeme, V591-51, and V582-58) under non-stress conditions in a mediterranean environment in Israel. They sprayed magnesium chlorate, a chemical desiccant, 14 days after anthesis. This induced earlier stem dry matter loss in two cultivars (Lakhish and V591-51, group I), and not in the other two (Cajeme and V582058, group II). The pattern of stem dry matter loss in the group II cultivars did not differ between sprayed and unsprayed treatments. Kernel growth rate was reduced by the treatment, to a relatively

lesser extent in group I than in group II. They concluded, therefore, that cultivars of group I were better than cultivars of group II in sustaining kernel growth in the absence of photosynthesis and this difference was associated with a respective difference in stem reserves remobilization. From the breeders' point of view, however, it should be emphasized that a highly productive cultivar should be capable of remobilizing reserve assimilates under both stress and non-stress conditions. A high yielding cultivar that does not remobilize reserves under non-stressed seasons may not be the best yielder under stressed conditions.

Maintenance of Turgor

As water deficits develop, water is removed from the cell and as a result, the solutes inside the plasmalemma get concentrated leading to reduction in water potential. Water moves from high to low water potential. Therefore, this acts as a driving force to replenish the cellular water content. In some species water stress not only concentrates solutes but induces solute accumulation, a process alluded to earlier called 'osmotic adjustment' or 'osmoregulation.' This can be explained if solute accumulation does not follow the Boyle-van't Hoff relationship which is expected if concentration of solute occurs with only loss of water. Using six potato (*Solanum tuberosum* L.) cultivars, Levy (1983a) reported genotypic variability in osmoregulation

capacity. Cultivar 'Alpha' had the highest and 'Troubadour' had the lowest osmotic adjustment. Concomitantly, Alpha had maintained the highest turgor potential under drought whereas Trobadour had the lowest values indicating a relationship between the degree of osmotic adjustment and maintenance of turgor. Alpha produced the highest tuber dry matter yield under drought whereas Troubadour produced the lowest yield under similar conditions (Levy, 1983b).

Osmotic adjustment in a range of crop species has been observed in response to diurnal and seasonal changes in water status (Hsiao et al., 1976) leading to full or partial turgor maintenance. Turner and Jones (1980) reported that full or partial turgor maintenance during a drying cycle has been shown in the leaves of 14 species, in the root and hypocotyl of two more species, and in both the leaves and floral parts of wheat. Osmotic adjustment has also been shown in rice (*Oryza sativa* L.) (Cutler et al., 1980), sorghum (*Sorghum vulgare* L.) (Hsiao et al., 1976), sunflower (Takami et al., 1981) and maize (Turner, 1975). However, it has been shown not to occur in soybeans (Turner et al., 1978) and sugarcane (*Saccharum Officinarum* L.) (Ingram and Moore, 1985).

Diurnal changes in osmotic adjustment help maintain physiological processes such as leaf expansion and photosynthesis that otherwise would be impaired by low turgor (Hsiao et al., 1976). They also hasten the unrolling of leaves wilted by low turgor (O'Toole and Moya, 1978).

Osmotic adjustment that occurs during a drying cycle, while rarely fully maintaining physiological functions, slow the rate of loss of physiological activity (Turner and Jones, 1980). Morgan (1980) has also reported genotypic variability in osmotic regulation among wheat genotypes. He crossed cultivars that showed osmotic adjustment with those that did not and selfed the progeny to the F4 generation. He showed that this character is heritable and can be selected for. After selfing, he came up with two populations that differed significantly in osmotic adjustment. These two populations were then grown under both drought and non-stress conditions. The group that was able to osmoregulate produced significantly higher grain yields than the other, possibly due to higher photosynthetic rates, lower respiration rates, and higher partitioning coefficients. However, negative associations between osmotic adjustment and productivity are expected because there is a biological cost in solute accumulation (Jefferies, 1981).

Changes in Tolerance to Dehydration

The ability of tissues to withstand dehydration becomes very important under conditions of severe and prolonged drought when other mechanisms have either failed or been exhausted. The cell membranes constitute a central site of activity for cellular metabolic processes. Their tolerance for dehydration stress is important (Bewley, 1979). It is

believed that dehydration tolerance may involve a complex of mechanisms at the enzyme and membrane levels that reduce protein denaturation and membrane degradation. Sullivan (1983) developed a fairly rapid method of assessing the rate of injury to cell membranes of sorghum by dehydration through the measurement in vitro of electrolyte leakage from water stressed leaf discs. This method seems applicable to other crop species (Blum and Ebercon, 1981) including bean plants (Tesda, 1984). Changes in dehydration tolerance occur with different rates of drying. Slow rates of drying enhance dehydration tolerance (Gaff, 1980), possibly due to the accumulation of solutes such as sugars and proline that protect proteins and aid in recovery. Free proline amino acid accumulation occurs in leaves of many plant species subjected to environmental stresses, including drought (Stewart and Hanson, 1980). However, that proline accumulation constitutes a drought-adaptive trait is rather controversial.

Working with barley, Hanson (1980) concluded that proline accumulation actually is an indicator of drought susceptibility rather than drought resistance. He used two barley cultivars that differed in dehydration avoidance. The nondehydration-avoiding genotypes accumulated more proline when grown under drought in the field. Similar results were reported in cotton (Ferreira et al., 1979). However, when proline accumulation is assayed at a given water potential in all cultivars this characteristic seems

to be related to leaf survival rate during stress and recovery of growth upon rehydration (Singh et al., 1973; Blum and Ebercon, 1976). The possible role of proline may be to serve as an energy pool to be used upon recovery (Blum and Ebercon, 1976; Bogges et al., 1978) or as an osmotic agent (Gould and Measures, 1977). Proline is probably an effective cryoprotectant against freeze-induced dehydration of cells, possibly through its effect on membrane stabilization.

Mycorrhizae

'Mycorrhiza' is a term that refers to a mutualistic, symbiotic relationship formed between fungi (Greek *mukes*) and living roots (Greek *rhiza*) of higher plants (Miller et al., 1986). This type of association has been observed in most plant species except the Cruciferae and Chenopodiaceae. Mycorrhizae have been classified (Harley and Smith, 1983) through a description of 7 types, namely vesicular-arbuscular, ecto-, ectendo-, arbutoid, ericoid, monotropoid, and orchid. The vesicular-arbuscular mycorrhizae (VAM) comprise the major type observed in crop plants. They produce structures known as vesicles and arbuscules, as well as hyphae and spores. Arbuscules are intracellular, haustoria-like structures that develop by a repeated, dichotomous branching of hyphae. Vesicles are sac-like, usually terminal swellings at the tip of hyphae. The hyphae can be formed both within the root and outside it. The

transfer of mineral nutrients and other materials from the soil to the host plant is mediated by these hyphae.

Safir et al. (1971, 1972) was the first group to report changes in the water relations of a plant when infected by a VAM fungus (*Endogone mosseae* L.). Soybean plants have been observed to suffer from drought stress in central Illinois under adequate soil moisture levels (Boyer et al., 1980). They contributed this to lack of enough root density to absorb enough water to meet atmospheric demand for moisture. However, Safir et al. (1971, 1972) showed that under well-watered conditions and low soil nutrition, mycorrhizal soybean plants had hydraulic conductivities 40% higher than nonmycorrhizal controls and showed no symptoms of drought stress. Addition of nutrients nullified these differences. It was suggested (Safir et al., 1972) that roots were the sites of the increased hydraulic conductivities of mycorrhizal plants based on comparisons of recovery rates from moderate water stress of whole plants with severed roots. Two possible explanations for increased conductivity exist. One is that it is possible that the mycorrhizal hyphae in the soil enable mycorrhizal plants to take up water. The other, which was discounted by Safir et al. (1972), is that mycorrhizal hyphae within the root could provide a low resistance pathway for water movement.

Under limited water conditions in the short term, Safir et al. (1971, 1972) demonstrated that mycorrhizal soybean leaves recovered from moderate water stress faster than

nonmycorrhizal controls after soil rehydration. These differences were eliminated under high nutrient levels. Nelsen and Safir (1982) conducted a long term study by exposing onion (*Allium cepa* L.) plants (mycorrhizal and nonmycorrhizal) to 7 cycles of drought. The regime started 4 weeks after seeding and lasted 8 weeks. Mycorrhizal plants at 8 and 12 weeks, which were given low P levels, were more drought tolerant than nonmycorrhizal onions given high P levels. Drought tolerance of mycorrhizal plants was shown by greater fresh and dry weights and by higher tissue P concentrations. Nutrient analysis showed that the P concentrations of the nonmycorrhizal plants were at levels (0.1 to 0.3% dry weight) known to retard the growth of plants (Epstein, 1972). But P was not limiting in the mycorrhizal plants. It is not surprising that mycorrhizal plants are able to absorb P during drought considering their extensive fungal network in the soil.

Water-use Efficiency

Wittwer (1975) identified water as the second-most important factor, behind land area, to increasing food production. He argued that a high research priority should be given to improvement in the efficiency of water use by crops. And knowledge of the factors influencing water-use efficiency has continued to be an objective in many studies. As opposed to the sense of the word 'efficiency' in the physical sciences, water-use efficiency (WUE) does not tend

toward unity if it is increased and can never reach it in a crop (J. L. Monteith, personal communication). However, the term is widely applied in crop studies where its place has been established.

Sinclair et al. (1984) defined WUE as a ratio of biomass accumulation, expressed as carbon dioxide assimilation (A), total crop biomass (B), or crop grain yield (G), to water consumed, expressed as transpiration (T), evapotranspiration (ET), or total water input to the system (I). The time-scale for defining WUE can be instantaneous (i), daily (d), or seasonal (s). Water-use efficiency is written symbolically as a function of these three variables. For example, WUE (B, I, s) refers to water-use efficiency expressed as total crop biomass (B) to total water input into the system (I) for a seasonal observation. It is calculated using the following formula:

$$\text{WUE (B, I, s)} = \frac{\text{Total biomass production (g)}}{\text{Total water applied (kg)}} \quad \dots(7)$$

One approach to increasing the use of the total available water is the development of crops with better rooting systems. Greater rooting density and deeper rooting depths increase the surface area exposed to soil moisture leading to an increase in the amount of soil moisture absorbed by the plant (Taylor, 1983). Water reserves previously

unavailable to the transpiring plant could be made available with an improved root system. However, a deeper and more extensive rooting system may have disadvantages. A greater root biomass would result in lowered harvest index. Carbohydrates would be diverted to construction and maintenance of a larger root mass. In a prolonged drought, rapid and more efficient use of stored soil water may be deleterious. A less effective, slow growing root system may leave some water reserves that would be partially available for surviving a drought.

Improvements in harvest index result directly in increased water-use efficiency based on seed yield. Substantial improvement in harvest index seems to be a desirable selection objective under conditions of limited moisture where drought stress, especially during reproductive growth, can lead to greatly reduced harvest indices. In Australia, Passioura (1972) describes manipulation of the water conducting system in plants for stress and nonstress environments. Conservation of soil moisture for later extraction is sought by narrowing the diameter of the vascular vessels by genetic selection. Shorter season cultivars that complete their life cycle and produce a high harvest index before the available water supply is exhausted is another approach. Cowpea (*Vigna unguiculata* (L.) Walp.) yields have been increased in a drought environment by developing lines with shorter growing seasons (Turk et al., 1980).

Drought and Crop Yield

Crop growth and development can be divided into phases, namely; vegetative and reproductive growth periods and various stages within either of these periods (Fehr and Caveness, 1977). During the early part of the summer field-grown soybeans and maize are frequently under moisture stress which limits leaf expansion and stem growth during the day and may be sufficiently severe to limit photosynthesis during part of the day. Usually there is sufficient soil moisture to rehydrate the plants at night (Slatyer, 1967). As the season progresses and if there is limited rainfall the roots extract water from the surface and as they grow downward the depth of soil depletion gets deeper. During years when combined fall and spring rainfall does not recharge the moisture reserves droughts during July reduce canopy size. This is a conservative characteristic because if conditions are reversed the amount of leaf area attained will limit assimilate production for seed filling. Severe droughts will cause reduction in light interception and numbers of pod-bearing nodes.

The most damaging drought in crops is that which occurs during the reproductive period and causes massive reductions in seed yields. In maize, a determinate species, a severe 4-day drought during some phases of the reproductive period is critical. From silking and a fortnight thereafter seems to be the most sensitive period of crop growth to drought (Claassen and Shaw, 1970). The number of kernels per ear is

the most drastically reduced yield component. Drought during this period causes barrenness in maize. In small cereal grains drought during the flower initiation and booting stages can reduce grain yields by about 25% and 65%, respectively (Hanson and Nelsen, 1980). Drought stress at different stages of indeterminate soybean development and its effect on seed yield and yield components was investigated by Shaw and Laing (1966). Indeterminate varieties have the potential to flower over longer periods of time and as a result may not be as sensitive to drought as determinate varieties. Short periods of drought during early flowering of soybean causes little reduction in seed yield; even though water stress caused flower abortion, the plant has time to generate a new flush of flowers after the drought. The number of pods per plant is the yield component most affected. And the growth stages most sensitive to drought are late pod development and mid-seed filling. At late pod development, Shaw and Laing (1966) observed pod abortion, poorer pod development (fewer seeds per pod), and reduced photosynthesis (reduced seed weight). During later stages of seed filling, although there was some effect on pods per plant and seeds per pod, the greatest influence was on seed weight. Determinate soybeans, however, behave similar to other determinate species, e.g. maize.

Therefore, drought resistance should ultimately be related to yield as a major economic consideration and as an integrator of the effects of plant drought stress in time and space. Yield under drought stress is a function of the genotype's yield potential (Mederski and Jeffers, 1973; Fischer and Maurer, 1978). Yield under such conditions may not be a reliable selection criterion because the genetic component of variation relative to the environmental component of variation is usually low (Daday et al., 1973). If drought is uniform over the population and it is shown to be the major environmental factor then yield under drought is an important factor. The problem of dissociating the effect of drought resistance from that of potential yield was resolved by Fischer and Maurer (1978) using an index of susceptibility (S):

$$Y_d = Y_p(1-SD) \quad \dots\dots\dots(8)$$

where Y_d is stress yield, Y_p is potential yield under nonstress conditions, and D is the drought intensity. D is calculated as $1-(X_d/X_p)$, where X_d and X_p are the mean yields over all cultivars tested under stress and nonstress conditions, respectively, and ranges from 0 to 1. S is the drought susceptibility index. A cultivar with lower S than another has higher drought resistance. Although S should be independent of drought intensity, its exact value will depend on cultivars included in the calculation of D . Using

S, Samper (1984) was able to show significant differences among dry bean genotypes in drought resistance. Although yield differential has been used to show differences in drought resistance between snap bean cultivars (Bonanno and Mack, 1983) it is a poor method.

Stability analysis (Finlay and Wilkinson, 1963; Eberhart and Russell, 1966) is very useful in defining drought resistance in terms of yield, provided that the major component of variation in the environmental index as used in the analysis can be attributed to the water regime (Nor and Cady, 1979; Blum, 1980). Laing and Fischer (1977) used the approach to show genotypic differences in drought resistance of wheat as shown by their yield under different environmental indices. Two cultivars, Mirian and 676, performed better than others at low soil moisture conditions. Their intercept (a) was higher than the other cultivars, Lakhish and Cajeme, which performed poorly. Therefore, differences in drought resistance among cultivars can be obtained by the intercept (a) of the regression line in a stability analysis. Potential yields under nonstress conditions are evaluated through their relative slopes (b). In their case, Laing and Fischer (1977) concluded that Mirian and 676 were both drought resistant but 676 had a higher yield potential than Mirian.

