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Comparative Ecophysiology of Cowpea, Common Bean, and Peanut

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1 INTRODUCTION

The comparative ecophysiology of yield and environmental adaptation of grain legumes is discussed. Emphasis is placed on opportunities for enhancing yield potential and resistance to abiotic stresses through breeding-improved cultivars and developing management methods that complement the new cultivars. This work concentrates on biotic stresses that interact with resistance to abiotic stresses and factors influencing yield potential. Symbiotic associations involving rhizobia and mycorrhizal fungi are particularly relevant to the function of grain legumes in cropping systems and are examined.

Few comparisons have been made about the ecophysiology of different grain legume species. Such comparisons can be valuable in that what has been learned about one species may be relevant to another. Also, in the future, genetic engineering should make it possible to transfer genes and, possibly, traits between species. Cowpea (*Vigna unguiculata* L. Walp.) is emphasized and compared with common bean (*Phaseolus vulgaris* L.), peanut (*Arachis*

hypogaea L.), and some other grain legumes to illustrate similarities and contrasts, and concepts that are not covered well in the cowpea literature.

Comprehensive reviews are available on breeding with cowpea (Hall et al., 1997a; Ehlers and Hall, 1997), common bean (Kelly et al., 1999; Kelly, 2000), and peanut (Knauff and Wynne, 1995); they contain some information on the ecophysiological traits conferring adaptation. Cowpea, common bean, and peanut are annual legumes which are adapted to warm conditions and are sensitive to chilling. Consequently, they are cultivated either in the tropics or during the warm season in subtropical or temperate zones. Cowpea, common bean, and peanut are mainly grown to produce dry grain. Cowpea is also grown to produce fresh southern peas, edible pods, edible leaves, hay, or forage, and as a green-manure crop. Common bean is likewise grown to produce edible pods, while peanut is often grown as a dual-purpose grain/hay crop. Cowpea and common bean are grown either as sole crops or as intercrops with other species, such as cereals. I will mainly focus on the sole-crop system because I feel this will be the dominant cropping system for grain legumes in the future. Future directions that are relevant to the breeding of all grain legumes are described at the end.

Prior to considering the phenological, morphological, and physiological traits that confer adaptation, I will provide a practical recommendation concerning a major principle that is particularly relevant to cowpea and common bean. Improved cultivars should produce the type of product that is desired by farmers, markets, and consumers. For grain legumes, consumer acceptance of the grain can be strongly influenced by the size and shape of the grain and the nature of the seed coat including the following factors: its color, how easily it takes up water during cooking, its cracking tendency, and whether it leaks pigments when cooked (Hall et al. 1997a). Selection of parents and progeny must place substantial emphasis on grain quality traits. For cowpea, this can be accomplished by making a large initial segregating generation (i.e., the F_2), and then practicing rigorous selection for grain quality traits within this and all subsequent generations. This aspect is of paramount importance because there have been too many cases where cowpea cultivars or advanced breeding lines have been developed which have outstanding adaptation and yields but which have not been adopted by farmers because of flaws in the quality of the grain (Kelly et al., 1999 discuss this issue for common bean).

2 GRAIN YIELD WITH OPTIMAL SOIL WATER AND OTHER CONDITIONS

Currently, the yield potential of grain legumes is not as high as that of cereals. This may be attributed to the inherent differences that constrain carbohydrate

production in grain legumes, in comparison with cereals, such as the metabolic costs of fixing atmospheric nitrogen and producing grain with high protein or oil contents. Moreover, less research effort has been devoted to most grain legume species than to the major cereal species. In addition, evaluation of segregating lines and yield testing tend to be less efficient with grain legumes because of the need for larger plots and more hand labor and time during harvest than with small grain cereals. Currently, most cowpea and common bean cultivars cannot be combine-harvested as a standing crop due primarily to the fragility of the grain (Hall and Frate, 1996). Empirical approaches based on yield testing are an essential part of most breeding programs with annual grain crops. Selection for ecophysiological traits should be regarded as complementing and not replacing empirical approaches. If lack of research and insufficient yield testing and information on ecophysiological traits have been major constraints, substantial opportunities may still exist for enhancing the yield potential of grain legumes through the development of improved cultivars and management methods.

In optimal conditions, grain yield of grain legumes per unit ground area (Y) can be modeled by using the following equation (Hall, 2001):

$$Y = \sum_{i=d}^{i=1} \text{PFD}_i \times \text{GC}_i \times Q_i \times \text{CP}_i \quad (1)$$

where Σ is the summation of daily values of $\text{PFD} \times \text{GC} \times Q \times \text{CP}$ over the period of days (d) when photosynthesis significantly contributes carbohydrate to the developing grains, which often ranges from an early flowering stage to the date when most grains are physiologically mature. According to the model, grain yield depends on the flux density of photosynthetically active photons (PFD; expressed in $\text{mol}[\text{photon}] \text{m}^{-2} \text{day}^{-1}$), the proportion of ground covered by the crop (GC; in $\text{m}^2 \text{m}^{-2}$) as this determines the interception of PFD, the efficiency of conversion of intercepted photons into carbohydrate through photosynthesis (Q in $\text{g}[\text{CH}_2\text{O}] \text{mol}[\text{photon}]^{-1}$), and the proportion of carbohydrate that is partitioned to grain (CP in $\text{g}[\text{CH}_2\text{O}] \text{g}[\text{CH}_2\text{O}]^{-1}$) on each day. The CP is conceptually related to harvest index (HI), which is often calculated as the ratio of grain yield to total shoot biomass at harvest. The CP will have a variable metabolic energy component for cases where grain carbohydrate substantially varies in oil or protein content. For grains with high protein content, a negative interaction may occur between CP and Q because of the breakdown of photosynthetic enzymes in leaves providing the amino acids, which are translocated to grains and synthesized into proteins (Sinclair and deWit, 1975).

Achieving high grain yields requires that cultivars have a reproductive period (approximated by d) of optimal length, as determined by the length

of the growing season or cropping system considerations. Cultivar and management methods should be designed to insure that ground cover is nearly complete (GC approaches 1.0) during the reproductive period. Cultivars should have maximal canopy efficiency for photosynthetic conversion of intercepted photons into carbohydrates (Q) and optimal values for partitioning of carbohydrate into grain (CP). In ideal environments, most of the carbohydrates for developing grains come from current photosynthesis, but some do come from carbohydrate that was previously stored in stems or roots. Methods for optimizing d and CP while maximizing Q and GC are discussed below.

2.1 Phenology and Reproductive Duration

Typically, the reproductive period of grain legumes consists of one or more discrete flushes encompassing overlapping periods of development by individual pods. Erect indeterminate cowpeas are able to produce two distinct flushes of pods (Gwathmey et al., 1992a). In California, the crop is harvested after producing either only the first flush of pods or after accumulating both flushes of pods (Hall and Frate, 1996). The duration of the reproductive period is influenced by temperature, as shown by studies where cowpeas were subjected to different night temperatures while growing in the same field (Nielsen and Hall, 1985a). The rate of development of individual cowpea pods was strongly influenced by night temperature. The period from anthesis to maturity of individual pods decreased linearly from 21 days with minimal night temperature of 15.5°C, typical of cool subtropical zones, to 14 days with minimal night temperature of 26.6°C, which is typical of hot tropical environments (Nielsen and Hall, 1985b). Genotypic variation during the pod development period is observed in cowpea, which is positively associated with individual seed weight (Wien and Ackah 1978). For very small seeds (50 mg per seed), the pod development period was 17 days, whereas with moderately large seeds (200 mg per seed), the pod development period was 21 days. The duration of the flush of pod production also depends on the rate at which reproductive nodes are produced and the total number of reproductive nodes that are produced. The rate of production of nodes is the same as the rate of production of leaves. Leaf appearance rate (RLA, in day⁻¹) in cowpea has exhibited a linear dependence on mean air temperature above a base temperature (T_b), with no effect of photoperiod (Craufurd et al., 1997).

$$RLA = (T - T_b)/P \quad (2)$$

where T represents the mean air temperature; P is the phyllochron, which is constant for a genotype but varied among genotypes with a mean value of about 42°C day; while T_b varied between 9 and 12°C for different genotypes

(Craufurd et al., 1997). According to Eq. (2), a genotype with a T_b of 10°C would produce a leaf (and a node) about every 4 days when subjected to a cool mean temperature of 20°C , and about every 2 days when subjected to very hot conditions with a mean temperature of 30°C . Craufurd et al. (1997) reported that peanut and soybean (*Glycine max* L. Merr.) can have greater phyllochrons of about 56°C day , which means that they would produce leaves and nodes at a slower rate than cowpea.