MATERIALS AND METHODS

Empirical equations are available that can be used to predict net primary productivity (NPP) at a particular location given environmental variables (Lieth, 1976). Each equation requires the use of but a single environmental variable. Such equations are given below:

$$NPP = 30[1 - e^{-0.000644W}] \dots\dots\dots(9),$$

where W = mean annual precipitation (mm);

$$NNPP = 30/[1 + e^{1.315 - 0.119T}] \dots\dots\dots(10),$$

where T = mean annual temperature (C);

$$NPP = [(1.5 \times PET) - 100]/100 \dots\dots\dots(11),$$

where PET = potential annual evapotranspiration (mm).

Such equations can be used to determine the most probable limiting environmental factor on crop productivity at any one location. Based upon Malawi Weather Tables (Malawi Government, 1982), three environmental variables were obtained from 19 different locations across that country. These variables were mean annual precipitation (mm), mean annual temperature (C) and PET (mm). PET was calculated as was done by Turc (1955) using the equation below:

$$PET = P(mm) / [0.9 + (P(mm)/L)^2]^{0.5} \dots\dots\dots(12)$$

where P = precipitation (mm), $L = 300 + 25T + 0.05T^2$, and T = mean annual air temperature (C). Calculations were done by the CALC procedure of the MSTAT (version 4) statistical package and NPP values were obtained and on an assumption of a growing season of 90 days and harvest index of 50% these values were adjusted to those in Table 1.

This type of analysis helps identify the most limiting environmental variable on crop productivity. From the table, mean air temperature consistently gave the highest amount of yield and therefore it does not seem to be limiting. On the other hand, mean annual precipitation consistently gave the least yields at all locations except at Mimosa, Bvumbwe, Chichiri, Nkhata-Bay, Mzuzu, and Thyolo, where evapotranspiration was probably more limiting than precipitations. As a result, one would conclude that moisture is the most limiting environmental factor in crop productivity and is the factor that plays the greatest role in evolution of crop plants under Malawian conditions. Therefore, the studies conducted here were limited to moisture stress as a factor to which some Malawian bean components are adapted in order to maintain themselves and the mixtures in general.

Malawi landrace bean genotypes were grown in three experiments at the Crop Science Field Laboratory in East Lansing, Michigan during 1984, 1985, and 1986. The

Table 1. Comparison of environmental parameters by their effect on net primary productivity across 19 locations in Malawi.

Location	Mean ann. temp.	Mean ann. precip.	A	B	C
	(C)	(mm)	-----kg/ha-----		
Chitipa	21.0	1038.8	2588	1653	2150
Karoga	24.8	1164.8	2827	1788	2414
Mzimba	19.7	864.3	2491	1447	1670
Mzuzu	17.9	1218.3	2339	1842	1474
Nkhata-Bay	23.3	1694.6	2742	2249	1637
Chitedze	20.1	919.1	2522	1514	1661
Lilongwe	19.7	847.5	2491	1426	1775
Nkhota-kota	23.8	1630.8	2767	2202	2223
Salima	24.2	1281.2	2796	1903	2350
Chichiri	19.9	1122.1	2506	1744	1652
Dedza	17.7	905.2	2326	1498	1524
Makoka	20.5	1044.1	2556	1659	1627
Chileka	22.4	857.5	2685	1439	2485
Mangochi	24.3	823.6	2799	1396	2250
Mimosa	21.6	1724.5	2631	2271	1383
Bvumbwe	19.3	1158.9	2455	1782	1262
Thyolo	20.9	1273.1	2578	1896	1411
Ngabu	26.2	811.4	2902	1380	2167
Makhanga	25.5	764.5	2867	1318	2119

A = seed yields calculated based on mean annual temperature;

B = seed yields calculated based on mean annual
precipitation;

C = seed yields calculated based on mean annual
evapotranspiration.

experiment conducted in 1984 was a field maize and bean intercropping study. A similar experiment was carried out in 1985 at the Montcalm Potato Research Facility about 80 miles north-west of East Lansing. The experiments conducted in 1985 and 1986 at East Lansing were near and under the rain-out shelter, respectively, in a field-simulated crop culture to determine water-use efficiency of the bean genotypes under both well-watered and drought conditions.

Intercropping Experiments

East Lansing, 1984

By planting maize and beans in one row it was envisaged that the aggressive species, maize, would out-compete the bean for moisture, especially if the maize was sparsely populated to reduce shading and both crops were fertilized adequately. Eighteen selected pure bean lines (arranged as accessions 1 to 18), three of which were Type I's (accessions 2,3 and 17) and the rest mostly Type IV's, were grown in single-row plots in a split-plot design. The main plots consisted of two rows of a bean genotype. Sub-plots were cropping systems consisting of a single bean row in monoculture and another single bean row intercropped with maize in the same row. Each main plot was replicated three times.

Land Treatment and Crop Culture

A site consisting of heavy, medium, and light soils was selected. Three replications were arranged so as to reflect the soil differences, with the first replicate on the light soil, the second replicate on the medium soil, and the third replicate on the heavy soil. The area was first plowed with a disc plow. On 12 June 1984 metolachlor and chloramheu were applied convert to at 2.36 kg/ha a.i. and 1.46 liters/ha, respectively, to control weeds. Adequate fertilizer Compound -10:20:20- was applied at 230 kg/ha on 13 June to remove interspecies competition for the major nutrients. Plating was done on 14 June. A main-plot consisted of two rows 3m long. The length of rows was dictated by availability of seed. To minimize competition through shading of the bean plants by maize, the inter-row spacing was 1m, conforming to the recommended space between ridges in Malawi. An early Michigan single cross maize hybrid (M422) was used in all intercropping sub-plots to provide competition for soil moisture. The maize was planted at an intra-row spacing of 1m and four seeds to a hole, again to conform to three plants of maize per hill after thinning two weeks after emergence. The beans were planted at an intra-row spacing of 20 cm in the same row with maize, a typical cropping system in Malawi, as one sub-plot, and in monoculture, at the same spacing, in the other row as a second sub-plot.

Soil Moisture Tension

The availability of moisture was monitored using the 'Quick Draw' soil moisture probe (Soil Moisture Equipment Corp., Santa Barbara, Ca) by determining moisture tension (kPa). Soil moisture tension was read at 15 cm away from the maize hill, between the hill and a bean plant in intercropping and anywhere inside 0.5 m borders in monocultures. Readings were recorded at 47, 68, and 82 days after planting (DAP). Using this method one can irrigate beans if soil moisture tension approaches or exceeds about 50 kPa; in other words, the sub-plot that exceeds 50 kPa has reached moderate drought stress levels.

Porometry and other related characteristics

Using a steady state porometer (LiCor Inc., Lincoln, NE) leaf diffusive resistance (s/cm), leaf transpiration [$\mu\text{g H}_2\text{O}/\text{cm}^2/\text{s}$], quantum [$\mu\text{E}/\text{cm}^2/\text{s}$], relative humidity (%) near the leaf, and leaf temperature (C) were obtained from both sub-plots in the entire experiment at 70, 78, and 85 DAP. In this study readings were taken both just before dawn (pre-dawn) and in mid-afternoon. Diffusive resistance was the resistance offered by the leaf to the escape of moisture as opposed to that of carbon dioxide uptake. The two are different only due to differences in molecular weights of the two compounds. Leaf diffusive resistance was the combination of both the mesophyll and the stomatal resistances.

Leaf Moisture Retention Capacity (LMRC)

At 72 DAP three young, fully expanded leaves were sampled from bean plants in each sub-plot. Their separate fresh weights (FW) were recorded. The leaves were then placed in shaded open air to dry for 24h. After this period the leaves were weighed again and these data are here-in-after called air-dried weight (ADW). At this point the leaves were oven-dried at 70C for 96h. These data are here-in-after called oven-dried weight (ODW). Leaf moisture retention capacity was calculated using the following formula:

$$\text{LMRC} = [\text{ADW} - \text{ODW}] \times 100 / [\text{FW} - \text{ODW}] \quad \dots\dots\dots(13)$$

where ADW is air-dried weight (g); ODW is oven-dried weight (g); and FW is fresh weight (g).

Specific Leaf Weight (SLW)

At 74 DAP, five young, fully expanded leaves were sampled from all sub-plots. The leaves were dissected into leaflets which were then run on a portable area meter (model LI-3000, LiCor, Lincoln, NE) to determine their leaf area (LA). After determining leaf area the leaves were oven-dried at 70 C for 96h to obtain their oven-dried weights (ODW). Specific leaf weight (SLW) is a growth analysis parameter that was calculated as follows:

$$SLW = ODW/LA \quad \dots\dots\dots(14)$$

where ODW is leaf oven-dried weight (mg), and LA is leaf area [cm²].

Yield and Yield Components

At maturity three plants were sampled at random from each plot. The stem was cut at the base. At the field laboratory each plant was dissected into various plant parts, although much fewer leaves were retained on the stem at this stage. All plant parts were oven-dried at 70 C for 72h and the following data were obtained: stem weight, number of pods, seed number and seed weight. Harvest index was 'apparent' due to lack of some leaves that had been shed in most bean genotypes but was calculated as follows:

$$AHI = \text{seed weight} \times 100 / \text{total biomass} \quad \dots\dots\dots(15)$$

Montcalm, 1985

A site consisting of a slight gradient in slope and a sandy soil (Montcalm sandy loam/ loamy sand) was selected in 1985. This was thought to provide rapid percolation of water, especially on the upper side, so as to emulate drought conditions. Dual (2.36 liters/ha) and Eptam (1.46 liters/ha) were applied on 10 June 1985 to control weeds. A mixed fertilizer -19:19:19- was applied at 341 kg/ha. Planting was done on 13 June and 14 June for bean and maize,

respectively. The same short season Michigan maize (M422) used in 1984 was planted in 1985. An experimental design similar to that used in 1984 was used in 1985. One difference was the length of rows which were extended to 5m. The following additional cultivars were included: Montcalm (from Michigan State University, U.S.A.), BAT 47, BAT 85, BAT 337, and BAT 798 (from C.I.A.T., Colombia) and Bayo Madero (from I.N.I.A., Mexico). Germination of the untreated materials (all except maize and Montcalm cultivars) was very poor and replanting was done on 30 June, 1985. As a result limited data were obtained from that nursery.

Two young, fully expanded leaves were sampled at 53 DAP for water retention capacity data. Fresh weights (FW) were obtained and the leaves were put in a shaded space to air dry for 48h. Air dry weights (ADW) were obtained and the leaves were then oven dried at 70 C for 72h to obtain ODW. The formula (12) was used in calculating leaf water retention capacity.

Porometry was done in a similar manner to that followed in 1984.

Water-use Efficiency Experiments

1985 WUE Experiment

Crop Culture

In 1985, five landrace dry bean genotypes (from Bunda College of Agriculture, University of Malawi), Montcalm (from Michigan State University, U.S.A.), BAT 47 and BAT 477 (from C.I.A.T., Colombia), Chiapas 7 (from I.N.I.A., Mexico) and three cowpea cultivars (from I.I.T.A., Nigeria) were grown in 20cm diameter and about 1m high seam-sealed black plastic bags secured in place by wire mesh. Fifty-five kg of field soil was put in each bag. Five grams of a mixed fertilizer -19:19:19- were placed 10cm deep. Seeds were pre-germinated for 48h and seedlings that were as uniform as possible were selected for planting. Two treatments were imposed and these were: a. adequate supply of water constituted well-watered plots and b. restricted supply of water constituted the drought plots. Well-watered treatments received 6 liters of water at planting, and additional water being supplied as necessary until a total of 9 liters of water had been applied by the stage of physiological maturity. The drought plots received only 2 liters at planting, and additional water being given fortnightly during the reproductive period until a total of 3 liters had been applied by physiological maturity. Planting was done on 30 June 1985, 24h after the initial and heavy dose of water was applied. Sevin was applied at 1.42 hg/ha on 28 July 1985 to control the mexican bean beetle.

Porometry and related characteristics

A steady state porometer (LiCor, In., Lincoln, NE) was used at 28 DAP in 1985 to determine leaf diffusive resistance, leaf transpiration, quantum, relative humidity near the leaf, and leaf temperature. Again, diffusive resistance was the resistance imposed by the leaf to moisture escape as opposed to that against carbon dioxide uptake.

Stem and leaf elongation rate

The length of the stem from the base to the terminal bud was measured at 32 and 56 DAP as H1 and H2 in cm, respectively. The difference between H2 and H1 represented growth in 14 days and the rate was expressed on a daily basis. Leaf lengths were taken from small developing terminal leaflets at 32 DAP as L1. Leaf lengths were measured from the same leaflets at 35 DAP as L2. The length difference between L2 and L1 in cm in 3 days was expressed as rate on a daily basis. In 1986 the equation cited by Gardner et al. (1985) was used to calculate leaf area from which leaf area expansion was derived.

Pod weight and other characteristics

Harvesting was done on 10 October 1985. Plants were cut at the base and taken indoors where they were dissected into various plant parts, i.e. stems, leaves, and pods. The number of pods was obtained. Plant parts were then placed

in the oven to dry for 72h at 70 C. Total biomass was the sum of all the dried plant parts. Leaf weight ratio (LWR) was calculated using the following formula:

$$\text{LWR} = \text{Leaf weight (g)} / \text{total biomass (g)} \quad \dots\dots(16)$$

Water-use efficiency was calculated using formula (7).

1986 WUE Experiment

Crop Culture

In 1986 a similar experiment to that conducted in 1985 was carried out under the rain-out shelter. This time a different set of genotypes was used as given in Table 2 below. Planting was done on 10 June and all cultural practices were conducted as in the previous experiment. However, the imposition of treatments was slightly different from that in 1985. No large doses of water were applied at planting. Instead all plots were well-watered up to the beginning of flowering. From then onwards well-watered plots were supplied with water every other week. Data were obtained as described in the previous WUE experiment.

Table 2. Bean genotypes used in the water-use efficiency experiment (1986).

Entry	Acc. #	Origin	Pedigree
1	I86030	WH Tepary, Az	WH Tepary, Az
2	I86032	LEF-2-RB MX	LEF-2-RB MX
3	B76001	61065 MSU	N2/BTS
4	I86033	II-900-5-m MX	II-900-5-M MX
5	N80068	802702 MITA/MSU	N76001,61068, I81110,B-351
6	B82008	80B001-53 MSU	49-242/TUS/2xBM /3/MID
7	N81017	77011-F3 MSU	Kent/N2//PIJ/ BUN
8	I86040	Vita 3, IITA	
9	I86037	Acc.# 5, MALAWI	
10	I86039	Acc.# 6, MALAWI	

Statistical Analysis

All data obtained during the three years that these studies were carried out were analyzed using MSTAT version 4, a micro-computer statistical package developed, revised, and updated by the Department of Crop and Soil Science at Michigan State University, East Lansing, Michigan, U.S.A.