Because the rate of production of nodes increases with increasing temperature, day-neutral cultivars exhibit fewer days to first flowering because they begin flowering at a specific nodal position on the main stem. A heat-unit model was developed to describe this effect (Ismail and Hall, 1998). Rate of development ($1/D$, the inverse of the period from sowing to flowering as expressed in days) increased linearly with average daily air temperature above a base temperature (T_b) up to a threshold level of $25\text{--}30^\circ\text{C}$, depending on the genotype (and day length), where the rate of development reached a plateau and remained constant.

$$1/D = (T - T_b)/\text{HU} \quad (3)$$

where T is the mean air temperature and HU is the heat unit requirement, which can vary substantially among genotypes. The base temperature, T_b , exhibits less genotypic variation than HU. For a set of early flowering, erect, indeterminate breeding lines developed for subtropical conditions in California, HU was 734°C day and T_b was 8.5°C . With a cool mean air temperature of 20°C , these lines would begin flowering 64 days after sowing. In contrast, with a very hot mean air temperature of 30°C , the response would depend on whether the genotype is heat-sensitive and exhibits suppression of floral development under hot long-day conditions. In these hot conditions, heat-tolerant lines would begin flowering 34 days after sowing under either long or short days. Under short days, heat-sensitive lines would also exhibit rapid development in these conditions and begin flowering 34 days after sowing. In contrast, under hot long-day conditions, the rate of reproductive development of heat-sensitive lines would reach a plateau and not increase as much, such that they would begin flowering at about 44 days after sowing.

The period from first flowering to physiological maturity also decreases with hotter temperatures. Consider an early flowering, erect, indeterminate cowpea cultivar, e.g., "California Blackeye 5" (CB5), growing in a subtropical zone (Shafter, CA) and a tropical zone (Bambey, Senegal). During the summer growing season, night temperatures are much higher in Bambey (with average nightly minimum of 23°C) than in Shafter (average nightly minimum of 15°C ; see Ismail and Hall, 1998 and Hall, 2001 for additional temperature data from these and other locations in the world.) This cultivar begins flowering about 50 days after sowing in Shafter and can reach physio-

logical maturity of the first flush of pods about 100 days after sowing, resulting in a reproductive period of about 50 days. In contrast, the same cultivar begins flowering about 34 days after sowing in Bambey and reaches physiological maturity about 65 days after sowing, resulting in a reproductive period of about 31 days. Under optimal soil conditions, with careful management of pests, no significant diseases, and high levels of solar radiation, this cultivar achieved very high first-flush grain yields of about 5 ton/ha at Shafter and about 2.5 ton/ha at Bambey. Thus in sunny, cloud-free conditions in California, this cultivar has the potential ability to produce about 100 kg grain ha⁻¹ per day of reproductive period. Much of the difference in yield between California and Senegal can be explained by the large difference in the length of reproductive period (50 vs. 31 days). However, the productivity per day of CB5 was slightly less in Senegal at only 81 kg grain ha⁻¹ per day, but then CB5 is not well adapted to this environment. The relationship between grain yield and length of the reproductive period has been evaluated in other studies in California. Well-managed cowpeas were sown on different days and years, and showed a strong positive linear correlation between grain yield and the duration of the reproductive period as it varied due to temperature differences with a regression slope of about 84 kg grain ha⁻¹ per day of reproductive period (Turk et al., 1980).

In optimal soil conditions, it is apparent that grain yield can be positively correlated with the length of the period from first flowering to physiological maturity. Cultivars of grain legumes can be bred with different durations of the reproductive period. This can be done by selecting for different numbers of days to first flowering and different plant habits. Genetic variation is present in cowpea for days to first flowering, and genotypes have been classified for this trait as it varies due to temperature and photoperiod (Patel and Hall, 1990; Ehlers and Hall, 1996). In all genotypes, temperature influences the rate of node production. In contrast, photoperiod determines the first node at which floral buds are initiated in genotypes that are sensitive to photoperiod in this way. These cowpea genotypes have a short-day response to photoperiod, and floral buds are initiated when the photoperiod becomes less than a critical day length of about 12.5 hr (Lush et al., 1980; Lush and Evans, 1980). Interaction between photoperiod and temperature can influence the rate of floral bud development in certain genotypes (Ehlers and Hall, 1996). In these cases, floral bud development is slowed down or completely suppressed in hot long-day conditions, but not in cooler long-day or short-day conditions. In general, cowpea plants that have earlier first flowering and are more erect have a shorter first-flush reproductive period than plants that have later first flowering and are more prostrate, which have a greater tendency to produce more branches and more reproductive nodes. For subtropical target production regions in the continental United States,

breeders of cowpea for dry grain or fresh southern pea production have emphasized the development of erect cultivars that do not have a strong photoperiod requirement for first flowering. Erect cultivars are needed because they exhibit synchronous production of mature pods, which facilitates mechanical harvesting. Cultivars with a strong photoperiod requirement are not effective because they would not begin flowering until late September, because they must first undergo some days when the photoperiod is shorter than a critical value of about 12.5 hr. Generally, conditions become too cool after this date in the continental United States, such that pod filling by this warm-season species either ceases or is very slow. Exceptions to this are the low-elevation valleys in the southern United States, such as the Coachella Valley of California, which can remain warm through November.

Two approaches of developing cowpea cultivars for subtropical zones with greater yields due to an extended reproductive period are examined. The first approach involves managing the crop to produce two flushes of pods (Gwathmey et al., 1992a). Record grain yields for cowpea have been achieved on large plots at Shafter, CA, through this technique. As was described earlier, cowpea in California has the potential to produce about 5 ton/ha on the first flush of pods. These plants will begin producing a second flush of flowers about 15 days after the first flush has ended, and then will take about 30 days to potentially produce another 2 ton/ha (Ismail and Hall, 1998), giving a total grain yield of 7 ton/ha. In the rain-free environment of the summer in the San Joaquin Valley of California, these pods can accumulate without suffering much damage after which both flushes are harvested. There are two problems with this approach. The first is that in some soil conditions, plants die after producing the first flush of pods (this phenomenon has been observed in many fields in California and also in Bambey, Senegal; Hall et al., 1997b). The soil organism that causes premature death in cowpea is probably *Fusarium solani* f. sp. *phaseoli* and it may also be responsible for the premature death observed in soybean and common bean. A delayed-leaf-senescence (DLS) trait, which was discovered in cowpea, can overcome this problem and appears to be simply inherited and is easy to incorporate; however, it confers a modest yield penalty on the first-flush grain yield of about 400 kg/ha (Ismail et al., 2000). A possible explanation is that the delayed-leaf-senescence trait confers resistance to premature death by causing more carbohydrate to be translocated to stem bases and, presumably, roots during the first flush of podding, thereby reducing the carbohydrate available for the first-flush yield (Gwathmey et al., 1992b). In some way, roots with higher levels of carbohydrates appear to have greater resistance to fungal disease. Another problem with this approach is that it makes inefficient use of the growing season in that there is a period between the two flushes of about 15 days when the plants are not producing flowers. Eliminating this inactive period by improved management has the

potential to enhance grain yields. Unfortunately, no management methods that can eliminate or reduce the length of the inactive period have, so far, been identified. The inactive period when no flowers are produced appears to be internally programmed in that it still occurs when young or older pods are continually removed during the duration of the first flush (Kwapata and Hall, 1990a; Gwathmey et al., 1992b). An alternative approach for achieving high grain yields would be to develop erect day-neutral cultivars that produce one pod flush of extended duration, which has the potential to produce a large number of pods. A hypothetical approach for doing this would involve selecting plants with a longer juvenile period that begin flowering later on a higher main-stem node. These plants would produce a larger vegetative base at first flowering, which would provide more reproductive nodes on branches, thereby supporting a single, longer and greater first flush of reproduction than current cultivars.

Cowpea breeders in tropical zones have several options for breeding cultivars with extended reproductive durations in that they can use either day-neutral or photoperiod-sensitive cultivars, and either erect or prostrate cultivars—depending on the patterns of the rainfall season and photoperiod, and degree of mechanization. Usually, prostrate cultivars are very sensitive to photoperiod, whereas erect cultivars can be either day-neutral or have varying degrees of sensitivity to photoperiod (Ehlers and Hall, 1996). With day-neutral, erect cultivars, a longer reproductive period may be achieved with a genotype that begins flowering early on a low node on the main stem by incorporating a gene causing “skipping.” For most cowpea genotypes, as soon as floral buds are initiated on the main stem, subsequent nodes on the main stem are also reproductive. However, under hot short-day conditions, the main stem of certain genotypes produces a few vegetative nodes, then two to four reproductive nodes, then one or two vegetative nodes, and then more reproductive nodes—this has been called “skipping” (Ehlers and Hall, 1996). The vegetative nodes produce branches, and therefore “skipping” increases the number of reproductive nodes that occur on branches and thereby lengthens the reproductive period.

Photoperiod sensitivity may also be useful for lengthening the reproductive period in some environments. For common bean, it has been established that plasticity in days to first flowering may be adaptive under rainfed conditions in the semiarid highlands of Mexico, and that some photoperiod-sensitive cultivars have this plasticity (Acosta-Gallegos and White, 1995). In this region, common beans are sown at the onset of the summer rains, which can vary from early June to late July. The crop must be harvested before temperatures become too cool, or water becomes scarce owing to the cessation of summer rains, which often occurs in late September or early October. An adapted cultivar would have a shorter period from sowing to first flow-

ering when sown later in this environment, and photoperiod-sensitive cultivars of common bean exhibit this type of phenological plasticity. Similar but more complex circumstances occur in the Savanna zone of West Africa, which is a major cowpea production zone (Wien and Summerfield, 1980). The sowing date is determined by the onset of the rains, which can be highly variable, whereas the end of physiological activity is determined by water limitations due to the cessation of the summer rains and is less variable. A cowpea cultivar that is well adapted to rainfed production in the Savanna zone would be plastic and begin flowering at the same date in the summer, irrespective of variation in the date of sowing. Achieving this plasticity also requires a degree of sensitivity to photoperiod in which long days either prevent the initiation of floral buds, or through an interaction with elevated night temperatures that slow down the development of floral buds during the early part of the cropping season (Ehlers and Hall, 1996). The complexity arises in that different local land races of cowpea grown by farmers in the Savanna zones of West Africa were adapted to different latitudes and photoperiods, and had different sensitivities to photoperiod (Wien and Summerfield, 1980). This enabled the different land races to begin flowering at the end of the rains in their specific regions, although they experienced different photoperiods just prior to flowering in these different locations.

For both common bean (Kornegay et al., 1993) and cowpea (Ehlers and Hall, 1996; Hall et al., 1997a), photoperiod sensitivity mainly depends on a few major genes, such that the trait can be manipulated by breeding. In common bean, there is substantial genotypic variation for the photoperiod response of flowering (White and Lang, 1989), and as for cowpea (Ehlers and Hall, 1996), this response can be influenced by temperature, which can make inheritance more complex (White et al., 1996). Most studies of environmental effects on days to first flowering in common bean did not discuss whether any suppression of floral bud development occurred as it does in cowpea under hot long-day conditions. However, the qualitative studies of Shonnard and Gepts (1994) indicate that some genotypes of common bean may exhibit high-temperature-induced suppression of floral bud development during long days. Therefore the increased photoperiod sensitivity of days to first flower observed in some common bean genotypes under hotter conditions (White et al., 1996) may be attributed to either floral bud suppression, which is induced under hot long-day conditions, as also occurs in some cowpea genotypes (Ehlers and Hall, 1996), or an interactive effect of photoperiod and temperature on floral bud initiation.

For peanut, studying the length of the period from first flowering to maturity is constrained by difficulties in defining and determining maturity for an indeterminate, nonsenescent plant whose fruits mature below the ground. Consequently, inheritance of phenological traits is poorly understood in

peanut, and these traits are difficult to manipulate during breeding (Knauff and Wynne, 1995). Peanut has been considered as a photoperiod-insensitive species, but in some cases, the extent of flowering may be slightly less under long hot days than short hot days (Knauff and Wynne, 1995).

For stable production environments, an important strategy in breeding grain legumes is to develop a cultivar that has a duration from sowing to grain maturity which fits into the available growing season, and also a date of first flowering that divides the growing season into vegetative and reproductive stages that have optimal durations.

2.2 Canopy Photosynthetic Efficiency (Q)

In grain legumes and other crop species, it has proven difficult to increase the photosynthetic efficiency of the canopy in converting PFD to carbohydrate (Q) by breeding. One approach for increasing Q under optimal soil conditions is to breed plants with higher rates of photosynthetic assimilation of carbon dioxide per unit leaf area because their leaves have either more open stomata and/or greater mesophyll capacity for fixing carbon dioxide. Genotypic differences in the potential grain yield of cowpea have been positively associated with leaf stable carbon isotope discrimination (Δ), indicating that more productive genotypes had higher internal carbon dioxide concentration in their leaves (Hall et al., 1997b; Condon and Hall, 1997). A genotype with higher internal carbon dioxide concentration would have higher stomatal conductance in relation to its mesophyll capacity for fixing carbon dioxide. This positive association between grain yield and Δ has been observed in other crop species with C_3 photosynthetic metabolism (reviewed by Hall et al. 1994a; Condon and Hall, 1997). The higher Δ in more productive genotypes of cowpea, cotton (*Gossypium barbadense* L.), and wheat (*Triticum* sp.) was probably due to their having more open stomata, which could have resulted in greater rates of photosynthesis due to diffusion effects (Condon and Hall, 1997), or beneficial effects on the plant resulting from greater evaporative cooling (Lu et al., 1998), but which could also be associated with either no change or a reduction in the mesophyll capacity for photosynthesis. Selection for higher Δ would only result in an increase in photosynthetic capacity if it is accompanied by an even greater increase in stomatal conductance. An alternative explanation for the higher grain yields in cowpea, cotton, and wheat is that Δ has also been positively correlated with HI (Menéndez and Hall, 1996). The mechanism for this association is unknown but genotypes with greater HI may also have more open stomata because of feedback effects associated with their greater reproductive sink activity. The evolutionary basis of the positive genotypic association observed between biomass production and stomatal conductance with several crop species has been dis-

cussed by Condon and Hall (1997). They speculated that the evolution of these crop species favored conservative stomatal function—that is, a tendency for stomata to be at least partially closed under many circumstances. This could have arisen if plant performance during very dry years, where conservative stomatal performance would be adaptive, had disproportionate influences on seed production and long-term evolutionary success over many years owing to soil “seed banks” becoming considerably less effective after 1 year. Interestingly, F_1 hybrids of cowpea usually have strong early vegetative vigor, as well as Δ values that are higher than midparent means under well-watered field conditions (Ismail and Hall, 1993, but also see Ismail et al., 1994 for a discussion of pot rooting volume effects on Δ). The extent in which grain yield can be increased by selecting for higher Δ and/or greater stomatal conductance will be constrained when these parameters approach optimal levels.

For peanut, in contrast with cowpea and wheat, biomass production was shown to be negatively correlated with Δ because of a positive genotypic correlation between biomass production and mesophyll capacity for photosynthesis (Wright et al., 1993). For peanut, a strong positive association was observed between Δ and the ratio of leaf area/leaf dry weight, which, for selection purposes, is much easier to measure than either Δ or photosynthetic capacity (Nageswara Rao and Wright, 1994). Consequently, in peanut, there is an opportunity to select for increases in photosynthetic capacity of leaves by selecting for reductions in leaf area/leaf dry weight and this may increase Q . In several crop species, however, there has been a trade-off in that genotypes with greater photosynthetic capacity had smaller leaves (Bhagsari and Brown, 1986), but this may not be the case with the peanut genotypes used by Wright et al. (1993). However, in peanut, there is a strong negative genotypic correlation between biomass production and HI, such that genotypes with the highest biomass production usually do not produce the greatest grain yields (Wright et al., 1993).

In common bean, it is not clear whether a general relation exists between genotypic differences in potential biomass production and gas exchange traits. In some cases, genotypic differences in Δ positively correlated with stomatal conductance and biomass production (Ehleringer, 1990; White et al., 1990). However, for other sets of common beans, genotypic differences in photosynthetic rate, leaf thickness, and stomatal conductance that were positively correlated with relative growth rates measured during the first month after sowing were observed (Sexton et al., 1997). Small-seeded Meso-american lines tended to have greater photosynthetic rate, leaf thickness, stomatal conductance, and relative growth rate than large-seeded Andean lines. The authors concluded that the previously reported negative association of seed size with relative growth rate in common bean appears to be a function

of higher photosynthetic capacity, and consequently, faster assimilation rate and faster relative growth rates for small-seeded lines (Sexton et al., 1997). However, where greater growth rates and biomass production in common bean are associated with higher Δ (White et al., 1990), this would mean that the genotypes producing more biomass would have a greater ratio of stomatal conductance to photosynthetic capacity, and are therefore unlikely to have a greater photosynthetic capacity.

Leaf canopy architecture can influence Q through the effects on the distribution of light within the canopy. Leaflets of cowpea and other grain legumes tend to be diaheliotropic under optimal soil conditions (Shackel and Hall, 1979). The leaflets track the sun, such that they are perpendicular to the direct beam of solar radiation, which results in substantial absorption of sunlight in the upper canopy and nonuniform distribution of light within the canopy. Cultivars with more uniform light distribution in the canopy may have higher Q values. Comparison between cowpea genotypes with broad leaflets and genotypes with smaller, much narrower leaflets showed no differences in light distribution within canopies or shoot dry matter production (Wien, 1982). Under drought stress, cowpea leaflets became paraheliotropic and were oriented parallel to the direct beams of solar radiation (Shackel and Hall, 1979). Canopies with paraheliotropic leaflets can have more uniform light distribution than canopies with diaheliotropic leaflets. A small number of cowpea accessions have paraheliotropic leaflets under optimal soil conditions, and this trait might be used to enhance Q and thus yield potential, providing it is not associated with other conservative stress-response traits such as partial stomatal closure. But I anticipate that the effect on Q of genotypic differences in leaf movement and orientation would not be large in cowpea. Seventy-five common bean cultivars were screened for variation in leaflet movements (Kao et al., 1994). Mesoamerican types were slightly more paraheliotropic, which could enhance Q , compared with Andean types. However, there was strong genotype \times environment interaction and some inconsistency in the responses of lateral and terminal leaflets that could constrain selection for this trait in breeding.