RESULTS

Microclimatology

In 1984 planting was done on 14 June. There was no significant precipitation from this date until 26 days later on 10 and then 11 July when about 33 mm of precipitation were received (Figure 1). This was convenient because a week later the early genotypes (accessions 2, 6, 10 and 14) started flowering and the precipitation received at this time prevented large losses in seed yields especially through reductions in number of pods/plant. However, there was no significant precipitation again for another 23 days until 4 August when 20 mm and then 30 mm four days later were received. It was during this second drought period that soil moisture was first sampled (31 July) with the tensiometer. Another stress period of 21 days ensued up until August 30 when 7 mm were received. The second soil moisture sample was taken during this stress period (21 August). The third sample was taken 5 days after the small drizzle (4 September). Generally, the 1984 crop season was highly moisture stressed, receiving only 287 mm over the entire period of May, June, July, August, and September, distributed as 102, 4, 50, 65, and 66 mm, respectively. June had virtually no rainfall. On the other hand, pan evaporation totalled 810 mm over the same crop season. Therefore, although there might have been adequate moisture

1984

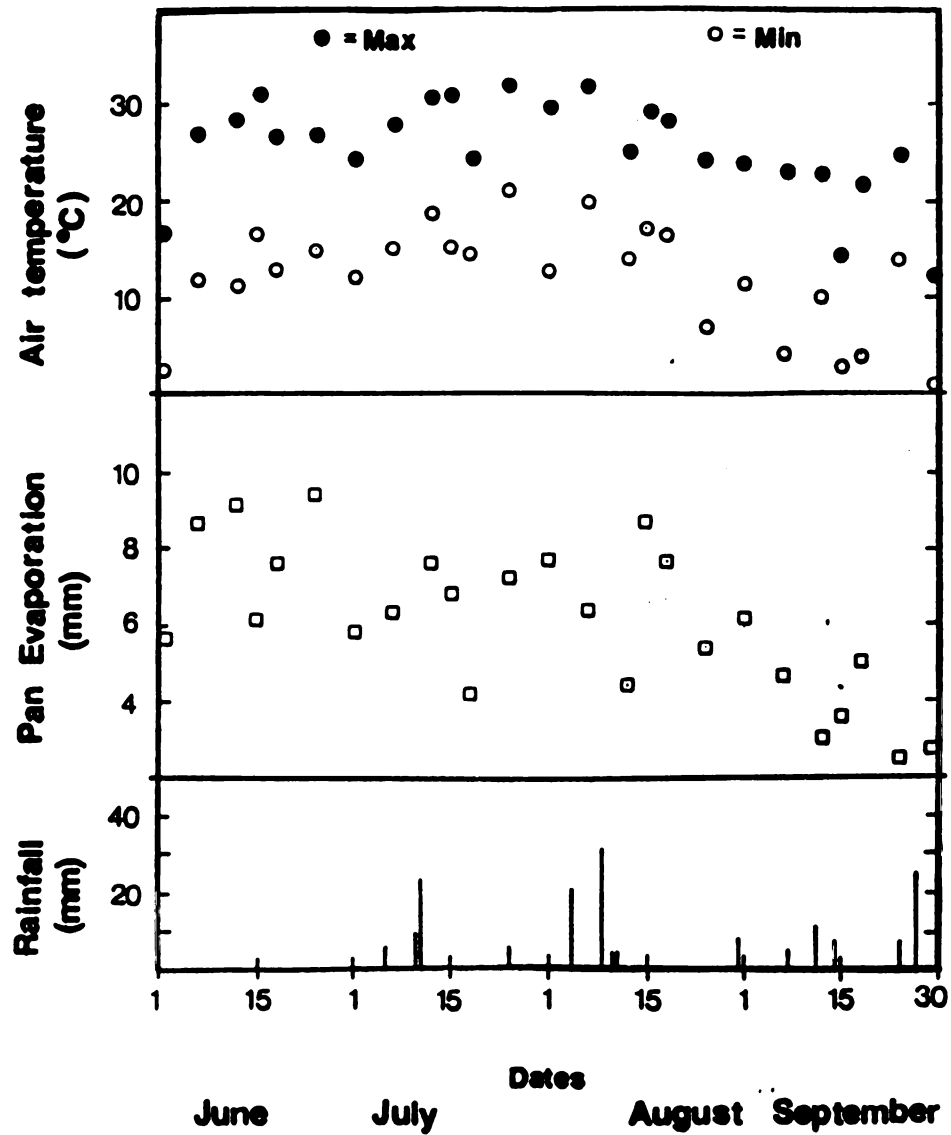


Figure 1. Meteorological characteristics at East Lansing, Michigan, 1984.

reserves, drought stress was rampant merely due to poor distribution of precipitation and high atmospheric demand expressed here in terms of evaporation.

In 1985, at East Lansing, the amount of water applied to beans was controlled. However, the distribution of precipitation during this crop season was better (Figure 2) than in the previous year. Amounts of precipitation obtained were 71, 57, 53, 96, and 88 mm for May, June, July, August, and September, respectively. This represented almost 100 mm over the previous season. However, atmospheric demand for moisture (858 mm) was comparable to the previous year.

The distribution of precipitation at Montcalm in 1985 was good and much better than that at East Lansing in 1984 (Figure 3). A total of 351 mm was obtained and distributed as follows: 40, 72, 67, 121, and 51 mm in May, June, July, August, and September, respectively. A pan evaporimeter was not installed as yet and so pan evaporation data were not obtained.

1985

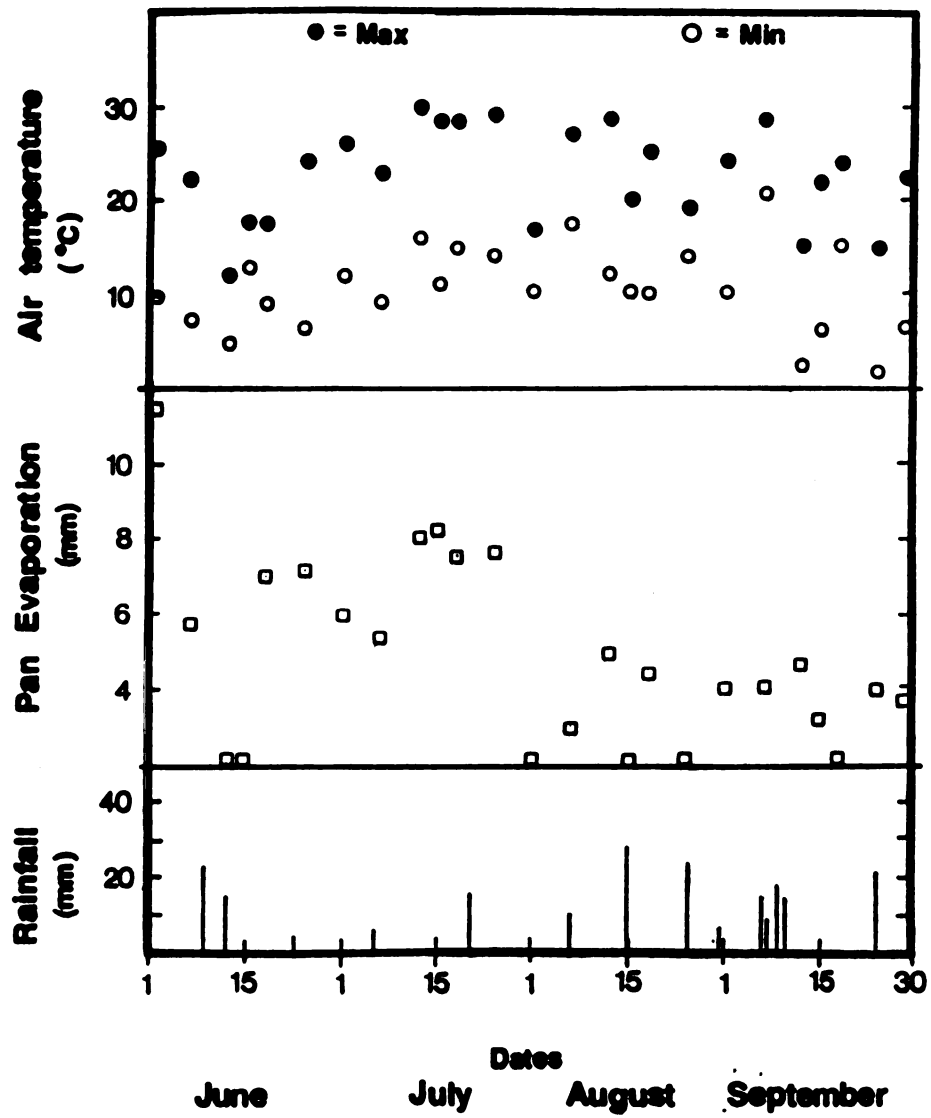


Figure 2. Meteorological characteristics at East Lansing, Michigan, 1985.

1985

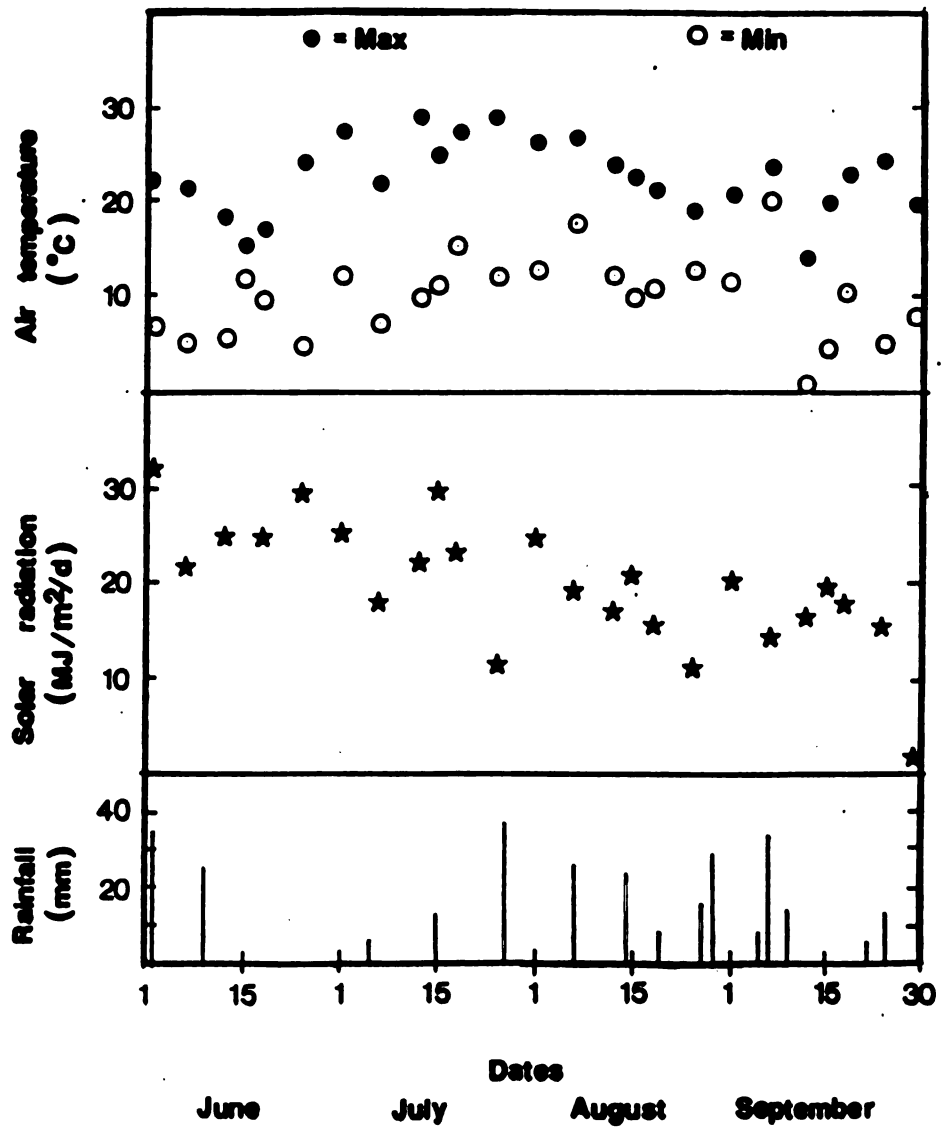


Figure 3. Meteorological characteristics at Montcalm, Michigan, 1985.

Intercropping Experiments

1984 Intercropping Experiment

As was shown earlier (Figure 1), there was lack of precipitation from plating up to near flowering and then another period of lack of precipitation that extended into the seed-filling stage. The result of these stress periods was a general increase in soil moisture tension from 47 to 81 DAP (Figure 4). The increase meant that as water evaporated and/or was taken up by the plants the remaining water had to be taken up by a larger force than previously. This indicates that the amount of moisture in the soil was decreasing. This decrease was generally faster between 68 and 82 DAP than between 47 and 68 DAP, the mean increases being 24.1 kPa and 8.75 kPa, for the respective periods. This was probably due to a rather active reproductive period (seed-filling) when water is needed in the plant for translocation of assimilates from current photosynthesis and/or remobilization of assimilates from previous sinks. Moisture depletion was significantly greater in the soil under intercrops than under monocultures. At the first sampling (two weeks after a rain of 33 mm) the amounts of soil moisture were similar in soil under intercrops as those under monocultures. However, with subsequent lack of precipitation and with high atmospheric moisture demand, there was significantly less soil moisture under intercrops than under monocultures. This difference became even wider

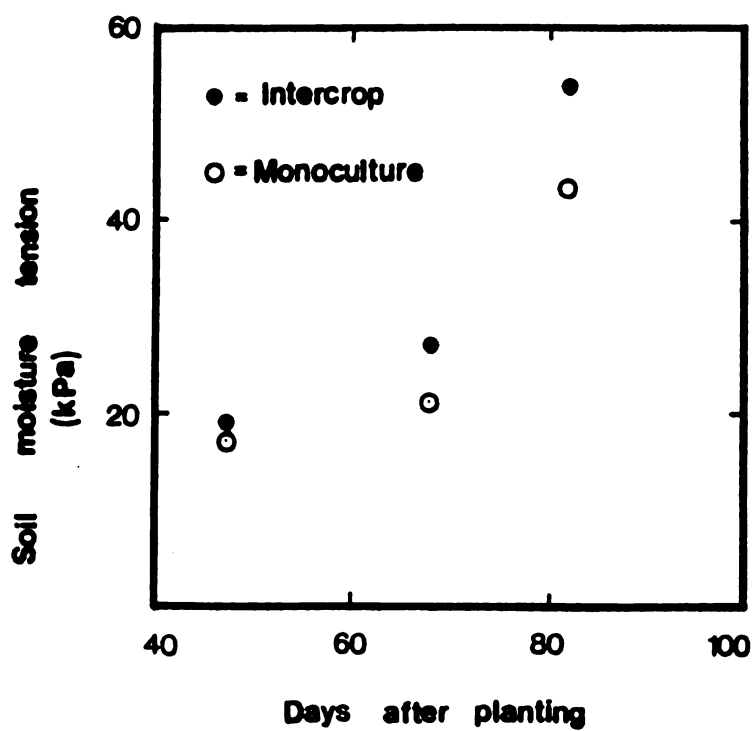


Figure 4. Moisture tension of soil under monoculture and intercropped Malawian landrace dry beans (1984).

(Figure 4) by 82 DAP. By this time, intercropped beans had reached a point where irrigation would have been necessary (at least 50 kPa) whereas those under monocultures had not reached that point as yet (Figure 4). This observation indicates that beans grown in intercropping systems with maize rely on reduced soil moisture levels and, should a drought occur, it would affect them before it would affect beans grown under monoculture systems. One could speculate that some Malawian landraces, selected naturally under intercropping systems, are expected to tolerate drought conditions better because the two stresses (intercropping and drought) seem to be confounded and not quite separable. Stated differently, drought seems to be a factor of the environment that some Malawian landraces of beans have had to overcome in order to have been selected naturally as they did and maintain themselves under the cropping systems prevalent in Malawi. In most of these systems, main crops out-compete the intercrops for water, light and nutrients.