Another approach for increasing the uniformity of light distribution would be to select for leaves that reflect more PFD due to their having either less chlorophyll content or reflective trichomes, but I anticipate that this may also only have a small effect on Q . There appears to be no advantage from selecting for high chlorophyll content per unit leaf area in that a cowpea mutant with yellowish leaves and 36% less chlorophyll content (Kirchhoff et al., 1989b) had similar quantum efficiencies (Habash et al., 1994), rates of leaf photosynthesis per unit of intercepted PFD (Kirchhoff et al., 1989c), and grain yield (Kirchhoff et al., 1989a) as its parent, which had dark green leaves. Possibly, leaves with light green appearance may have optimal levels of chlorophyll.

Breeding for some canopy traits can result in Q decreasing below maximum values. Under optimal conditions, the maximum Q value of cowpea may be about 600 mg dry matter/mol of intercepted photosynthetically active photons (Kwapata et al., 1990). This could result in crop growth rates of 300 kg dry matter ha⁻¹ day⁻¹ for a canopy that completely covers the ground and sunny conditions with PFD of 50 mol photon m⁻² day⁻¹. Surprisingly, a cowpea genotype with many pods displayed above the canopy had a Q value that was only 46% of the value of a genotype whose pods were retained within the canopy but had a similar genetic background (Kwapata et al., 1990). The authors hypothesized that this effect was a result of absorption of PFD by pods, which had much lower rates of photosynthesis than leaves. Green cowpea pods can exhibit even a net loss of carbon dioxide when exposed to full sunlight (Littleton et al., 1981). Removal of young pods would be expected to reduce pod interference with PFD interception by leaves and was shown to substantially increase the Q rate of a genotype that displayed its pods above the canopy, and have little effect on the Q rate of a genotype that retained its pods within the canopy (Kwapata et al., 1990). Cowpea cultivars having canopies with pods displayed above the leaves have advantages with respect to providing fewer oviposition sites for pod borer (*Maruca testualis* Geyer). Pod borer is a major pest of cowpea in tropical zones such as the Savannas of West Africa (Hall et al., 1997a). Under rainy conditions, pods displayed above the canopy are also less likely to be damaged by various wet and dry pod rot organisms because they dry out more rapidly after the rain ends than pods retained inside the canopy. Moreover, pods displayed above the canopy are easier to harvest by hand than pods retained within the canopy. Consequently, there is some merit in having cultivars with pods displayed above the canopy for rainfed production in wetter areas of Africa, where the crop is manually harvested. However, such cultivars have likely reduced ability to produce biomass compared with canopies in which the pods are covered by leaves. In California, cowpea is grown under irrigation in environments where it rarely rains, there are few problems with pod rots, pod borer is not present, and the crop is mechanically harvested. Consequently, cultivars for use in California should and do have canopies where pods do not project above the leaves.

2.3 Partitioning of Carbohydrate to Grain (CP) and Harvest Index (HI)

Grain legume breeders have not been as successful as cereal breeders in achieving increases in grain yield by enhancing the partitioning of carbohydrate to grain (CP) and thereby increasing HI. Earlier analysis indicated that, under optimal conditions, cultivars of cowpea can achieve Q values of about 600 mg dry matter/mol of intercepted photons, which with PFD of about

50 mol photon $\text{m}^{-2} \text{day}^{-1}$ would result in biomass production of 300 kg $\text{ha}^{-1} \text{day}^{-1}$. Under optimal conditions, rates of grain production of about 100 kg grain $\text{ha}^{-1} \text{day}^{-1}$ of the reproductive period have been achieved in sunny conditions with PFD of about 50 mol photon $\text{m}^{-2} \text{day}^{-1}$. This suggests that CP values were about 0.3, but this is an underestimation, in that biomass production would have decreased in the last half of the reproductive period due to leaf senescence.

Earlier studies of partitioning simply measured the ratio of grain yield to total shoot biomass at harvest (HI), which is somewhat different from, but conceptually similar to, CP. For cowpea, Kwapata and Hall (1990b) suggested that selecting bush types with greater HI could produce cultivars with potential for greater productivity under high plant densities, and that this selection could be conducted in early generations with widely spaced plants. This hypothesis concerning HI and yield potential was tested by using pairs of cowpea breeding lines with similar genetic backgrounds and either have, or do not have, heat tolerance during reproductive development. The heat-tolerance trait was shown to be associated with shorter internodes, dwarfing, and greater HI (Ismail and Hall, 1998, 1999). One of the semidwarf lines with heat tolerance, California Blackeye No. 27 (CB27), was released as a cultivar in California (Ehlers et al., 2000). Three semidwarf and three standard-height cowpea lines with similar indeterminate plant habit and phenology were evaluated at row spacings of 51, 76, and 102 cm in four productive field environments that varied in soil conditions and the extent of early vegetative vigor (Ismail and Hall, 2000). Semidwarf lines produced relatively greater first-flush grain yield than standard lines at narrower row spacings (15%, 11%, and 4% greater yield than standard lines at 51-, 76-, and 102-cm row spacing, respectively). Semidwarf lines produced greater grain yield than standard lines at narrow row spacing in soil conditions that promoted moderate to vigorous early plant growth. The smaller grain yield of the standard lines was caused by their impaired reproduction on branches compared with the semidwarf lines when competition for light was strong. Genotypic mean grain yield averaged over the two narrower row spacings (51 and 76 cm) and four environments was positively correlated with HI ($r = 0.97$, $n = 6$) with the slope of regression predicting an increase of 587 kg/ha in grain yield per 0.10 change in HI. Among the six genotypes, the range in first-flush grain yield was 2992–3597 kg/ha, and the range in HI was 0.41–0.51. Genotypic mean grain yield was also positively correlated with the average number of pods per peduncle on the first five reproductive nodes on the main stem ($r = 0.86$, $n = 6$). An even stronger positive correlation was observed between HI and the number of pods per peduncle ($r = 0.94$, $n = 6$). These correlations suggest that grain yield was responding to increases in HI that resulted from increases in pod

setting ability. In contrast, the genotypic mean grain yield was negatively correlated with vegetative shoot biomass ($r = -0.90$, $n = 6$). The slope of regression for the combined data from 51- and 76-cm row spacing predicted that an increase of 578 kg/ha in grain yield would be accompanied by a 1000 kg/ha decrease in vegetative shoot biomass, and therefore a substantial decrease in total shoot biomass and possibly GC or Q . At the narrowest row spacing (51 cm), however, the average total shoot biomass production of the semidwarf lines over the four environments was very similar (7534 kg/ha) to that of the standard lines (7528 kg/ha). This indicates that, with dense plant spacing, GC and Q may have been similar for standard and semidwarf lines. These studies are consistent with the hypothesis of Kwapata and Hall (1990b), stated above, that selecting for high HI could produce cowpea cultivars with the potential for high grain yields under high plant densities. However, selecting for higher HI only would be effective until an optimal HI had been achieved.

Erect or semierect semidwarf grain legume cultivars with high HI may only be suitable for intensive single-flush production under high plant densities in environments with low levels of abiotic and biotic stresses, such as drought and weed competition. Dwarf determinate accessions with very high HI are also available in cowpea, but they have not been used in breeding for subtropical zones because the plants are very small and have less adaptive plasticity than the indeterminate semidwarf types. For tropical zones, neither dwarf nor semidwarf cowpeas may be effective because the higher night temperatures accelerate plant development and cause more extreme dwarfing than occurs in subtropical zones.

Empirical breeding in over 50 years for grain yield in peanut in the United States has resulted in plants with greater HI because of an earlier transition to reproductive growth, shorter main stem lengths, smaller vegetative mass, and greater CP (Wells et al., 1991). This is similar to what has occurred in breeding cowpea for intensive production in California (Ismail and Hall, 2000). Peanut cultivars with extremely high CP and HI may, however, be less tolerant to some of the stresses that damage leaves in midseason (Knauff and Wynne, 1995). Optimal levels of CP and HI may have been achieved in breeding peanut and cowpea for some intensive production environments, such that further increases in CP and HI may not result in additional increases in grain yield, except for possible effects of increases in atmospheric $[CO_2]$ (refer to the discussion in Section 6 on future directions for plant breeding).

Achieving high grain yields probably requires that GC be close to 1.0 (100% ground cover) during the reproductive period. In many cases, this may require using narrower rows and higher plant densities than were used in the

past, especially when growing erect semidwarf cultivars. For common bean, however, early canopy closure may have disadvantages in some regions, in that it can enhance the extent of infection by *Sclerotinia sclerotiorum* Lib. De Bary and thus, the extent of the white mold disease (Kelly, 2000).

An ideotype approach to breeding common beans, which was pioneered by M.W. Adams (reviewed by Kelly, 2000), bears similarities with the approach described above for cowpea and provides guidelines concerning canopy architecture. This approach initially emphasized erect determinate types but subsequently focused on erect indeterminate types when it was discovered that the grain yields of indeterminate Mesoamerican-type common beans were greater and more stable than those of determinate common beans. Small leaflets that achieve a more vertical orientation (paraheliotropic) were considered useful in that this trait would result in more uniform distribution of light in the canopy. In addition to enhancing Q , this trait might also reduce the extent of the white mold disease. Stem and root storage of starch and its complete remobilization to pods during grain filling was considered to be a desirable trait. This would enhance grain yield by enhancing CP and HI in single-flush production systems, but may enhance susceptibility to *F. solani* f. sp. *phaseoli*, which may cause premature death in some cases. A strong stem was considered desirable to reduce lodging, which is needed in both common beans and cowpeas. Some consideration was given to the number of main stem nodes and basal branches that would be optimal. However, Kelly (2000) concluded that because there is a wide diversity in grain sizes required by different market classes of common beans and production environments, it is likely that different ideotypes would be needed for these different conditions. As an example, Kelly (2000) pointed out that decumbent (less erect) common bean cultivars are needed in the semiarid highlands of Mexico. Also, spreading cowpea cultivars have some advantages in West Africa in that they exhibited more stable yields of grain and greater yields of hay than erect cultivars in environments where the rainy season is not too short. However, spreading cultivars are not as early to first flowering and do not have as short a period to maturity of the first flush as the earliest erect cowpea cultivars.

3 ADAPTATION TO TEMPERATURE EXTREMES

3.1 Chilling

In subtropical zones, warm-season grain legumes are often sown early in the spring to ensure a long growing season and permit harvest prior to cool weather or rain in the fall. With early sowing, chilling soil temperatures that reduce maximal emergence of seedlings can occur. For cowpea, the

threshold temperature for some chilling damage to occur during germination (El-Kholy et al., 1997) and emergence (Ismail et al., 1997) is about 18°C. Germination studies with peanut (Mohamed et al., 1988) indicate a similar threshold temperature for germination and emergence as cowpea, but some genotypic differences were reported. Common bean is more chilling-tolerant than either cowpea or peanut, with a threshold temperature for the initiation of chilling damage during germination and emergence of about 15°C (Scully and Waines, 1987).

Genotypic differences in chilling tolerance during emergence were observed in cowpea (Ismail et al., 1997). A hypothesis was developed to explain the chilling tolerance as a result of the presence in the seed of a specific dehydrin protein with a positive nuclear effect and an independent additive effect associated with the extent of electrolyte leakage from the seed as a negative maternal effect. Near-isogenic lines were bred with and without the specific dehydrin and by using reciprocal crosses to distinguish between nuclear and cytoplasmically inherited effects associated with differences in electrolyte leakage. Studies with these lines (Ismail et al., 1999b) supported the hypothesis that the presence of the dehydrin is associated with an increment of chilling tolerance during seedling emergence that is independent of electrolyte leakage effects. The maternal electrolyte leakage effect was not shown to be cytoplasmically inherited, and may involve a nuclear trait that influences the seed coat. The dehydrin protein, which has been associated with chilling tolerance, was purified (Ismail et al., 1999a). The cDNA corresponding to the dehydrin was isolated and its sequence determined (Ismail et al., 1999b). A set of recombinant inbred cowpea lines that had been used to develop a genetic-linkage map of cowpea (Menéndez et al., 1997) was screened with gene-specific oligonucleotides derived from the cDNA and an immunoblot assay for the presence of the dehydrin (Ismail et al., 1999b). The dehydrin structural gene and dehydrin presence/absence trait mapped to the same position on the genetic-linkage map (Ismail et al., 1999b; Ouédraogo et al., 2002).

Only 3 out of 61 U.S. cultivars contain the dehydrin protein, indicating that there is substantial opportunity to enhance chilling tolerance during emergence in U.S. cultivars (Ismail and Hall, 2002). The dehydrin can be readily incorporated into cowpea by using conventional breeding by selecting based on an immunoblot assay of a chip taken from a cotyledon with the seed still being capable of germination (Ismail et al., 1999b). For other warm-season grain legumes, chilling tolerance during seedling emergence might be enhanced by incorporating a similar seed dehydrin through conventional breeding, or if a gene conferring its expression is not present in the germplasm by transgenic approaches using the cowpea gene. The specific dehydrin protein only confers an increment of chilling tolerance during seedling emer-

gence. Obtaining more complete chilling tolerance requires incorporating genes for other aspects of chilling tolerance, such as those that confer slow electrolyte leakage under chilling conditions as an indicator of greater membrane thermostability. Cowpea accessions are available with slow electrolyte leakage from seed under chilling conditions (Ismail and Hall, 2002). Breeding for this trait can be efficient, in that instruments that can simultaneously determine electrolyte leakage from 100 individual seeds (Ismail and Hall, 2002) are available.

When warm-season species, including cowpea, common bean, and peanut, are subjected to chilling nights followed by high levels of solar radiation, photoinhibitory damage can occur to photosystem II, and other components of the photosynthetic system can be damaged by photooxidation (Hall, 2001). I am not aware of any attempts to overcome this problem by breeding with grain legumes.

3.2 Heat

High temperatures can reduce yields of grain legumes in some production environments. In breeding to enhance heat tolerance, it is important to know the extent to which grain yield is being reduced by heat in the particular target production zone and the types of plant processes and temperatures that are responsible for the yield reductions. Reviews are available that provide information on these points (Hall, 1992, 1993 and www.plantstress.com). For many grain legumes, reproductive development is particularly sensitive to heat stress.

Heat resistance is defined as the ability of a cultivar to yield more than other cultivars when subjected to heat. For cowpea, heat damage can occur in a developmental sequence influencing a series of reproductive processes that, in turn, influence different components of grain yield. A yield component model can be used to describe these effects of heat, which is effective when the size of the reproductive sink is strongly limiting yield, such that there are few negative correlations among the yield components. It should be noted that yield component models of this type may be of little value in more optimal environments, where the size of the reproductive sink does not limit the yield because of the very effective yield-component compensation that can occur in grain legumes.

$$Y = (\# \text{ flowers/m}^2) \times (\# \text{ pods/flower}) \times (\# \text{ seeds/pod}) \\ \times (\text{g dry weight/seed}) \quad (4)$$

where Y is the grain yield in g m^{-2} . I will begin by discussing the effects of heat on pod set ($\#$ pods/flower or pods/peduncle) because this may represent the most damaging effect of heat stress on cowpea. We had observed that grain

yield and the number of pods/ground area were negatively correlated with a degree day estimate of day-time heat stress, °C above 35°C during each day summed for the 30 days after the first appearance of floral buds (Turk et al., 1980). We then determined the extent that day or night, or root, or shoot temperatures were causing the effect by using growth chambers (Warrag and Hall 1984a,b). We discovered that the pod set can be reduced to zero by high night shoot temperature (30°C). This effect was surprising in that hotter day shoot temperatures (33°C) did not damage pod set. Additional growth chamber studies (Warrag and Hall, 1983) demonstrated that pod set can be substantially reduced by the combination of moderately hot nights (27°C) and very hot days (36°C). Reciprocal artificial pollination between plants grown under optimal and high night temperatures indicated that the low pod set was caused by male sterility in that the pistils did not appear to be damaged by high night temperature. The detrimental effects of high night temperature on pod set were also shown to occur in field conditions (Nielsen and Hall, 1985b). In these experiments, a unique approach was used in which field plots of cowpea plants were subjected to different increments of higher night temperatures during early stages of flowering by using enclosure systems placed over the plots only during the nighttime (Nielsen and Hall, 1985a). In these studies, pod set and grain yield exhibited similar linear decreases for minimum daily nighttime temperature increasing from 15°C, with 50% reductions occurring at 27°C. These results suggested that heat stress may be causing substantial reductions in grain yield in the warmer target production zones where cowpea are grown (Nielsen and Hall, 1985a).

Possible mechanisms for the sensitivity of pod set and pollen development to high night temperatures have been proposed. Limitations in carbohydrate supplies were suggested as being responsible for reproductive failure, but this does not appear to account for the low pod set induced by high night temperature in cowpea. Damage to pod set caused by high night temperature is greater for plants in long days when they would be expected to have greater supplies of photosynthate compared with short days (Mutters et al., 1989b). Also, elevated atmospheric carbon dioxide concentration resulted in higher overall carbohydrate levels in plants but did not increase their heat tolerance with respect to either flower production or pod set (Ahmed et al., 1993a). In field conditions, high temperatures have greater effects on the reproductive development and grain yield of cowpea than they do on shoot biomass production (Ismail and Hall, 1998), indicating that effects of heat on photosynthesis do not constitute the major factor behind the reductions in grain yield. It appears that high night temperature may have a direct damaging effect on reproductive development. Mutters and Hall (1992) demonstrated that there is a distinct period during the 24-hr cycle when pollen development in cowpeas is sensitive to high night temperatures. Plants subjected to high night

temperature during the last 6 hr of a 12-hr night exhibited substantial decreases in pollen viability and pod set, whereas plant subjected to high temperature during the first 6 hr of the night exhibited no damage. Mutters and Hall (1992) hypothesized that these results could be explained if a heat-sensitive process in pollen development is under circadian control and only occurs in the late night period. The damaging effect of high night temperature on pod set was greater in long days than in short days, and red and far-red light treatments indicated that it is a phytochrome-mediated response (Mutters et al., 1989b). The phytochrome effects also involve circadian rhythms.