Leaf diffusive resistance was measured on three dates, namely; 70, 78, and 85 DAP in 1984. Both pre-dawn and mid-afternoon resistances were measured. Pre-dawn leaf diffusive resistances were similar in leaves of different genotypes and between cropping systems but were significantly lower than mid-afternoon diffusive resistances (Tables 3, 4, and 5). There were no differences among genotypes nor between cropping systems in mean leaf diffusive resistance at 70 DAP (Table 3). At 78 DAP there

Table 3. Leaf diffusive resistance of 18 Malawian landrace dry beans at 70 DAP (1984).

Accession number	Leaf diffusive resistance					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	-----s/cm-----					
1	0.55	0.45	0.50	4.63	4.27	4.45
2	0.21	0.33	0.33	2.96	3.31	3.13
3	0.38	0.34	0.36	4.74	4.81	4.77
4	0.75	0.68	0.71	3.65	2.79	3.22
5	0.13	0.15	0.14	3.72	3.50	3.61
6	0.49	0.49	0.49	4.21	3.32	3.76
7	0.45	0.32	0.38	3.57	4.26	3.91
8	0.56	0.55	0.55	4.79	3.98	4.38
9	0.40	0.31	0.35	4.62	5.27	4.94
10	0.44	0.47	0.45	4.21	3.99	4.10
11	0.33	0.33	0.33	4.49	4.37	4.43
12	0.41	0.69	0.55	3.67	4.31	3.99
13	0.30	0.37	0.33	3.99	4.47	4.23
14	0.24	0.37	0.30	4.06	5.11	4.58
15	0.27	0.14	0.20	3.91	3.53	3.72
16	0.55	0.78	0.66	4.09	4.52	4.30
17	0.29	0.32	0.30	3.09	3.07	3.08
18	0.34	0.36	0.35	4.40	5.21	4.80
Mean	0.40	0.41	0.40	4.04	4.12	4.08
CV (%)	33.3					

M = monoculture;

I = intercrop.

Table 4. Leaf diffusive resistance of 14 Malawian landrace dry beans at 78 DAP (1984).

Accession number	Leaf diffusive resistance					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	-----s/cm-----					
1	0.50	0.43	0.46	3.92	6.53**	5.22
2	0.30	0.30	0.30	4.58	5.32	4.95
4	0.36	0.61	0.48	2.54	4.07**	3.30
5	0.36	0.41	0.35	4.16	4.42	4.29
7	0.39	0.56	0.47	3.20	4.22**	3.71
8	0.26	0.36	0.31	3.88	4.88*	4.38
9	0.29	0.42	0.35	5.37	7.19**	6.28
10	0.16	0.38	0.27	4.00	5.65**	4.82
11	0.54	0.66	0.60	5.37	5.97	5.67
13	0.52	0.46	0.49	3.54	4.83**	4.18
15	0.25	0.41	0.33	5.87	6.05	5.96
16	0.56	0.59	0.57	4.12	5.18*	4.65
17	0.15	0.48	0.31	3.57	5.12**	4.34
18	0.25	0.32	0.28	4.37	4.64	4.50
Mean	0.34	0.45	0.39	4.18	5.28	4.73
CV (%)	48.3					

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

Table 5. Leaf diffusive resistance of 12 Malawian landrace dry beans at 85 DAP (1984).

Accession number	Leaf diffusive resistance					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	-----s/cm-----					
1	1.23	1.20	1.21	4.56	4.96	4.76
2	1.69	1.67	1.68	5.10	5.94	5.52
4	1.42	1.45	1.43	4.47	5.64*	5.05
7	1.57	1.41	1.49	3.82	5.41	4.61
8	1.07	1.02	1.04	4.63	5.06	4.84
9	0.99	1.03	1.01	4.66	4.68	4.67
11	1.17	1.97	1.57	4.75	7.52**	6.13
13	2.01	1.89	1.95	5.27	6.85**	6.06
15	1.73	1.94	1.83	6.23	7.34	6.78
16	1.91	2.03	1.97	4.75	5.77*	5.26
17	1.61	1.67	1.64	4.68	5.83	5.25
18	1.98	2.13	2.05	3.96	5.22**	4.59
Mean	1.53	1.62	1.57	4.74	5.85	5.29
CV (%)	50.8					

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

was a significant increase in mean leaf diffusive resistance in leaves on intercropped beans over those in monoculture (Table 4). Genotypes were not significantly different in leaf diffusive resistance. Accessions 1, 4, 7, 8, 9, 10, 13, 16, and 17 significantly increased their diffusive resistance in leaves under intercropping. This indicates that at 78 DAP these genotypes were already reacting to stress conditions under intercropping conditions by closing their stomata. As a result, these genotypes probably conserved more moisture than others. At 85 DAP there still was a significant increase in mean leaf diffusive resistance on leaves of intercropped beans over those in monoculture (Table 5). This came about because accessions 4, 7, 11, 13, 16, 17, and 18 significantly increased their leaf diffusive resistances under intercropping at 85 DAP. Some of these landraces (accessions 4, 7, 13, 16, and 17) had partially closed stomata at 78 DAP.

Leaf diffusive resistance should be related to leaf transpiration rates because the partial closing of stomata under high leaf diffusive resistance causes less moisture to escape. The overall result is water conservation and loss of productivity, due to less photosynthesis, although much of it is regained in this case as opposed to plants that do not conserve water. At 70 DAP only 2 genotypes, accessions 7 and 13, were able to significantly reduce their rates of transpiration in the process of conserving water (Table 6). At 78 DAP all genotypes, except accession 11, significantly

Table 6. Leaf transpiration of 189 Malawian landrace dry beans at 70 DAP (1984).

Accession number	Leaf transpiration					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	----- ug H ₂ O/cm ² /s-----					
1	1.22	1.11	1.16	1.40	1.11	1.26
2	1.00	0.91	0.95	1.67	1.54	1.60
3	1.10	1.01	1.06	1.43	1.16	1.30
4	1.15	1.08	1.11	1.60	1.61	1.60
5	1.12	1.07	1.10	1.57	1.46	1.52
6	1.12	1.06	1.09	1.40	1.43	1.41
7	1.13	1.13	1.13	1.51	1.03**	1.27
8	1.10	1.02	1.06	1.40	1.22	1.31
9	1.18	0.95	1.07	1.36	1.13	1.25
10	1.20	1.04	1.12	1.52	1.31	1.41
11	1.10	0.99	1.04	1.51	1.32	1.41
12	0.94	0.92	0.93	1.57	1.23	1.40
13	1.06	0.97	1.01	1.48	0.95**	1.21
14	1.04	1.12	1.08	1.44	1.23	1.34
15	0.91	0.92	0.91	1.50	1.51	1.51
16	0.93	0.86	0.90	1.47	1.34	1.41
17	1.03	0.99	1.01	1.63	1.39	1.51
18	0.88	0.79	0.83	1.45	1.27	1.36
Mean	1.07	0.99	1.03	1.50	1.29	1.39
CV (%)	33.5					

M = monoculture;

I = intercrop;

** significant between cropping systems at P=0.01.

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reduced their rates of transpiration under intercropping (Table 7) due to stomatal closure. Similarly, at 85 DAP some genotypes (accessions 1, 4, 7, 11, 16, and 18), most of which had significantly higher leaf diffusive resistance under intercropping, significantly reduced (Table 8) their rates of transpiration due to partial stomatal closure.

Generally, the leaf temperature of leaves on plants under drought stress rises above that of leaves of nonstressed plants. On the contrary, in this study the mean leaf temperature of stressed plants (i.e. those under the intercropping system) was significantly lower than that of nonstressed plants (Tables 9, 10, and 11). Significant reductions were in accessions 3, 4, 5, 7, 8, 10, and 13. Some of these (4, 7, and 13) had both significant increases in leaf diffusive resistance and reductions in transpiration rates. Reductions in leaf temperature under intercropping may have been due to partial shading by the maize, although this was avoided by the sparse maize planting pattern, or to changes in leaf orientation under stress. At 78 DAP only three genotypes, accessions 2, 9, and 10, had significantly lower leaf temperatures (Table 10). However, at 85 DAP leaves from intercropped plants were at temperature similar to those of monoculture plants (Table 11).

Specific leaf weight (SLW) has been shown to be an adaptive characteristic under evolutionary processes. Plants evolving in extremely low moisture environments (xerophytic plants) have very large SLW as opposed to those

Table 7. Leaf transpiration of 14 Malawian landrace dry beans at 78 DAP (1984).

Accession number	Leaf transpiration					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
----- ug H ₂ O/cm ² /s-----						
1	0.97	0.83*	0.90	0.97	0.71**	0.84
2	0.83	0.76	0.79	0.98	0.76**	0.87
4	0.86	0.91	0.88	1.21	0.80**	1.00
5	0.82	0.81	0.81	0.97	0.68**	0.82
7	0.89	0.81	0.85	1.05	0.80**	0.92
8	0.89	0.77	0.83	0.96	0.78**	0.87
9	0.86	0.85	0.85	0.89	0.74**	0.81
10	0.82	0.78	0.80	1.04	0.78**	0.91
11	1.04	1.00	1.02	0.90	0.79	0.84
13	0.82	0.74	0.78	1.00	0.67**	0.83
15	0.78	0.78	0.78	0.87	0.68**	0.77
16	0.90	0.83	0.86	0.97	0.81**	0.89
17	0.85	0.77	0.81	1.12	0.61**	0.89
18	0.87	0.80	0.83	0.97	0.75**	0.86
Mean	0.87	0.82	0.84	0.99	0.74	0.86
CV (%)	13.2					

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

Table 8. Leaf transpiration of 12 Malawian landrace dry beans at 85 DAP (1984).

Accession number	Leaf transpiration					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	----- ug H ₂ O/cm ² /s-----					
1	1.13	1.15	1.14	1.17	0.95*	1.06
2	1.01	1.03	1.02	1.12	0.95	1.03
4	1.12	1.06	1.09	1.16	0.91**	1.03
7	1.11	1.05	1.08	1.20	0.93**	1.06
8	1.12	1.12	1.12	1.11	1.11	1.11
9	1.11	1.01	1.06	1.15	1.08	1.11
11	1.13	1.23	1.18	1.16	0.96*	1.01
13	1.14	1.08	1.11	1.19	0.97*	1.08
15	1.07	1.02	1.04	1.12	0.99	1.05
16	1.13	1.10	1.11	1.16	0.83**	0.99
17	1.07	1.00	1.03	1.15	0.99	1.07
18	1.18	1.06	1.12	1.19	1.00*	1.09
Mean	1.11	1.07	1.09	1.15	0.95	1.05
CV (%)	44.3					

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

Table 9. Leaf temperature of 18 Malawian landrace dry beans at 70 DAP (1984).

Accession number	Leaf temperature					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	----- C -----					
1	15.5	15.8	15.6	21.2	21.4	21.3
2	14.8	15.0	14.9	22.4	21.9	22.1
3	15.1	15.4	15.2	22.1	21.3*	21.7
4	15.9	16.4	16.1	22.3	21.7*	22.0
5	14.8	14.9	14.8	22.4	21.6*	22.0
6	15.3	15.6	15.4	21.1	21.1	21.1
7	15.1	15.1	15.1	22.1	21.3*	21.7
8	15.6	15.6	15.6	21.5	20.8*	21.1
9	15.5	15.5	15.5	21.7	21.3	21.5
10	15.5	15.7	15.6	21.9	21.3*	21.6
11	16.5	16.7	16.6	22.5	22.5	22.5
12	15.0	15.5	15.2	22.1	22.0	22.0
13	14.9	15.0	14.9	21.7	20.8*	21.2
14	15.3	15.3	15.3	22.0	21.5	21.7
15	14.9	14.9	14.9	22.1	21.6	21.8
16	15.7	15.9	15.8	22.1	22.0	22.0
17	14.8	14.9	14.8	22.1	21.5	21.8
18	14.6	14.8	14.7	22.4	22.0	22.2
Mean	15.3	15.4	15.3	22.0	21.5	21.7
CV (%)	9.7					

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

Table 10. Leaf temperature of 14 Malawian landrace dry beans at 78 DAP (1984).

Accession number	Leaf temperature					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	----- C -----					
1	13.7	13.2	13.4	25.2	25.1	25.1
2	11.3	11.5	11.4	27.6	25.8*	26.7
4	12.8	13.1	12.9	26.5	26.0	26.2
5	11.0	11.2	11.1	25.6	25.2	25.4
7	12.0	12.1	12.0	26.0	25.3	25.6
8	12.5	12.7	12.6	25.6	25.8	25.7
9	12.4	12.4	12.4	27.2	23.0*	25.1
10	9.6	14.9*	12.2	27.9	25.9*	26.9
11	14.1	14.4	14.2	28.4	27.1	27.7
13	11.7	11.8	11.7	26.4	25.4	25.9
15	11.2	11.4	11.3	27.4	26.7	27.0
16	13.6	13.2	13.4	27.2	26.3	26.7
17	11.1	11.5	11.3	27.5	26.1	26.7
18	10.8	10.7	10.7	26.4	25.6	26.0
Mean	12.0	12.4	12.2	26.8	25.6	26.2
CV (%)	19.4					

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

Table 11. Leaf temperature of 12 Malawian landrace dry beans at 85 DAP (1984).

Accession number	Leaf temperature					
	Pre-dawn			Afternoon		
	M	I	Mean	M	I	Mean
	----- C -----					
1	17.2	17.0	17.0	19.9	19.7	19.8
2	17.1	16.9	17.0	19.9	19.8	19.8
4	17.6	17.3	17.4	19.8	19.5	19.6
7	17.2	17.1	17.1	19.9	19.9	19.9
8	16.7	16.7	16.7	19.8	19.9	19.8
9	16.6	16.7	16.6	20.0	19.9	19.9
11	17.9	18.8*	18.3	20.5	20.2	20.3
13	18.4	18.1	18.2	20.9	20.2	20.8
15	17.2	17.2	17.2	20.5	20.1	20.3
16	18.4	18.0	18.2	20.1	19.8	19.9
17	17.2	17.2	17.2	19.8	19.5	19.6
18	19.3	18.8	19.0	20.5	20.4	20.4
Mean	17.5	17.5	17.5	20.1	19.9	20.0
CV (%)	29.2					

M = monoculture;

I = intercrop;

* significant between cropping systems at $P=0.05$;

growing under fair to adequate moisture environments (mesophytic plants). Measured under both intercropped and monoculture conditions at 74 DAP, specific leaf weight tended to be lower, though insignificantly, in intercropped bean leaves. The eighteen genotypes tested differed significantly in SLW (Table 12). Accession 14 had the highest SLW. Leaf moisture retention capacity (LMRC) measured at 72 DAP did not differ between cropping systems but was significantly different among the malawian landrace genotypes (Table 12). Accessions 2, 15, and 17 had significantly more moisture retained in the leaves than other genotypes whereas 12 and 14 had significantly less moisture retained in their leaves. SLW was similar (Table 13) in leaves of beans grown on the different soil types (heavy, medium, and light). However, there was a significant decline in LMRC in leaves on plants growing on heavier soil. Rapid water percolation leads to faster moisture depletion in the light-textured soil and earlier drought as a result. These data show that LMRC is probably a better characteristic that plants use to adapt to soil moisture deficits than the SLW. One difference between SLW and LMRC is that SLW becomes a permanent adaptation as opposed to LMRC. When the soil is rehydrated total leaf area will have been set and limited by leaf thickness as opposed to expansion. Therefore, LMRC is not as conservative a trait as SLW and it responded more flexibly to the environment.