Processes influencing pod set were shown to be most sensitive to high night temperature 9–7 days before anthesis by experiments in which plants were transferred between growth chambers with either optimal or high night temperatures (Warrag and Hall, 1984b; Ahmed et al., 1992). This sensitive period takes place after meiosis and coincides with the release of pollen microspores from tetrads (Ahmed et al., 1992; Mutters and Hall, 1992). Damage due to high night temperature was associated with the premature degeneration of the tapetal layer that provides nutrients to developing pollen. The transfer of proline from the tapetal layer to pollen was inhibited by high temperatures (Mutters et al., 1989a). Healthy pollen contains large quantities of proline. Just prior to anthesis, proline constitutes 55% of the amino acids in anthers and pollen. In very hot field conditions, proline content of pollen in heat-sensitive cowpea genotypes was only half of the content in more optimal field conditions (Mutters et al., 1989a). Proline has been hypothesized to play a role in protecting pollen from heat-induced damage during germination (Hong-Qui and Croes, 1983). Heat-induced damage to pod set of cowpea has been associated with high levels of infertile pollen, but for some genotypes, anthers also may not dehisce (Mutters and Hall, 1992; Ahmed et al., 1992).

Another component of the heat-tolerance model for yield [Eq. (4)] can be strongly affected by heat. Early floral bud development can be damaged, such that sensitive plants produce few or no flowers. Two weeks or more of consecutive or interrupted hot nights during the first month after germination can cause complete suppression of floral bud development (Ahmed and Hall, 1993). In both growth chamber and field conditions, the damage can be much more pronounced under long days than short days (Dow El-Madina and Hall, 1986; Patel and Hall, 1990). However, responses to red and far-red light indicated that the effect was only partially consistent with the system being mediated by phytochrome (Mutters et al., 1989b). The damaging effect of high night temperature and long days on floral bud development also depends on light quality (Ahmed et al., 1993b). When growth chambers were used with relatively large amounts of fluorescent light and little incandescent light, such that the red/far-red ratio was high (the photon flux density at 660 ± 5

nm/photon flux density at 730 ± 5 nm was 1.9), floral buds were not suppressed in long-day, high night temperature conditions (but pod set was very low). In contrast, when growth chambers were used with a lighting system that had a lower red/far-red ratio of 1.2, which is similar to sunlight, floral buds were suppressed in long days with high night temperature and no flowers were produced, i.e., the same as occurs in field conditions. There are two implications of the results of these studies. First, the use of growth chambers with lighting systems that mainly depend on fluorescent lights can result in serious artifacts when studying plant reproductive responses to heat stress. Second, in field conditions, intense shading of floral buds can reduce the red/far-red ratio far below 1.2 and may intensify the floral bud suppression effect. In densely sown fields of cowpea, individual plants that are suffering from competition are tall and spindly and can exhibit floral bud suppression, although night temperatures are not too hot.

Another component of the heat-tolerance model for yield [Eq. (4)] can be strongly affected by heat and other stresses. Pods of different cowpea genotypes produce 9–20 ovules with many cultivars having 15, but they rarely produce this many seeds per pod. Under optimal conditions, two-thirds of the ovules may produce seed, whereas with high day or high night temperatures (Warrag and Hall, 1983) and other stresses, such as drought (Turk et al., 1980), fewer seed are produced per pod. For most cowpea cultivars and stresses, it is the ovules at the blossom end of the pod, which are furthest from the carbohydrate supply, that suffer embryo abortion and do not produce seed, resulting in the production of “pinched” pods. The acceleration of reproductive development caused by high night temperature (Nielsen and Hall, 1985b) would enhance the demand by embryos for carbohydrate and where the demand is not met by the supply, it could lead to increased embryo abortion. Drought could have a similar effect but by reducing photosynthesis and the supply of carbohydrate to developing embryos.

Temperature can influence seed quality. Cowpea seeds produced under high day temperatures can have asymmetrically twisted cotyledons (Warrag and Hall, 1984a). Germination of the seed is not influenced and this effect of heat stress may not be a major problem. In contrast, heat-induced brown discoloration of cowpea seed coats can occur with some cultivars and be a major problem in that consumers reject the grain. Higher night temperatures resulted in a progressively larger numbers of seed of accession TVu 4552 with larger areas of brown discoloration of their seed coats (Nielsen and Hall, 1985b). The important breeding line TVx 3236 has also exhibited brown discoloration of seed coats as it grows during the main cropping season in Senegal. The accelerated pod development associated with higher night temperatures is associated with the production of smaller seed (Nielsen and Hall, 1985b) influencing yield as indicated in Eq. (4).

The traditional method for breeding to enhance adaptation to hot conditions is to grow advanced lines in a hot target production environment and select lines that have greater grain yields than current cultivars (by definition, such lines would have greater heat resistance). This approach is not very effective with crops such as cowpea and common bean, where yield evaluation requires considerable land and labor. Also, the presence of other stresses can confound the evaluation of heat stress effects. For example, insect pests such as lygus bugs (*Lygus hesperus* Knight) and flower thrips (*Megalurothrips sjostedti* Trybom) can cause damage to developing flower buds of cowpea, an effect which appears similar to that caused by high night temperatures. Irrespective of these problems, some slow progress may have been made in enhancing heat resistance of cowpea in West Africa by breeding programs that made selections based on grain yield in hot target production environments (Ehlers and Hall, 1998).

Efficient approaches to breeding for heat resistance involving early generation selection for specific traits that confer heat tolerance have been developed. The first step in this approach is to discover accessions with heat-tolerance traits. We have screened cowpea accessions in field environments with very high night and day temperatures for heat tolerance during reproductive development. Our current most effective field nursery for screening for heat tolerance is located in the Coachella Valley of California, with sowing in mid-June. Plants are provided with optimal irrigation, fertilizer, and pest management practices. For the 3-week period beginning 1 week prior to the start of flowering, minimum daily (night) air temperatures are 23–27°C, and maximum daily air temperatures are 42–50°C. This is one of the hottest crop production environments on earth. The plants also experience long days (14.5 hr) and sunny skies. We screened hundreds of cowpea accessions and only three, accounting for less than 1%, showed the ability to abundantly produce flowers and set pods in this very hot environment. Two of the heat-tolerant accessions, TVu4552 and Prima, came from hot environments in West Africa (Warrag and Hall, 1983), while one, MN13, was bred for the very cool conditions of Minnesota (Davis et al., 1986) and was presumably selected in nurseries where plants were not exposed to heat. Some chilling-tolerant snap beans also have heat tolerance during reproductive development (Dickson, 1993). However, we suspect that, for cowpea line MN13, the association is between heat tolerance and extreme earliness (Ehlers and Hall, 1996), and not between heat tolerance and chilling tolerance. Screening for heat tolerance was conducted by the International Institute of Tropical Agriculture (IITA) at Kano in northern Nigeria, using screenhouses to reduce attacks by insect pests. With sowing set in March, the plants experience minimum daily (night) air temperatures between 24 and 27°C, maximum daily air temperatures between 38 and 42°C, and short-day conditions during the early flowering

stage. In this hot short-day environment, lines TVu4552, IT88D-641-1, IT88D-867-11, and IT97K-472-12 produced many pods, while many other cowpea lines showed infertile pollen and little or no pod set (B.B. Singh, personal communication, March, 2001).

Most cowpea breeding programs do not have field nurseries or screenhouses with consistently high night and day temperatures, but have otherwise optimal growing conditions. Consequently, we have developed a glasshouse environment for screening cowpea to detect differences in reproductive-stage heat tolerance. The plants are subjected to minimum and maximum 24-hr air temperatures of 27 and 36°C, respectively, and sunny long-day conditions. This glasshouse environment is very effective for screening cowpea for reproductive-stage heat tolerance, but only a few hundred plants can be grown in it, compared with the thousands of plants that can be screened in field nurseries. One advantage of using a hot glasshouse compared with most field conditions is that air temperatures are relatively stable overtime, and genotypes that begin flowering at various dates can be reliably screened. In contrast, the Coachella Valley field nursery is mainly effective for screening genotypes that begin flowering at about the same time because temperatures vary substantially from day to day and exhibit seasonal changes.