Table 12. Specific leaf weight (SLW) and leaf moisture retention capacity (LMRC) of 18 Malawian dry beans at 74 and 72 DAP, respectively (1984).

Accession number	SLW			LMRC		
	M	I	Mean	M	I	Mean
	-----mg/cm ² -----			-----%-----		
1	3.33	3.31	3.32 cdef	28.5	30.9	29.7 bcd
2	3.61	3.88	3.74 bcdef	41.7	40.9	41.3 a
3	4.49	4.08	4.28 b	21.7	25.3	23.5 d
4	3.60	3.17	3.38 cdef	21.6	31.2	26.4 cd
5	3.67	3.33	3.50 bcdef	22.7	27.9	25.3 d
6	4.47	3.81	4.13 bc	24.8	34.0	29.4 bcd
7	2.97	2.84	2.91 f	27.8	30.9	29.3 bcd
8	4.44	3.51*	3.98 bcd	22.8	25.3	24.0 d
9	3.30	2.73	3.02 ef	36.2	37.2	36.7 ab
10	3.44	3.37	3.41 cdef	38.5	31.8	35.1 abc
11	3.08	2.69	2.89 f	28.9	34.3	31.6 abcd
12	3.84	3.77	3.81 bcde	18.9	17.4	18.1 e
13	3.61	3.86	3.74 bcdef	34.6	35.9	35.3 abc
14	5.75	6.07	5.91 a	13.3	16.0	14.7 e
15	3.44	3.22	3.33 cdef	44.2	36.3	40.2 a
16	3.33	3.11	3.22 def	22.3	27.3	24.8 d
17	3.59	3.64	3.62 bcdef	42.9	39.2	41.1 a
18	3.35	3.09	3.22 def	34.2	38.7	36.4 ab
Mean	3.74	3.53	3.63	29.2	31.1	30.1
CV (%)		14.5			32.2	

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

Means followed by the same letter are not significantly

(P=0.01) different.

Table 13. Specific leaf weight (SLW) and leaf moisture retention capacity (LMRC) of 18 Malawian dry bean genotypes grown in three different soil types (1984).

Soil type	SLW	LMRC
	-- mg/cm ² --	-- % --
Light	3.55	33.7 a
Medium	3.68	29.4 b
Heavy	3.72	26.6 c
Mean	3.63	29.9
CV (%)	14.5	32.2

There was a significant mean biomass yield reduction under intercropping as compared with monoculture. However, only four of the sixteen genotypes that were harvested yielded significantly lower biomass under intercropping than the monoculture cropping system (Table 14). Because there were no differences between cropping systems for apparent harvest index (AHI) (Table 17), economic yield production responded much the same as biomass production (Table 14). Assuming similar biomass production under either cropping system, some Malawian landraces of beans yield well under the intercropping system just as they do in monocultures.

Four methods (Table 15) were used in assessing adaptability of the landraces to the intercropping systems and possible consequent drought stresses. Yield differential seemed to be a poorer method than the other three. For example, accession 9 had one of the smallest differentials but the other methods except S indicated that it was drought susceptible. The arithmetic mean identified accessions 4, 10, 7, 6, (2), 13, 5, and 17 to be better adapted to intercropping and drought stress, in that order, than other genotypes. Accessions 9, 1, 3, and 14 were least adapted to such conditions. The geometric mean identified 10, 4, 7, 6, 5, and 17 to be better adapted and 9, 1, and 3 to be least adapted. The drought susceptibility index (S) excludes the yielding potential of a genotype in assessing its drought resistance. In this case it identified 2, 4, 5, 3, 8, 12, and 17 to be better adapted and 13, 1, 16, 15, and

Table 14. Biological and economic yield of 16 Malawian dry bean genotypes (1984).

Acc. no.	Biological yield			Economic yield		
	M	I	Mean	M	I	Mean
-----g/plant -----						
1	119.9	66.0**	93.0 abcd	43.2	17.8**	30.5 de
2	116.5	100.8	108.6 abc	38.3	50.4	44.3 abcd
3	64.1	50.1	57.1 d	37.3	31.6	34.4 cde
4	132.0	123.0	127.5 a	58.7	69.9	64.3 a
5	84.0	77.4	80.7 bcd	57.2	49.0	53.1 abcd
6	100.5	80.7	90.6 abcd	69.2	51.0*	60.1 ab
7	123.0	96.9	109.9 ab	69.2	55.0	62.1 ab
8	99.4	75.6	87.5 abcd	50.1	42.1	46.1 abcd
9	79.6	98.4	89.0 abcd	16.2	12.3	14.3 e
10	115.7	90.4	103.1 abc	74.0	52.9*	63.5 ab
12	70.0	55.7	62.9 cd	45.0	36.5	4.08 abcd
13	148.0	76.2**	112.1 ab	87.9	24.9**	56.4 abc
14	80.5	45.8	63.2 cd	51.5	27.3**	39.4 bcd
15	133.4	69.5**	101.5 abc	53.5	27.2**	40.3 abcd
16	116.8	56.1**	87.0 abcd	61.4	27.5**	44.5 abcd
17	123.7	107.0	115.3 ab	58.0	47.1	52.6 abcd
Mean	106.7	79.4	93.0	54.4	38.9	46.6
CV (%)		23.9			20.3	

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

Means followed by the same letter are not significantly (P=0.01) different.

Table 15. Yield differential, arithmetic mean, geometric mean, and drought susceptibility index (S) of 16 Malawian landrace dry beans grown in monoculture and intercropping with maize (1984).

Accession	$[Y_m - Y_i]$	$\frac{[Y_m + Y_i]}{2}$	$[Y_m \times Y_i]^{1/2}$	S
number	(1)	(2)	(3)	(4)
1	25.4	30.5	27.7	2.06
2	-12.1	44.3	43.9	-1.11
3	5.7	34.4	34.3	0.54
4	-11.2	64.3	64.0	-0.67
5	8.2	53.1	52.9	0.50
6	18.2	60.1	59.4	0.92
7	14.2	62.1	61.7	0.72
8	8.0	46.1	45.9	0.56
9	3.9	14.3	14.1	0.84
10	21.1	63.5	65.6	1.00
12	8.5	40.8	40.5	0.66
13	63.0	56.4	46.8	2.51
14	24.2	39.4	37.5	1.65
15	26.3	40.3	38.1	1.71
16	33.9	44.5	41.1	1.94
17	10.9	52.6	52.3	0.67

Y_m = monoculture seed yield;

Y_i = intercrop seed yield;

1 = yield differential;

2 = arithmetic mean;

3 = geometric mean; and

4 = drought susceptibility index.

Table 16. Number of pods/plant and number of seeds/plant of 16 Malawian dry bean genotypes (1984).

Acc.	No. pods/plant			No. seeds/plant		
no.	M	I	Mean	M	I	Mean
----- no. -----						
1	74.3	36.2**	55.2 a	234	101**	167 abc
2	34.1	35.1	34.6 abc	108	120	114
3	25.1	24.9	25.0 c	103	94	98
4	56.1	41.9	49.0 ab	170	165	167
5	38.7	32.3	35.5 abc	220	185	202 a
6	35.4	31.8	33.6 abc	163	113	138 abc
7	38.7	37.3	38.0 abc	137	126	131 abc
8	38.7	32.2	35.4 abc	139	107	123 abc
9	22.4	16.8	19.6 c	41	28	34 d
10	28.2	27.9	28.0 bc	203	133*	168 abc
12	42.7	18.9**	30.8 abc	207	155	181 ab
13	47.6	21.2**	34.4 abc	261	72**	166 abc
14	29.8	18.3	24.0 c	112	79	95 cd
15	33.3	14.8**	24.0 c	118	60	89 cd
16	43.1	21.4*	32.2 bc	158	75*	116 bc
17	37.9	26.9	32.4 bc	125	92	108 bcd
Mean	39.1	27.4	33.2	156	107	131
CV (%)		31.5			28.8	

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01.

Means followed by the same letter are not significantly different.
(P=0.05 and P=0.01 for pods and seeds, respectively)

14 to be least adapted to intercropping and consequent drought conditions.

The number of pods/plant is a characteristic used by those genotypes that were better adapted to intercropping to produce similar economic yields as in monoculture. There was a significant reduction in number of pods/plant (Table 16) in accessions 1, 12, 13, 15, and 16 under monoculture. It seems that the number of pods/plant largely controlled number of seeds/plant produced (Table 16).

Genotypic variability existed for stem weight (Table 18). There was a significant reduction in stem weights of bean plants under intercropping as compared with those in monoculture in 1984. Shaded plants usually increase in height faster than unshaded plants so that they can be exposed to light. The less investment of assimilates into stem tissue leads to slender stems. Assuming a positive correlation between stem weight and amount of reserves, one expects that in the event of a drought occurring during seed-filling intercropped bean plants rely on significantly reduced amounts of reserves for remobilization to support seed growth. Most drought tolerant genotypes, identified by other criteria, did not have significantly smaller stem weights. Landrace 9 had higher stem weight under intercropping than under monoculture. This was probably due to the better climbing ability of this landrace which made it grow more than without support in monoculture.

Table 17. Apparent harvest index (AHI) and 100-seed weight of 16 Malawian dry bean genotypes (1984).

Accession number	AHI			100-seed weight		
	M	I	Mean	M	I	Mean
	----- % -----			----- g/100 seeds -----		
1	37.9	27.2	32.5 e	18.5	17.7	18.1 c
2	33.4	50.9	42.1 cde	35.8	41.8	38.8 abc
3	58.1	63.0	60.5 ab	36.3	33.9	35.1 abc
4	44.1	57.4	50.7 abcd	34.3	44.2	39.2 abc
5	68.0	63.3	65.6 a	25.9	26.6	26.2 abc
6	70.7	63.3	67.0 a	42.3	45.4	43.8 ab
7	59.1	57.2	58.1 abc	50.2	43.6	46.9 a
8	50.9	58.1	54.5 abcd	36.1	59.5	47.8 a
9	20.4	12.7	16.5 f	41.9	45.4	43.6 ab
10	63.9	59.0	61.4 ab	36.5	39.9	38.2 abc
12	62.8	65.3	64.0 ab	22.0	23.5	22.7 bc
13	64.1	33.3	48.7 abcde	33.7	35.2	34.4 abc
14	63.8	60.4	62.1 ab	65.0	34.7	49.8 a
15	40.5	39.2	39.8 de	46.8	47.4	47.1 a
16	52.0	48.9	50.4 abcd	40.8	36.6	38.7 abc
17	47.0	44.6	45.8 bcde	46.9	51.0	48.9 a
Mean	52.3	50.2	51.2	38.3	39.1	38.7
CV (%)		14.1			32.7	

M = monoculture;

I = intercrop;

Means followed by the same letter are not significantly
(P=0.01) different.

Table 18. Other agronomic characteristics of 16 Malawian landrace dry beans (1984).

Accession number	No. non-seeded pods/plant			Stem weight		
	M	I	Mean	M	I	Mean
	----- no. -----			----- g/plant -----		
1	12.0	11.5	11.8 abc	60.6	39.7*	50.1 ab
2	6.7	6.4	6.5 a-d	60.2	30.0**	45.1 abc
3	3.7	6.1	4.9 bcd	14.7	9.4	12.1 e
4	4.0	4.5	4.3 cd	51.9	33.0	42.5 a-d
5	4.8	2.7	3.8 cd	16.9	18.1	17.5 de
6	7.3	6.0	6.7 a-d	15.5	14.4	15.0 e
7	4.0	3.5	3.8 cd	37.8	25.6	31.7 b-e
8	6.3	5.2	5.8 a-d	34.3	21.2	27.7 b-e
9	15.7	10.5	13.1 a	50.3	77.9**	64.1 a
10	8.7	8.8	8.8 a-d	20.9	21.4	21.2 cde
12	6.7	5.1	5.9 a-d	13.7	9.5	11.6 e
13	4.1	3.9	4.0 cd	33.2	37.1	35.1 b-e
14	12.6	12.7	12.6 ab	15.7	7.9	11.8 e
15	3.9	3.5	3.7 cd	56.1	29.2*	42.7 a-d
16	3.9	1.8	2.9 d	36.8	21.6	29.2 b-e
17	8.3	3.4	5.9 a-d	39.5	43.3	41.1 a-d
Mean	7.0	6.0	6.5	34.9	37.5	31.2
CV (%)		58.4			37.7	

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01;

Means followed by the same letter are not significantly
(P=0.01) different.

1985 Intercropping Experiment

Leaf diffusive resistances tended to be higher in some genotypes, though not significantly, in beans grown under the intercropping system than those grown in monocultures (Table 19). However, leaf diffusive resistance differed significantly among the dry bean genotypes. Accessions 2 and 5, and BAT 47 had significantly higher leaf diffusive resistances. Probably as a result of similar leaf diffusive resistance under the two cropping systems, leaf transpiration rates did not differ in beans grown under either intercropping or monoculture. But genotypes differed significantly in rates of leaf transpiration (Table 19). Accessions 2, 5, and 6, and BAT 47 had lowest leaf transpiration rates, thereby conserving the most water. There were no differences in leaf temperature between cropping systems and among the dry bean genotypes, probably due to lower levels of solar radiation. On the day these readings were taken there was a partly cloudy sky and a consequent decline in solar radiation.

There was a significant decline in mean economic yield (Table 20) in beans under the intercropping system (20.9 g/plant) from those in monoculture (27.6 g/plant). The dry bean genotypes also differed significantly in economic yield. The highest yielders were Montcalm (an adapted cultivar), BAT 798, BAT 85, and accessions 10 and 7, in that order, although 6 and 5 were close behind these. The four methods of determining relative drought tolerance were again

Table 19. Leaf diffusive resistance, leaf transpiration, and leaf temperature of 22 dry bean genotypes (1985).

Acc./ cv.	Leaf diffusive resistance			Leaf transpiration			Leaf temperature			
	M	I	Mean	M	I	Mean	M	I	Mean	
	----- s/cm ---			ug H ₂ O/cm ² /s			----- C ----			
1	0.48	0.60	0.54	14.5	12.6*	13.6	cd	22.4	22.3	22.3
2	0.61	0.67	0.64	13.0	11.8	12.4	d	22.3	22.2	22.2
3	0.54	0.44	0.49	15.7	16.8	16.3	a-d	22.6	22.5	22.5
4	0.40	0.38	0.39	18.2	18.3	18.2	abc	22.6	22.7	22.6
5	0.66	0.56	0.61	13.2	14.0	13.6	cd	22.5	22.6	22.5
6	0.40	0.51	0.45	15.8	14.3	15.0	bcd	22.2	22.2	22.2
7	0.48	0.35	0.42	15.3	18.8*	17.0	a-d	22.3	22.0	22.1
8	0.54	0.52	0.53	13.7	14.3	14.0	cd	22.2	22.1	22.1
9	0.46	0.50	0.51	15.9	14.7	15.3	bcd	22.4	22.6	22.5
10	0.64	0.41	0.53	13.7	16.8*	15.3	bcd	22.3	22.2	22.2
12	0.57	0.54	0.55	15.4	16.5	15.9	bcd	23.1	23.1	23.1
13	0.38	0.57	0.48	18.8	15.2	17.0	a-d	22.2	22.2	22.2
14	0.40	0.40	0.40	18.7	17.1	18.2	abc	22.3	22.4	22.3
15	0.28	0.31	0.30	21.4	20.8	21.1	a	22.2	22.2	22.2
16	0.39	0.47	0.43	18.5	16.4*	17.5	a-d	22.6	26.0	24.3
17	0.27	0.31	0.30	21.0	19.1*	20.0	ab	22.3	22.2	22.3
BM	0.42	0.50	0.46	16.3	16.3	16.3	a-d	21.9	21.9	21.9
BAT337	0.40	0.33	0.36	16.2	17.9	17.1	a-d	22.0	21.8	21.9
BAT47	0.57	0.64	0.61	13.6	12.0	12.8	cd	22.2	22.1	22.1
BAT798	0.47	0.48	0.47	16.0	15.7	15.9	a-d	22.9	22.9	22.9
BAT85	0.44	0.38	0.41	16.3	17.9	17.1	a-d	22.2	22.1	22.2
MC	0.34	0.42	0.38	18.4	17.1	17.3	a-d	21.8	21.8	21.8
Mean	0.46	0.47	0.46	16.3	16.1	16.2		22.3	22.4	22.3
CV (%)	27.1			16.6				3.8		

M=monoculture, I=intercrop; Bm=Bayo Madero; MC=Montcalm; * significant between cropping systems at P=0.05; Means followed by the same letter are not significantly (P=0.01) different.

Table 20. Economic yield at physiological maturity and leaf moisture retention capacity (LMRC) at 45 DAP of 22 dry bean genotypes (1985)

Accession/ Cultivar	Economic yield			LMRC		
	M	I	Mean	M	I	Mean
	----- g/plant -----			----- % -----		
1	21.6	9.0**	15.3 de	21.1	52.9	47.0 ab
2	22.3	13.2**	17.8 cde	42.1	36.1	39.1 abc
3	17.3	14.1	15.7 de	53.7	41.2	47.5 ab
4	15.8	15.9	15.8 de	43.7	48.1	44.2 ab
5	31.0	27.2	29.1 bcd	40.2	48.1	44.2 ab
6	34.5	25.4**	29.9 bcd	50.2	50.0	50.1 ab
7	31.5	28.8	30.2 bcd	47.9	47.9	47.9 ab
8	32.3	24.5**	28.4 bcd	41.1	38.1	39.6 abc
9	23.7	20.4	22.0 b-e	44.5	46.1	45.3 ab
10	32.2	29.5	30.9 bc	45.7	45.0	45.4 ab
12	29.8	27.8	28.8 bcd	25.7	27.5	26.6 c
13	15.6	6.9*	11.2 e	48.2	40.3	44.3 abc
14	24.7	16.2*	20.5 cde	34.8	34.4	34.6 bc
15	36.6	16.0**	26.3 bcd	38.8	45.0	41.9 abc
16	15.7	6.9*	11.3 e	43.6	41.2	42.4 abc
17	28.3	22.6	25.5 b-e	45.2	61.2	53.2 a
Bayo Madero	15.7	14.3	15.0 de	40.4	50.6	45.5 ab
BAT 337	28.8	16.5**	22.7 b-e	47.5	49.1	48.3 ab
BAT 47	8.1	21.8**	15.0 de	41.9	41.8	41.8 abc
BAT 798	40.7	32.4*	36.5 b	52.9	51.3	52.1 ab
BAT 85	35.0	27.7*	31.3 bc	46.3	45.2	45.8 ab
Montcalm	66.9	41.8**	54.4 a	54.2	52.0	53.1 a
Mean	27.6	20.9	24.2	44.1	45.4	44.7
CV (%)		28.5			13.5	

M = monoculture;

I = intercrop;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01;

Means followed by the same letter are not significantly (P=0.05 and P=0.01 for yield and LMRC, respectively).

used during this year. Bat 47 was harvested before physiological maturity and so will not be used in comparisons. Some of the genotypes with smallest differences in yields between the two cropping systems were accession 4, Bayo Madero, and accessions 12, 10, and 7, in that order (Table 21). This method does not consider yielding ability of the genotypes. The arithmetic and geometric means do. These indicated that Montcalm, BAT 798, BAT 85, and accessions 10 and 7, were better adapted to intercropping conditions. The index of adaptability to stress conditions (S), which delineates adaptation apart from yielding potential, indicated that accessions 4, BAT 47, 12, and 7, Bayo Madero, accessions 5, 9, 17, and 3 were the most adapted, in that order, to intercropping systems.

The number of pods/plant, which was previously shown to be a factor for adaptation, again differed significantly among the dry bean genotypes (Table 22). And the number of pods on plants under the intercropping system (15.5) was significantly reduced from that on plants in the monoculture system (20.2). As expected, the number of pods/plant seemed to influence the number of seeds/plant, the latter also being significantly different among the dry bean genotypes (Table 22). Accession 5 (Katolika) produced the most seeds/plant (Table 22) probably due to more seeds/pod and small seedsize (Table 23). As previously, 100-seed weight seemed to play no direct role in adaptation of dry bean genotypes to the intercropping stress (Table 23).

Table 21. Yield differential, arithmetic mean, geometric mean, and drought susceptibility index (S) of 22 dry bean genotypes grown in monoculture and intercropping with maize (1985).

Accession/ Cultivar	[Y _m -Y _i]	$\frac{[Y_m+Y_i]}{2}$	[Y _m xY _i] ^{1/2}	S
	(1)	(2)	(3)	(4)
1	12.6	15.3	13.9	0.027
2	9.1	17.8	17.1	0.019
3	3.2	15.7	15.6	0.009
4	-0.1	15.9	15.8	-3.271
5	3.8	29.1	29.0	0.006
6	9.1	29.9	29.6	0.012
7	2.7	30.1	30.1	0.004
8	7.8	28.4	28.1	0.011
9	3.3	22.0	22.0	0.006
10	2.7	30.8	30.8	0.004
12	2.0	28.8	28.8	0.003
13	8.7	11.2	10.4	0.026
14	8.5	20.4	20.0	0.016
15	20.6	26.3	24.2	0.026
16	8.8	11.3	10.4	0.026
17	5.7	25.4	25.3	0.009
Bayo Madero	1.4	15.0	15.0	0.004
BAT 337	12.3	22.7	21.8	0.020
BAT 47	-13.7	15.0	13.3	-0.079
BAT 798	8.3	36.5	36.3	0.010
BAT 85	7.3	31.3	31.1	0.010
Montcalm	25.1	54.3	52.9	0.017

Y_m = monoculture seed yield;

Y_i = intercrop seed yield;

1 = yield differential;

2 = arithmetic mean;

3 = geometric mean;

4 = drought susceptibility index.

Table 22. Number of pods/plant and number of seeds/plant of 22 dry bean genotypes (1985).

Acc./ Cultivar	No. pods/plant			No. seeds/plant		
	M	I	Mean	M	I	Mean
	----- no. -----					
1	33.2	13.5	25.8 bc	153	75	114 abc
2	14.9	9.5	12.2 def	57	34	46 de
3	11.9	8.7	10.3 ef	48	36	42 de
4	13.6	13.9	13.8 def	55	52	54 de
5	20.1	18.8	19.4 cdef	157	145	151 a
6	20.4	15.1	17.8 cdef	81	47	64 de
7	23.1	18.0	20.6 bcde	78	68	73 cde
8	24.6	18.9	21.7 bcd	105	79	61 de
9	15.3	13.0	14.2 def	49	41	45 de
10	15.3	14.0	14.7 def	65	61	63 de
12	35.7	34.3	35.0 a	64	60	62 de
13	27.4	16.9	22.2 bcd	43	28	37 e
14	11.7	8.8	10.2 f	45	32	39 de
15	17.6	8.2	12.9 def	95	39	67 cde
16	12.9	5.4	9.2 f	55	24	40 de
17	16.7	11.7	14.2 def	69	50	61 de
Bayo Madero	10.9	8.9	9.9 f	48	40	44 de
BAT 337	15.7	9.0	12.3 def	46	25	36 e
BAT 47	10.6	20.1	15.4 def	38	70	54 de
BAT 798	44.4	28.3	36.4 a	158	164	161 a
BAT 85	31.9	27.7	29.8 ab	138	119	129 ab
Montcalm	17.4	12.4	14.9 def	106	74	90 bcd
Mean	20.2	25.5	17.8	80	62	71
CV (%)		29.2			30.8	

M = monoculture; I = intercrop; B. Madero=Bayo Madero;

* significant between cropping systems at P=0.05;

** significant between cropping systems at P=0.01;

Means followed by the same letter are not significantly (P=0.01) different.

Table 23. Number of seeds/pod and 100-seed weight of 22 dry bean genotypes (1985).

Acc./ cv.	No. seed/pod			100-seed weight		
	M	I	Mean	M	I	Mean
	----- no. -----			----- g/100 seeds -----		
1	4.54	4.09	4.32 def	14.2	12.0	13.1 k
2	3.86	3.60	3.73 efgh	39.0	38.5	38.8 defg
3	3.98	4.11	4.04 defg	36.4	39.5	38.0 efg
4	3.96	3.80	3.88 efgh	28.9	30.4	29.7 ghij
5	7.61	7.68	7.65 a	19.7	18.8	19.2 jk
6	3.98	3.13	3.55 gh	42.4	53.6	48.0 cde
7	3.44	3.77	3.61 fgh	40.4	42.6	41.5 def
8	4.26	4.15	4.20 defg	30.8	31.2	31.0 ghi
9	3.23	3.16	3.20 hi	48.1	49.6	48.9 cd
10	4.21	4.37	4.29 defg	49.4	48.3	48.9 cd
12	1.79	1.74	1.76 j	46.5	46.6	46.6 cde
13	1.66	1.64	1.65 j	34.2	24.8	29.5 ghij
14	3.89	3.55	3.72 efgh	54.6	51.4	53.0 bc
15	5.54	4.80	5.17 c	38.5	40.7	39.6 defg
16	4.32	4.34	4.33 def	28.4	29.5	29.0 ghij
17	4.09	4.32	4.20 defg	41.3	45.7	43.5 cdef
Bayo Madero	4.42	4.52	4.47 de	32.7	35.8	34.2 fgh
BAT 337	2.95	2.80	2.87 i	62.3	65.5	63.9 a
BAT 47	3.84	3.39	3.61 fgh	21.2	31.3	26.2 hij
BAT 798	3.87	5.70	4.78 cd	25.8	19.8	22.8 ijk
BAT 85	4.30	4.29	4.30 defg	25.4	23.3	24.3 hij
Montcalm	6.08	6.00	6.04 b	63.0	56.2	59.6 ab
Mean	4.08	4.04	4.06	37.4	38.0	37.7
CV (%)		11.9			10.7	

M = monoculture;

I = intercrop;

Means followed by the same letter are not significantly
(P=0.01) different.

It is interesting to observe that yield stability analysis on data obtained by the Bean Cowpea CRSP from sixteen locations in Malawi on the same 18 accessions showed that accessions 2, 6, 7, 14, and 17 performed well under poor environments (Table 24). Accessions 3, 4, 5, 9, 10, 11, 12, 15, and 16 were stable across environments. Accessions 1, 8, 13, and 18 performed poorly under poor environments. These environments were not limited to differences in soil moisture and the beans were grown in monoculture systems. However, the genotypes identified in this study as more adaptable to intercropping and consequent drought stress were those that were either good under poor environments or were stable across environments in the stability analysis.

WUE Experiments

1985 Experiment

There was a tendency by all genotypes used in 1985 to incur a reduction, but not significantly, in leaf elongation rates under drought stress (Table 25). However, because there was a high coefficient of variation (45.2%), no statistically significant differences were observed between the drought and well-watered treatments. There were significant differences among the genotypes. Cowpea genotypes generally had faster leaf elongation rates than dry bean genotypes. On the other hand, there was a general significant reduction in stem elongation rates in five

Table 24. Yield stability analysis of the 18 Malawian dry bean genotypes across 16 locations in Malawi.

Accession number	Slope (b)*
1	1.49
2	0.51
3	0.99
4	1.01
5	1.17
6	0.83
7	0.80
8	1.20
9	0.94
10	1.04
11	1.01
12	0.99
13	1.30
14	0.70
15	0.91
16	1.09
17	0.65
18	1.35

* Calculated from data obtained by Dr. E. Ayeh, Bean/Cowpea CRSP Project, Bunda College of Agriculture, University of Malawi.

Table 25. Leaf elongation and stem elongation rates of nine dry bean and three cowpea genotypes (1985).

Accession/ Cultivar	Leaf elongation rate			Stem elongation rate		
	WW	DS	Mean	WW	DS	Mean
	----- mm/day -----			----- cm/day -----		
4	2.02	0.98	1.50 cde	2.78	1.67	2.23 cde
5	2.02	1.24	1.63 cde	4.19	2.33*	3.26 b
6	3.06	0.36	1.71 cde	3.44	1.60*	2.94 bc
16	2.26	1.00	1.63 cde	4.34	1.54**	2.52 bcd
17	1.04	0.60	0.82 e	2.12	0.96	1.54 e
Chiapas 7	1.62	0.66	1.14 de	3.50	2.06*	2.78 bcd
BAT 477	2.74	0.52	1.63 cde	1.86	1.47	1.66 e
BAT 47	2.66	1.96	2.31 abc	6.23	3.32**	4.77 a
Montcalm	2.16	1.80	1.98 bcd	2.54	1.57	2.06 de
Vita 4	3.00	2.56	2.78 ab	1.78	1.44	1.61 e
Vita 5	3.16	3.16	3.16 a	1.57	1.47	1.52 e
Vita 7	3.34	3.20	3.27 a	1.61	1.39	1.50 e
Mean	2.42	1.50	1.96	3.00	1.73	2.36
CV (%)		45.2			27.2	

WW = well-watered treatment;

DS = drought stressed treatment;

* significant between treatments at P=0.05;

** significant between treatments at P=0.01;

Means followed by the same letter are not significantly (P=0.01) different.

genotypes: accessions, 5, 6, 16, and Chiapas 7 and BAT 47 (Table 25).

Genotypes did not differ among themselves in leaf diffusive resistance, leaf transpiration, and leaf temperature (Table 26). However, there was a significant increase in leaf diffusive resistance and leaf temperature under drought conditions as compared with well-watered conditions. Also, there was a significant reduction in leaf transpiration rates under drought conditions.

A significant reduction in total biological yield was observed in accessions 5 and 17, and BAT 47 and Vita 5 (Table 27). Means of total biological yield production among genotypes were significantly different. Chiapas 7 had the highest whereas accession 16 and BAT 477 had the lowest biological yield. Water-use efficiency (WUE), calculated on the basis of total biomass production, increased, but not significantly, under drought conditions from that under well-watered conditions (Table 27). Means of water-use efficiency were significantly different among genotypes. BAT 47 had the highest and accession 6 had the lowest water-use efficiency.

Pod weight was significantly reduced in all genotypes, except Chiapas 7, under drought as compared with the well-watered conditions (Table 28). Chiapas 7 was still forming pods when the entire experiment was harvested. The mean number of pods/plant differed significantly between drought and well-watered conditions in all genotypes except

Table 26. Leaf diffusive resistance, leaf transpiration, and leaf temperature of 9 dry bean and three cowpea genotypes at 40 DAP (1985).