In breeding for heat tolerance, we grow plants from the first segregating generation in a heat-screening nursery, and select single plants that are able to produce many flowers. We have shown that heat tolerance at early flowering is consistent with it being conferred by a single recessive gene with high heritability (Hall, 1993). Selection in the first segregating generation fixes the ability to produce flowers in most, but not all, selected plants. We also select for seed quality traits in the first segregating generation and all subsequent generations, and we feel it is effective. Genetic studies demonstrated that heat-induced seed coat browning, which is an undesirable trait, is consistent with the effect of a single dominant gene that is not linked to the gene conferring heat tolerance at early flowering (Patel and Hall, 1988). Consequently, both the absence of seed coat browning and the ability to produce flowers can be usually fixed via selection during the first segregating generation. In addition, we also selected single plants with high numbers of pods per peduncle (3–4) in the first segregating generation, but selection for this trait is not very effective at this stage with single plants. Heat tolerance during pod set was shown to be consistent with the effect of a single dominant gene, but with strong environmental effects and low, narrow-sense and realized heritabilities of 0.26 (Marfo and Hall, 1992). We also suspect that, with some crosses, at least two major genes and some minor genes are involved in conferring the ability to set pods under hot conditions. Consequently, we conduct family selection for high numbers of pods per peduncle on advanced lines in several subsequent generations. In all generations, we practice some selection for well-filled pods as

an indicator of less embryo abortion, but this selection may not be very effective. Embryo abortion is a complex factor that is influenced by many stresses, plant pod load, and age. Negative correlations among yield components can occur for this trait. For example, in some environments, there is a tendency for plants that set very many pods to have poorly filled pods, so it is necessary to select for both high pod set and pods that are not too pinched. Two cowpea accessions, TN88-63 and B89-600, exhibited no heat-induced reductions in the number of seeds per pod, even when they had a substantial pod load (Ehlers and Hall, 1998). These genotypes may provide an opportunity for breeding to enhance heat tolerance during embryo development. It should be noted that negative correlations among yield components is not as big a problem for cowpea under high night temperatures as it would be under more optimal conditions. Heat stress tends to reduce reproductive development of cowpea more than biomass production (Ismail and Hall, 1998), so that the plants are strongly limited by the size of the reproductive sink and thus exhibit few negative correlations among yield components in very hot conditions. Advanced lines that have been selected in the heat-screening and other nurseries are then evaluated for yield and other agronomic traits in multi-location trials conducted in experiment stations and commercial fields in the target production zone.

We have demonstrated that these methods can be effective in incorporating heat tolerance for subtropical environments with hot long-day conditions, such that heat resistance is enhanced. We did this by breeding six pairs of lines that either have, or do not have, a set of heat-tolerance genes in similar genetic backgrounds. These pairs of lines were evaluated in eight subtropical field environments with average night temperatures ranging from being cool to being very hot, but with other conditions being similar and near optimal (Ismail and Hall, 1998). The heat-sensitive lines, which included a commercial cultivar, CB5, exhibited a 13.5% decrease in grain yield per °C increase in average minimum night temperature above 16.5°C for the 3-week period starting 1 week prior to first flowering. The heat-tolerant lines had 50% greater grain yield and numbers of pods per peduncle than the heat-sensitive lines with average minimum night temperatures of 21°C, but similar grain yields as the heat-sensitive lines under cool night temperatures (Ismail and Hall, 1998; also see www.plantstress.com). Minimum night temperatures exceeding 21°C occur in several commercial production zones (Nielsen and Hall, 1985a). One of the heat-tolerant lines, CB27, was released as a cultivar in California (Ehlers et al., 2000). It should be noted that heat tolerance, by itself, will not justify the release of a new cultivar; the cultivar must have greater grain yield than current cultivars when grown in the target production environment (i.e., greater heat resistance is needed). In addition to greater grain yields than current cultivars when conditions are hot at flowering,

CB27 has also greater grain yields in some fields because of its resistance to a broader range of biotypes of root-knot nematodes and Fusarium wilt than previous California cultivars.

When breeding to incorporate heat tolerance or any other trait, it is important to evaluate the potential negative effects of the trait. In hot environments, the reproductive-stage heat tolerance genes caused cowpea to be more compact and dwarfed because their internodes are shorter. At a minimum night temperature of 18°C, the heat-sensitive cowpea lines had 50% longer main stems, and at 22°C, they had 50% more vegetative biomass than the heat-tolerant lines (Ismail and Hall, 1998; photographs of these plants are presented in www.plantstress.com). The performance of heat-tolerant semi-dwarf cowpea lines was compared with that of standard-height cowpea lines under different row spacing (Ismail and Hall, 2000). The heat-tolerant semi-dwarf lines were less effective than the standard-height lines at the wide row spacing of 102 cm used by some farmers, more effective with the widely used 76-cm row spacing, and even more effective with a narrow row spacing of 51 cm. Natural selection likely would not favor this type of heat tolerance in that the compact plant habit is not very competitive, such that careful weed management is needed.

Our approach for breeding heat-resistant cowpeas is effective in hot subtropical zones, but it is still not clear whether the approach and the genes will be effective in hot tropical zones. The six pairs of heat-tolerant and heat-sensitive cowpea lines used in the studies in California were evaluated in three experiments in northern Ghana and three experiments in the Peanut Basin of Senegal (Hall et al., 2002). The average minimum daily (night) air temperatures for the 3-week period beginning 1 week prior to the start of flowering ranged from 21 to 26°C in these six experiments. However, in all of the experiments, there were no differences in grain yield between the heat-tolerant and the heat-sensitive lines, and the average grain yields in the different experiments were small, ranging from 562 to 1866 kg/ha with an overall average of 1185 kg/ha. The low yields are partially attributed to the susceptibility of the California lines to both wet and dry pod rots under humid tropical conditions. Controlled environment studies provided some clues, which can be used to try to explain these results. In some cases in tropical zones, the day length may not be long enough to trigger heat \times photoperiod induced damage to floral bud development (the critical effective day length, defined as the period from sunrise to sunset plus any twilight effects, is estimated to be about 12.5 hr). With effective day length of less than 12.5 hr, heat may have little damaging effect on floral bud development and the number of flowers produced (Dow El-Madina and Hall, 1986; Patel and Hall, 1990), and only have a partial damaging effect on pod set (Mutters et al., 1989b). Consequently, heat-tolerance genes may be expected to have less beneficial effect on grain yield in

hot tropical environments with short days than in hot subtropical environments with long days. In developing the heat-tolerant lines used in the experiments in California and West Africa, accessions Prima and Tv4552 were used as sources of heat tolerance because they are extremely tolerant in long days. These accessions were also shown to exhibit heat tolerance for pod set under short days. In controlled environment chambers under hot 12-hr day conditions, Prima was shown to have higher grain yield per plant than IT84S-2246 because it has better ability to maintain peduncle and flower production and greater pod set (Craufurd et al., 1998). In hot short-day conditions in screenhouses in West Africa, TVu4552 exhibited much higher pod set and grain production than many other cowpea accessions and lines (B.B. Singh, personal communication, March 2001). Advanced breeding lines were developed by using Prima and TVu4552 as sources of heat tolerance, and these breeding lines were evaluated in hot glasshouses under both short-day and long-day conditions (Ehlers and Hall, 1998). The heat-tolerant lines had high grain yields under both short-day and long-day conditions, whereas heat-sensitive lines that gave zero grain yield under hot long-day conditions exhibited variable yields under hot short-day conditions ranging from being 20% to 100% of those of the heat-tolerant lines (Ehlers and Hall, 1998; Hall et al., 2002). In the hot short-day glasshouse, grain yields were positively correlated with the number of pods per peduncle and pods produced per day, and excessive suppression of floral buds was not detected (Ehlers and Hall, 1998). This suggests that enhanced pod set was a major factor in the heat tolerance exhibited by some genotypes under hot short-day conditions. My overall conclusions are that the genes that confer heat tolerance during pod set in the lines bred in California could enhance pod set in hot tropical conditions, but that they need to be combined with additional genes that confer local adaptation so that the pods become filled, and the effect on grain yield would not be as large as has been achieved in hot subtropical zones.

Common bean exhibited heat-induced damage to reproduction in hot subtropical (long-day) field conditions that bear some similarities to what has been observed in cowpea. Heat-sensitive common bean genotypes exhibited substantial flower bud abortion and low pod filling (Shonnard and Gepts, 1994), presumably due to ineffective fertilization (Gross and Kigel, 1994). Sensitivity to heat during early floral bud development may only occur in long days for common bean and may be consistent with the action of a single dominant gene (White et al., 1996) as it is in cowpea (Hall, 1993). However, in the study of White et al. (1996), it was not reported whether the genotypic differences in days to first flowering resulted from differences in time of floral bud initiation or differences in extent of floral bud suppression. In common bean, elevated night temperature was more detrimental to reproductive devel-

opment than high day temperature (Konsens et al., 1991) as it is in cowpea (Warrag and Hall 1984a,b). High night temperatures caused heat-induced reductions in number of seeds per pod and number of pods per plant, while even higher day temperatures had little effect, providing night temperatures were optimal (Konsens et al., 1991). This is similar to what was observed in cowpea, except that in cowpea, the number of seeds per pod can be reduced by both high night and high day temperature (Warrag and Hall, 1983; Ehlers and Hall, 1998). A major difference between the responses to heat is that, for most cowpea genotypes, it is the ovules at the blossom end of the pod that fail to produce seed, and the effect probably involves embryo abortion. In contrast, for common bean, it is the ovules at the peduncle end of the pod that fail to produce seed (Dickson and Petzoldt, 1989), and the effect probably involves impaired pollen tube growth and fertilization (Gross and Kigel, 1994).

Detailed studies have been conducted in which common beans were subjected to high night temperature (27°C), moderate day temperature (32°C), and long photoperiods (16 hr) for short durations (1 or 5 days) during different stages of reproductive development (Gross and Kigel, 1994). The most heat-sensitive stage was for pollen development occurring just after meiosis, as it was for cowpea (Warrag and Hall, 1984b; Ahmed et al., 1992). Pollen developed under heat stress were not viable, and anthers did not dehisce. As for cowpea, heat at this stage did not affect the gynoecium function. Similar detrimental effects on pollen and anther development of common bean were likewise observed under hot short-day (12 hr) conditions (Porch and Jahn, 2001). Gross and Kigel (1994) observed reductions in ovule fertilization and seed set that were greater at positions further away from the stigma and probably reflected heat stress constraints to pollen tube growth. In contrast with the results for cowpea, Gross and Kigel (1994) detected sensitivity of the gynoecium to heat occurring at anthesis, which contributed to reductions in the number of seeds per pod.