Acc./ Cv.	Leaf diffusive resistance			Leaf transpiration			Leaf temperature		
	WW	DS	Mean	WW	DS	Mean	WW	DS	Mean
	----- s/cm ---			ug H ₂ O/cm ² /s			----- C ----		
4	0.55	1.65	1.10	28.7	16.4	22.5	31.0	31.8	31.4
5	0.78	2.09	1.43	23.3	11.4	17.4	31.4	32.3	31.9
6	0.63	1.39	1.01	26.2	17.2	21.7	30.9	31.4	31.1
16	0.66	1.25	0.96	25.8	16.3	21.0	31.2	32.1	31.7
17	0.56	1.11	0.84	28.3	18.4	23.3	30.6	31.2	30.9
C. 7	0.65	1.87	1.26	25.6	16.6	21.1	31.1	31.3	31.2
BAT 477	0.66	0.91	0.79	25.0	20.4	22.7	31.0	31.1	31.0
BAT 47	0.59	1.40	1.00	28.8	19.8	24.3	30.5	31.5	31.0
MC	0.65	2.04	1.35	22.6	15.0	18.8	30.2	32.7	31.4
Vita 4	0.52	1.80	1.16	27.2	14.4	18.8	29.8	32.2	31.0
Vita 5	0.57	1.11	0.84	23.5	15.7	19.6	29.7	31.8	30.7
Vita 7	0.78	1.86	1.32	20.5	15.4	18.0	30.2	31.3	30.8
Mean	0.64	1.54	1.09	25.5	16.4	20.9	30.6	31.7	31.2
CV (%)	45.1			28.0			4.57		

WW = well-watered treatment;

DS = drought stressed treatment;

* significant between treatments at P=0.05;

** significant between treatments at P=0.01;

Table 27. Biological yield and water-use efficiency (WUE) of nine dry bean and three cowpea genotypes (1985).

Accession/ Cultivar	Biological yield			WUE		
	WW	DS	Mean	WW	DS	Mean
	----- g/plant ----			----- g/kg water ----		
4	53.1	26.2	39.7 abc	5.90	8.76	7.33 abc
5	58.6	27.6*	43.1 abc	6.51	9.21	7.86 ab
6	36.5	17.9	27.2 c	4.06	5.75	4.90 c
16	43.3	26.3	34.8 abc	4.81	8.78	6.80 abc
17	50.6	28.4*	39.5 abc	5.62	5.16	5.39 bc
Chiapas	62.3	43.3	52.8 a	6.93	6.87	6.90 abc
BAT 477	38.0	17.4	27.7 c	4.19	5.59	4.89 c
BAT 47	60.2	40.3*	50.2 ab	6.69	11.87	9.28 a
Montcalm	44.2	25.5	34.9 abc	4.92	6.99	5.95 bc
Vita 4	36.5	25.5	31.0 bc	4.27	8.22	6.24 bc
Vita 5	40.4	27.7	36.0 abc	4.93	9.22	7.07 abc
Mean	47.3	27.2	37.3	5.26	7.79	6.52
CV (%)		56.0			55.7	

WW = well-watered treatment;

DS = drought stressed treatment;

* significant between treatments at P=0.05;

Means followed by the same letter are not significantly
(P=0.01) different.

accession 17 and Montcalm. BAT 47 produced the most pods/plant (Table 28). Significant increases in apparent harvest index (AHI) were observed only in accession 5, and Montcalm (Table 28). BAT 47 showed a decrease in AHI. However, the mean apparent harvest indices were not different among genotypes. Pod yield was used in methods of assessing drought resistance (Table 29). The yield differential proved to be a poor indicator of drought resistance because it generally did not agree with other indicators. For example, Chiapas 7 and BAT 47 had the least differentials. However, both the arithmetic mean and the geometric mean indicated that BAT 47 was the most drought resistant genotype among those that were used and Chiapas 7 was the most susceptible. At harvest, Chiapas 7 had not as yet reached physiological maturity. Accession 5 had the largest differential whereas the other methods indicated that it was drought resistant. According to the arithmetic and geometric means, cultivars BAT 47 and Montcalm, and accession 5 were the most drought tolerant genotypes. The drought susceptibility index (S) identified BAT 47 and Montcalm as the most drought resistant genotypes.

Table 28. Pod weight, number of pods/plant, and apparent harvest index (AHI) of nine dry bean genotypes (1985).

Acc./ cv	Pod weight			No. pods/plant			AHI		
	WW	DS	Mean	WW	DS	Mean	WW	DS	Mean
	--- g/plant ----			----- no. -----			---- % -----		
4	25.6	10.7**	18.2 a	19.5	11.3*	15.4	31.3	34.3	32.8
5	34.2	13.2**	23.7 a	21.5	12.5*	17.0	18.7	22.1*	20.4
6	26.2	10.3**	17.7 a	19.5	8.3*	13.9	14.3	12.0	13.1
16	23.5	11.8**	18.2 a	17.3	10.2*	13.7	22.4	25.7	24.0
17	26.2	12.2**	19.2 a	12.0	8.0	10.0	24.0	27.5	25.7
C7	9.1	4.2	6.6 b	24.5	13.3*	18.9	48.7	45.4	47.0
B477	26.0	10.5**	18.2 a	19.7	8.8*	14.2	13.9	12.5	13.2
B47	28.3	21.5**	24.9 a	31.7	19.3*	25.5	38.0	34.1*	36.0
MC	29.1	15.2**	22.1 a	12.7	6.7	9.7	16.2	21.2*	18.7
Mean	25.3	12.2	18.7	19.8	10.8	15.3	22.3	26.1	24.2
CV (%)		40.9			41.3			28.9	

C7 = Chiapas 7; B477 = BAT 477; B47 = BAT 47;

MC = Montcalm;

WW = well-watered treatment;

DS = drought stressed treatment;

* significant difference between treatments at P=0.05;

** significant difference between treatments at P=0.01;

Means followed by the same letter are not significantly (P=0.01) different.

Table 29. Pod yield differential, arithmetic mean, geometric mean, and drought susceptibility index (S) of 9 dry bean genotypes grown under well-watered and drought conditions (1985).

Accession/ Cultivar	[Yww-Yds]	$\frac{[Yww+Yds]}{2}$	$[Yww \times Yds]^{1/2}$	S
	(1)	(2)	(3)	(4)
4	14.9	18.1	16.5	1.12
5	21.0	23.7	21.2	1.18
6	15.9	18.2	16.4	1.17
16	11.7	17.6	16.6	0.96
17	14.0	19.2	17.9	1.03
Chiapas 7	4.9	6.6	6.2	1.03
BAT 477	15.5	18.2	16.5	1.15
BAT 47	6.8	24.9	24.7	0.46
Montcalm	13.9	22.1	21.0	0.92

Yww = pod yield under well-watered conditions;

Yds = pod yield under drought-stressed conditions;

1 = pod yield differential;

2 = arithmetic mean;

3 = geometric mean;

4 = drought susceptibility index.

Table 30. Stem and leaf weights of 9 dry bean and three cowpea genotypes (1985).

Accession/ Cultivar	Stem weight			Leaf weight		
	WW	DS	Mean	WW	DS	Mean
	----- g/plant -----					
4	15.9	7.9	11.9	11.6	7.6	9.6
5	10.7	5.8	8.2	13.6	8.7	11.1
6	5.2	3.2	4.2	5.2	4.3	4.7
16	9.5	6.8	8.7	10.2	7.7	8.9
17	11.4	6.9	9.1	12.9	9.3	11.1
Chiapas 7	28.3	19.3	23.8	25.0	20.5	22.7
BAT 477	5.5	2.8	4.2	6.6	4.1	5.3
BAT 47	15.8	9.5	12.6	16.1	11.2	13.6
Montcalm	7.1	5.3	6.2	8.0	5.0	6.5
Vita 4	20.1	15.1	17.6	12.0	10.3	11.1
Vita 5	19.5	10.6	15.0	14.4	7.7	11.0
Vita 7	20.0	17.0	18.5	17.4	10.7	14.0
Mean	14.6	9.2	11.9	12.7	8.9	10.8
CV (%)		49.5			51.2	

WW = well-watered treatment;

DS = drought-stressed treatment;

Means followed by the same letter are not significantly
(P=0.01) different.

1986 WUE Experiment

In 1986, a different set of genotypes was used (Table 2) in the water-use efficiency (WUE) experiment. Total biological yield production decreased significantly in all genotypes except breeding line B76001, Vita 3, and accession 5 (Katolika) (Table 31). Genotypic variability was observed for total biological yield production. I86032, I96033, N80068, and accession 6 had the highest mean biomass production. Under drought stress Malawian landraces 5 and 6 had the highest biomass production. Genotypic variability was also observed for water-use efficiency (WUE). Accession 6, B82008, I86033, and N80068 had the highest WUE. Mean WUE increased significantly under drought over that under well-watered conditions. The significant genotype increases were observed only in accessions 5 and 6. The two Mexican lines also showed WUE over 5.0, although this was not significant statistically. The contention is that the Malawian landrace components probably had more rooting density that lead them to explore for moisture more efficiently than other genotypes, especially under drought conditions. But roots were not sampled in this study. Total biological yield was used in assessing relative drought resistance among genotypes using the various methods of numerical expression (Table 32). The yield differential and S identified accessions 5 and 6, B76001 and Vita 3 to be the most drought resistant genotypes. This contrasted with both the arithmetic and geometric means which identified

Table 31. Biological yield and water-use efficiency (WUE) of 9 dry bean and one cowpea genotypes (1986).

Line/ Accession	Biological yield			WUE		
	WW	DS	Mean	WW	DS	Mean
	----- g/plant ----			----- g/kg water ----		
I86030	41.7	21.1**	31.4 b	3.27	3.52	3.49 c
I86032	48.7	30.5**	39.6 ab	4.06	5.08	4.57 ab
B76001	40.7	28.7	34.7 b	3.39	4.79	4.09 bc
I86033	49.3	30.6**	39.9 ab	4.12	5.09	4.60 ab
N80068	49.8	28.5**	39.1 ab	4.14	4.74	4.44 abc
B82008	46.4	25.7**	36.0 b	4.34	4.74	4.53 ab
NB1017	44.8	27.0**	35.9 b	3.78	4.47	4.12 bc
Vita 3	39.1	28.1	33.6 b	3.26	4.68	3.91 bc
5 (Malawi)	35.9	32.6	34.2 b	2.99	5.20**	4.10 bc
6 (Malawi)	52.3	38.5*	45.4 a	4.36	6.42**	5.39 a
Mean	44.9	29.1	37.0	3.79	4.87	4.33
CV (%)		30.1			29.7	

WW = well-watered treatment;

DS = drought stressed treatment;

* significant between treatments at P=0.05;

** significant between treatments at P=0.01;

Means followed by the same letter are not significantly (P=0.01) different.

Table 32. Biological yield differential, arithmetic mean, geometric mean, and drought susceptibility index (S) of 9 dry bean genotypes and one cowpea genotypes (1986).

Line/ Accession	[Y _{ww} -Y _{ds}]	$\frac{[Y_{mm}+Y_{ds}]}{2}$	[Y _{ww} xY _{ds}] ^{1/2}	S
	(1)	(2)	(3)	(4)
I86030	20.6	31.4	29.7	0.029
I86032	18.2	39.6	38.5	0.022
B76001	12.0	34.7	34.2	0.017
I86033	18.7	39.9	38.8	0.022
N80068	21.3	39.1	37.7	0.025
B82008	20.7	36.0	34.5	0.026
N81017	17.8	35.9	34.8	0.024
Vita 3	11.0	33.6	33.1	0.017
5 (Malawi)	3.3	34.2	34.2	0.005
6 (Malawi)	13.8	45.4	44.9	0.016

Y_{ww} = potential; biological yield under well-watered conditions;

Y_{ds} = biological yield under drought stress;

1 = biological yield differential;

2 = arithmetic mean biological yield;

3 = geometric mean biological yield;

4 = drought susceptibility index.

accession 6, and lines I86033, I86032, and N80068 as the most drought tolerant genotypes. The difference here was caused because the latter two methods incorporate yield potential and drought resistance whereas the former two methods remove the yield potential from the drought resistance attributes. Genotypic variability was observed for leaf moisture retention capacity (LMRC) (Table 33). White tepary, I86033, N81017, accession 5 (Katolika), and accession 6 had the highest LMRC. Line N81017 was shown to be the most drought tolerant line in a study conducted by my colleague (Samper, 1984), I86033, Vita 3, and accession 5 (Katolika) had significantly lower leaf transpiration rates (Table 34). There was a significant reduction in leaf area expansion in all genotypes under drought conditions (Table 35). Vita 3 had the fastest mean leaf area expansion rate.

Table 33. Specific leaf weight (SLW) and leaf moisture retention capacity (LMRC) of 9 dry bean and one cowpea genotypes at 36 DAP (1986).

Line/ Accession	SLW	LMRC
	g/cm ²	-- % --
I86030	2.46	43.8 a
I86032	4.11	34.5 b
B76001	3.65	39.3 b
I86033	3.01	40.4 a
N82008	3.67	34.8 b
B82008	3.45	37.2 b
N81017	3.49	43.8 a
Vita 3	3.97	33.1 b
5 (Malawi)	3.10	44.4 a
6 (Malawi)	3.63	40.9 a
Mean	3.51	39.9
CV (%)	29.9	17.8

Means followed by the same letter are not significantly
(P=0.01) different.

Table 34. Leaf diffusive resistance, leaf transpiration, and leaf temperature of 9 dry bean and one cowpea genotypes at 47 DAP (1986).

Line/ Acc. #	Leaf diffusive resistance			Leaf transpiration			Leaf temperature		
	WW	DS	Mean	WW	DS	Mean	WW	DS	Mean
	----- s/cm -----			ug H ₂ O/cm ² /s			----- C -----		
I86030	2.21	4.16	3.18	9.00	7.72	8.36	26.6	28.5**	27.5
I86032	1.66	5.01	3.33	11.43	7.17	9.30	27.3	28.4*	27.9
B76001	2.07	3.72	2.90	9.95	8.45**	9.20	27.0	28.3	27.6
I86033	2.86	6.44	4.65	8.99	4.19	6.59	27.9	28.8	28.3
N80068	1.30	4.54	3.02	12.19	6.36**	9.28	27.9	29.8**	28.9
B82008	1.61	2.67	2.14	10.16	8.30	9.33	27.0	27.9	27.5
N81017	1.48	6.79	4.13	12.58	5.36**	8.97	27.6	28.0	27.8
Vita 3	2.03	8.48	5.25	8.66	3.57	6.12	28.0	28.5	28.2
5 (Malawi)	3.36	5.93	4.64	8.71	4.45	6.58	28.0	28.0	28.0
6 (Malawi)	1.34	7.14	4.24	13.26	6.05**	9.65	27.8	28.6*	28.2
Mean	2.01	5.49	3.75	10.49	6.18	8.33	27.5	28.5	28.0
CV (%)	49.6			40.4			6.90		

WW = well-watered treatment;

DS = drought-stressed treatment;

* significant between treatments at P=0.05;

** significant between treatments at P=0.01;

Table 35. Leaf area expansion of 9 dry bean and one cowpea genotypes (1986).

Line/ Accession	Leaf area expansion		
	WW	DS	Mean
	----- cm ² /day -----		
I86030	5.08	1.63**	3.35
I86032	4.43	2.15**	3.29 b
B76001	4.82	1.83**	3.32 b
I86033	4.85	2.83**	3.84 b
N80068	5.00	1.75**	3.38 b
B82008	5.42	2.46**	3.94 b
N81017	4.91	1.93**	3.42 b
Vita 3	7.18	3.50**	5.34 a
5 (Malawi)	5.01	2.86**	3.93 b
6 (Malawi)	5.48	1.48**	3.48 b
Mean	5.22	2.25	3.47
CV (%)		26.4	

WW = well-watered treatment;

DS = drought-stressed treatment;

** significant between treatments at P=0.01;

Means followed by the same letter are not significantly
(P=0.05) different.

DISCUSSION

It is important to understand causes of drought at any one location before a researcher proceeds into developing genotypes that are supposed to be drought tolerant at that particular location. Drought is caused by a number of factors that govern the supply of moisture (precipitation and initial soil moisture at planting) and the demand for moisture by the atmosphere (an interplay of air temperature, relative humidity, wind, and solar radiation) and the soil at the site (matric forces). When the cause of drought is known one can then proceed to strategically address the problem. For example, Boyer et al. (1980) have observed, through wilting symptoms, that soybeans growing on adequate supplies of moisture in central Illinois experience drought. They determined that this was due to failure by the root system to replenish, at the necessary rate, the moisture lost to the atmosphere. In such a case, one would perhaps employ methods dealing with the morphology of root systems to explore adequate amounts of moisture and also, perhaps, reduce hydraulic resistance to water conduction through the root system. Work done in this study aimed at identifying genotypes of dry beans that are tolerant to drought conditions, or characteristics that make them respond as such, under the Michigan environment.

This work was conducted during some of the most moisture stressed years in Michigan. As was shown in Figure 1, the month of June in 1984 had virtually no precipitation. This was during the vegetative phase of bean plant growth. Although there was precipitation during reproductive growth its distribution was poor; periods of three to four weeks of no precipitation occurred. One intercropping experiment was conducted during this particular year. Results indicated that beans growing in intercropping systems with maize suffered moderate levels of moisture stress (soil moisture about 50 kPa). Andow and Berkowitz (1985) indicated similar results using field bean and weed associations. Berkowitz (1985), however, reported similar moisture depletion in corn and sunflower monoculture systems as that when the two were intercropped. In their case the two species were of similar height and populations were grown in alternate rows and so inter-species competition was kept to a minimum. In the present study the planting patterns and populations used were those that are used by or recommended for the Malawian farmers. No special adjustments in plant populations were made. Berkowitz (1985) concluded that intercrops use the same amounts of water as monocultural stands. In this study intercrops used significantly more soil moisture than monocultural bean stands. Therefore, beans grown in intercropping seem more likely to encounter drought than those in monoculture systems. These landrace lines from Malawi have been naturally selected under these mixed

cropping systems for more than 300 years and some may have evolved in such a way as to contend with such competition for moisture under intercropping and have become more drought tolerant concomitantly. Two significant results here are: a, that one could identify drought tolerant bean genotypes though their performance under intercropping systems; and b, that when developing bean cultivars for Malawian farmers it is important to incorporate drought tolerance to assure high productivity under prevalent cropping systems. In the past two to three decades crop scientists have condemned intercropping as a primitive method of crop production. Farmers do not want to change because this system maximizes their labor and crop yield stability as well as minimizes risk. This study identifies drought as one of the most important factors that farmers have to deal with and against which natural selection probably has been operating over the last several decades.

One of the mechanisms characteristic of some Malawian landraces exposed to drought under intercropping was stomatal resistance. The more stress tolerant landraces [accessions 4 (Nyauzembe), 7, and 17] significantly increased their leaf diffusive resistances under intercropping as compared with monoculture. The possible ways in which such stomatal behavior can enhance drought resistance in plants are: a, conservation of a limited supply of water so that some remains for later stages of the plant's development; b, prevention of potentially damaging

drought; and c, maximization of total assimilation with the available water (Jones, 1980). However, although genotypic variation in stomatal conductance has been shown in soybean (Carlson et al., 1979), most later studies (Clarke and McCaig, 1982; Tesha, 1984) including these conducted here, have failed to detect genotypic variation for this characteristics. The approach, under conditions of unpredictable droughts, should be to breed for a genotype with low diffusive resistance (high stomatal conductance) under good conditions (to maximize photosynthesis) but under drought conditions such a genotype should efficiently close its stomata. Upon rehydration such stomata should rapidly reopen. The overall result of such an approach is an increase in water-use efficiency (WUE).

Xerophytic plants have very thick leaves as one of the characteristics they have acquired in adaptation to high moisture deficit environments. Mesophytic plants seem to show similar increases in specific leaf weight (SLW) when grown under drought conditions (Turner, 1979). Turk and Hall (1980a) indicated increases in SLW of cowpea with increasing levels of drought. A similar response was observed with the bean genotypes grown under the rain-out shelter. However, beans grown in intercropping had significantly lower SLW as compared to those under monoculture due to expanded area and reduced weight per unit area under partially shaded conditions. The response observed under intercropping was only invoked due to the

partial shading and not as a result drought. This raises a problem in using SLW, under intercropping and drought, as a criterion for selection of drought resistant genotypes. The way SLW is calculated (equation 14) one does not necessarily know whether it is due to an increase in leaf thickness or accumulation of nutrients and starch. With the three different soil types, SLW showed no adaptation to soil moisture content accruing to differences in water-holding capacity of such soils. The problem with SLW is that if a plant increased SLW of its leaves when it is exposed to a drought during one of its growth stages the result would be an increase in SLW and a concomitant limitation of leaf area expansion. On rehydration SLW does not change as a result of which maximum leaf area is never attained. In cowpeas, seed yield was correlated with LAI at the end of flowering (Turk and Hall, 1980a).

A more flexible characteristic than SLW is leaf moisture retention capacity (LMRC). This was significantly different among bean genotypes but no evidence of a change due to cropping systems was detected. Some of the genotypes shown to be drought tolerant in this study using other criteria (accessions 2 and 17) had significantly higher amounts of leaf moisture retained, whereas stress-susceptible ones, like accession 14, retained significantly less moisture. Beans grown under more drought (light soil type) retained significantly more moisture than those grown on less droughty (heavy soil types). These results show

that LMRC is a more reliable indicator of a genotype's capacity to adapt to increasing soil moisture deficits than SLW. LMRC does not seem to be as conservative a trait as SLW because it is expected not to respond permanently. There was no significant relationship between LMRC and SLW and between SLW and total biological yield production. There was also no significant relationship between LMRC and total biological yield production. This casts some doubt as to whether LMRC could be used as an alternative to the porometer although it is not as convenient. Genotypic variability was observed with LMRC but it was not detected with use of the porometer.

There was significant genotypic variability in both biological and economic yield production under both monoculture and intercropping systems. Mean economic yield in 1984 was significantly reduced by 28.5% under intercropping from yields obtained under monoculture. Comparable yield reduction in beans and soybeans have been reported (Mmbaga, 1980). See yield reductions in such cropping systems were explained as due mainly to partial shading. Interestingly, some genotypes did not yield differently under intercropping as compared with monoculture. This indicates that some dry bean genotypes are adapted to intercropping systems whereas others are not. Pooled over methods or criteria of quantifying drought tolerance in 1984, the data indicate that accessions 2, 4, 5, 6, and 17 were better adapted than others to

intercropping. Accessions 1 and 14 were the least adapted. Economic yield was significantly reduced (24.3%) under intercropping from the yields obtained under monoculture in 1985. Accessions 4, 5, 7, and 17, and Bayo Madero seemed better adapted to intercropping than the remaining entries in 1985.

Under controlled conditions biological yield production declined significantly (42.6%) under drought conditions from biomass productivity observed under well-watered conditions. Turk and Hall (1980a), Bonanno and Mack (1983) and Jones et al. (1980) also reported reductions in biological yield in cowpea, snap bean, and perennial ryegrass (*Lolium perenne* L), respectively. In 1985, there was significant genotypic variability in biological yield production. Chiapas 7 had the highest mean biomass whereas accession 6 and BAT 477 had the least mean biomass production. Only accessions 5 and 17, and BAT 47 and Vita 5 significantly reduced their biomass productivity under drought. However, all genotypes produced significantly less (51.8%) economic yield under drought conditions and no genotypic variability was observed. BAT 47 and accession 5 (Katolika) were the most adapted genotypes to drought conditions in 1985. During 1986 there was again a significant decline in biological yield productivity (35.2%) under drought conditions from the potential productivity observed under well-watered conditions, except breeding line B76001, Vita 3, and accession 5, which showed no significant decline. Genotypic

variability existed in mean biological yield productivity. Accessions 5 and 6, lines B76001, Vita 3, I86033, I86032, and N80068 were more drought tolerant than other genotypes.

Better adapted genotypes under intercropping did not reduce their number of pods/plant when grown under such a system as compared to their potential under monoculture. The less well adapted genotypes suffered significant reductions in this yield component. Mmbaga (1980) indicated similar results. It seems that the number of pods/plant largely controlled number of seeds plants produced.

Under controlled conditions in 1985, there was a significant reduction in the number of pods/plant under drought from the number observed under well-watered conditions. In cowpea Turk et al. (1980) indicated that drought reduced seed yield due mainly to reductions in pods per square meter. There was also significant genotypic variation in the mean number of pods produced. BAT 47, a genotype that showed higher relative drought tolerance, produced the most pods/plant. Frederick et al. (1985) indicated that older soybean varieties were drought tolerant in terms of yield due to a smaller relative decrease in pod number/branch. However, using a different set of genotypes, Boyer et al. (1980) indicated consider yield improvement in newer cultivars when their yields were compared with those of older cultivars under a high evaporative demand environment. Rooting densities of two cultivars showing extremes of water deficits indicate that the cultivar with

the least water deficit had a greater root density than the cultivar with the largest deficit. The implication is that older cultivars have larger root densities than newer ones. If this is the case with large-seeded legumes crops in general, one would expect the Malawian landraces to have large rooting densities. Such a characteristic would be important especially under unpredicted droughts as compared with terminal droughts. The major portion of the environment in Malawi is such that crops have to rely on current rainfall and unpredicted droughts often occur. Large rooting densities would be most appropriate as opposed to deep rooting systems. This might explain why Malawian landraces had higher WUE in 1986 and lower WUE in 1985. In 1985 the large initial doses of water in WUE experiments simulated terminal drought whereas in 1986 unpredicted droughts were simulated. Under such latter conditions deep rooting genotypes would be at a disadvantage because they would be wasting biomass in developing deep roots when moisture is not available lower in the soil profile. This is probably why the tepary bean had lower WUE than other genotypes.

Water-use efficiency (WUE) calculated on the basis of total biological yield production during both the vegetative and reproductive periods (equation 7) increased, but not significantly, under drought from that under well-watered conditions in 1985. In 1986 the increase was significant. This contradicts reductions in WUE of leaves indicated in

sorghum and soybeans (Rawson et al., 1978) with increasing soil water deficits. Turk and Hall (1980b) indicate that WUE (calculated on the basis of seed yield and evapotranspiration) increases when drought is imposed during the vegetative period and it decreases when drought is imposed during the reproductive period. It would seem that some Malawian landraces partially close their stomata to conserve water and maximize total assimilation with the available water, i.e. tend to have high WUE. This was indicated by an increase in leaf diffusive resistance and consequent decrease in leaf transpiration under stress.

Drought tolerant genotypes were identified by some characteristics. They showed increased leaf diffusive resistance, reduction in leaf transpiration rates, and reduction in leaf temperature under stress conditions. LMRC and SLW produced mixed results. The drought tolerant genotypes had lower SLW in the 1984 intercropping experiment. Genotypic variability in SLW was not observed in the 1986 WUE experiment. Some of the drought tolerant genotypes, on the other hand, had higher LMRC than other drought tolerant and susceptible genotypes in both of the above experiments. However, in the 1985 intercropping experiment, the drought tolerant genotypes were among those with higher LMRC. Montcalm, a cultivar adapted to the area, produced the highest economic yield and also had higher LMRC than other entries. The Malawian landrace components 5 and 6, which increased WUE under drought conditions, were among

genotypes with significantly higher LMRC. In the 1984 intercropping experiment most of the drought tolerant genotypes also escape drought by either maturing early or by a coincidence of a relief from drought (precipitation) and either pod development or seed-filling (Table 37 in the Appendix).

SUMMARY AND CONCLUSIONS

1. Intercropping maize and beans resulted in significantly lower soil moisture indicating that the bean would suffer from drought stress earlier under such a cropping system than when beans are grown in monoculture systems. Since most of the beans are grown in intercropping in Malawi, such droughts comprise most of the environmental limitations to crop productivity.
2. Genotypic variability was indicated in tolerance to stress caused by intercropping and/or drought in the selected genotypes of *Phaseolus* and *Vigna* species. This is probably a major explanation of why Malawian farmers use bean mixtures. They want to maximize seed yields during the good years by planting landraces of higher yielding potential while at the same time aiming at minimizing yield losses during drought years by including drought tolerant genotypes (a double-barrel strategy).
3. Under simulated unpredictable droughts Malawian landrace lines had significantly higher water-use efficiency. However, under simulated terminal droughts the Malawian were comparable to other genotypes in water-use efficiency.

4. Leaf moisture retention capacity (LMRC) was significantly different among genotypes, although it was not significantly related to economic yield. Drought tolerance and yield potential are two different characteristics that are possibly differently inherited. However, the combination of the two should produce high yielding drought tolerant genotypes (within limits). There was no evidence for either LMRC or SLW being good indicators of drought tolerance.
5. Intercropping maize and beans increased leaf diffusive resistance in beans and as a result decreased leaf transpiration. This indicates that some Malawian landraces overcome intercropping and consequent drought stresses by conserving moisture and probably utilizing it more efficiently.
6. Both biological and economic yields were significantly reduced in susceptible genotypes to intercropping stress. There was no evidence for such reductions in the adapted landraces and cultivars. Under simulated terminal droughts (WUE, 1985) virtually all genotypes had significant reductions in biological yield. However, under simulated unpredictable drought (WUE, 1986) there was no evidence for such reductions in the drought tolerant genotypes.

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APPENDIX

Table 36. Mean squares (ms) from analysis of variance for moisture tension of soil under monoculture and intercropped Malawian landrace day beans (1984).

Source of variation	df	ms	Pr > F
Rep (R)	2	3755.799	-
Genotypes (G)	17	37.038	0.030
R x G	34	17.427	-
Treatment (T)	1	3312.642	0.000
G x T	17	15.505	0.138
R x G x T	36	10.114	-
Stage (S)	2	21208.892	0.000
G x S	34	21.382	0.452
T x S	2	323.429	0.000
G x T x S	34	6.684	ns
R x G x T x S	144	21.017	-

Table 37. Patterns of response by the landrace genotypes to drought in 1984.

Entry	Stage when drought was critical
1	early pod development
2	escaped, early maturity
3	end seed-filling
4	escaped, synchronized*
5	escaped, synchronized
6	escaped, early maturity
7	escaped, synchronized
8	escaped, synchronized
9	problem related to fertility
10	late pod development
12	early pod development
13	early pod development
14	early pod development, seed-filling
15	early pod development
16	early pod development
17	escaped, early maturity

* 'escaped, synchronized' means that the genotype escaped the drought largely from the fact that drought occurred outside the important reproductive stages, namely; pod development and seed filling.

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