The ability of plants to acclimate to heat may be an important aspect of genotypic differences in resistance to heat if the production environment only experiences occasional periods of hot weather. Studies of high-temperature acclimation in common bean emphasized slow electrolyte leakage as a measure of membrane thermostability and heat tolerance (Li et al., 1991). For 74 common bean lines, genotypic differences were detected in the ability to acclimate to heat (24 hr at 37°C day and night air temperature) and exhibit longer periods (in min) before extremely high temperatures (50°C) caused 50% ion leakage from tissues (Li et al., 1991). Because neither the acclimation thermal regime nor the heat-stress temperature would be experienced by common bean in any reasonable target production environment, it is important to determine whether these differences in heat tolerance have any rele-

vance to heat resistance (cultivar ability to produce dry grain or fresh pods in hot environments). For a small subset of the cultivars investigated (13), Li et al. (1991) reported a positive correlation between the number of pods produced 2 weeks after the heat stress (1 week at 37/35°C day/night air temperature), as a percentage of controls, and a measure of heat acclimation potential based on electrolyte leakage from leaf disks ($r = 0.78, n = 13$). This indicates a possible association between heat tolerance and heat acclimation potential, but it does not provide information on the heat resistance of these lines under field conditions. Others have noted (e.g., Dickson, 1993) that some common bean genotypes reported to have high heat acclimation potential with respect to electrolyte leakage can be highly sensitive to heat, in terms of reproductive development, and produce low pod yields when subjected to heat just prior to bloom. Prior to recommending the use of heat acclimation potential as a selection criterion for use in common bean breeding programs, it would appear necessary to conduct genetic experiments to determine the heritability of this trait and its association with grain or pod yield of plants subjected to heat in field environments. I am not aware of any reports of genetic studies on common bean dealing with heat acclimation potential as determined by electrolyte leakage. For cowpea, an association between reproductive-stage heat tolerance and slow electrolyte leakage from leaves has been reported (Ismail and Hall, 1999). In an extremely hot field environment, negative correlations were observed between grain yield and electrolyte leakage ($r = -0.79, n = 9$), and pod set and electrolyte leakage ($r = -0.89, n = 9$) among nine cowpea breeding lines. Genetic selection studies with cowpea, however, indicated that the realized heritability of leaf electrolyte leakage was low and associations with pod set and grain yield under hot conditions were only moderate (Thiaw, 2003).

Heat-acclimation effects may be related to the fact that seedlings subjected to high temperatures synthesize a novel set of proteins that have been called heat-shock proteins, and the plants become more tolerant, in terms of plant survival, to more extreme temperatures (Vierling, 1991). These proteins are thought to enable cells to survive the harmful effects of heat by two general types of mechanisms: as molecular chaperones, and by targeting proteins for degradation. As an example of chaperone activity, it has been shown that a specific small heat-shock protein cooperates with other heat-shock proteins to reactivate a heat-denatured protein (Lee and Vierling, 2000). Heat shock proteins do not appear to be the only mechanism whereby plants differ in heat tolerance. Heat shock protein profiles were examined in six common bean cultivars that differ in heat acclimation potential with respect to differences in heat killing time based on electrolyte leakage (Li and Udomprasert, 1993). No relationship was observed between the patterns of heat-shock proteins and heat acclimation potential. Also, genotypes of cowpea have been bred

that have substantial differences in heat tolerance during reproductive development, but they produced the same set of low molecular weight heat shock proteins in their leaves when subjected to moderately high temperatures (A.S. El-Kholy, unpublished studies, 1996).

Progress has been made in breeding snap bean types of common beans with heat resistance through incorporating heat tolerance during reproductive development by selecting plants for high pod set in a glasshouse with high night temperatures (Dickson, 1993). With day/night temperatures of 35/27°C during the early floral bud and bloom period, narrow-sense heritabilities for pod production were only 0.11–0.30, but selection in these conditions over two generations produced lines with uniformly high pod production (Dickson, 1993). Some heat-resistant dry bean types of common bean cultivars have been developed (e.g., Beaver et al., 1999). For common bean, the detrimental effects of some diseases may be greater in some hot environments, so increased genetic resistance to these diseases may also be needed.

Peanut exhibits geocarpy in which flowers are produced above ground, and after fertilization pegs are produced that penetrate the soil, such that embryo development and pod formation occur in the soil. High day and night air temperatures occurring just prior to anthesis were shown to reduce pollen production and viability, and peg production (Vara Prasad et al., 1999a,b). As for cowpea (Mutters and Hall, 1992), peanut exhibited circadian variation in sensitivity to heat (Vara Prasad et al., 2000b). High air temperatures during the morning reduced fruit set, whereas high air temperatures during the afternoon had no effect on fruit set. Peanut flowers typically open early in the morning, self-pollination occurs just before opening, and fertilization is completed within 5–6 hr. The authors concluded that fruit number in peanut would be reduced when mean day air temperatures exceed 28°C (Vara Prasad et al., 2000b). High soil temperature reduced flower production, the proportion of pegs forming pods and individual seed weight, whereas high air temperature mainly reduced the proportion of flowers that set pegs (Vara Prasad et al., 2000a). Effects on pod yield of high soil and high air temperatures were additive.

In summary, pollen development and fertilization processes have been shown to be particularly sensitive to high temperatures in cowpea, common bean, and peanut, and to be mainly responsible for reductions in grain yield caused by high air temperatures. High temperatures occurring a few days prior to anthesis in either the late night (cowpea and common bean) or morning (peanut) appear to be most damaging. Heat-resistant cultivars of cowpea and common bean have been developed by selecting for high pod and seed set with plants in greenhouses subjected to high night air temperature (about 27°C daily minimum) plus high day air temperature (about 36°C daily maximum) and long days.

4 ADAPTATION TO WATER-LIMITED ENVIRONMENTS

Adaptation to water-limited environments can include both drought resistance—defined as where a cultivar has higher average grain yield than another cultivar when grown in the same water-limited environments—and drought escape. Cultivars with improved adaptation to water-limited environments can be bred by selecting lines with high average grain yield in tests conducted in several locations over several years in the target production environment. As was discussed before, this approach requires considerable effort and time with cowpea and common bean. Also, rainfall tends to be highly variable in semiarid zones, such that grain yields are highly variable and substantial genotype \times environment interaction can occur. Selecting lines that have both a low coefficient of variation (calculated over all test environments using mean values for the genotype in individual tests) and a high average grain yield can take some of this variability into consideration, but many tests can be required to produce reliable results.

Conducting trials under both rainfed (stressed = Y_s) and irrigated (non-stressed = Y_p) conditions may speed up the process of empirical selection for grain yield. Based on trials of this type with common bean, Schneider et al. (1997) proposed that initial selection should be based on high geometric mean ($Y_s \times Y_p$)^{0.5} grain yield, followed by selection for high Y_s . It should be noted that geometric mean yield selects genotypes with high yield in both stress and nonstress environments, whereas arithmetic mean yield $(Y_s + Y_p)/2$ can favor genotypes with high nonstress yields, and either $(Y_p - Y_s)$ or $(1 - Y_s/Y_p)$ can favor genotypes with high yields under stress (Fernandez, 1993). Kelly et al. (1999) reported that some progress in enhancing drought resistance was achieved with the procedure of Schneider et al. (1997). In addition, selection for phenological, morphological, physiological, and biochemical traits that confer adaptation to drought could complement a breeding program that is mainly based on empirical selection for grain yield and make it more efficient. Progress in defining traits that confer drought adaptation in cowpea, peanut, and common bean is discussed.

4.1 Drought Escape

Optimal days to first flowering and cycle length have proved to be effective indicators for cowpea adaptation to rainfed environments with terminal drought. Since 1968, droughts have occurred in the Sahelian zone of Africa that shortened the rainy season to less than 2 months during some years (Dancette and Hall, 1979; Khalfaoui, 1991). Traditional land races of cowpea are prostrate and begin flowering 50–70 days after sowing, and are ready for harvest of dry grain 80–100 days after sowing. In many of the dry years since 1968, these land races often suffered terminal droughts that began while they were flowering (Khalfaoui, 1991) and produced little grain. Erect lines were

bred at the University of California, Riverside, that begin flowering about 35 days after sowing and are ready for harvest in 55–65 days. In dry years in the Sahelian zone of Senegal and Sudan with about 200 mm of rain, these “60-day” cowpea lines have produced grain yields of 500–1000 kg/ha, while local land race only produced about 150 kg/ha (Hall and Patel, 1985). The “60-day” cowpea lines also have reasonably high yield potential in that they produced about 2400 kg/ha of grain when grown at the wetter boundary of the Sahelian zone with rainfall of 452 mm (Hall and Patel, 1985). Note that, in environments with terminal drought, the cycle length of these “60-day” lines can be as short as 55 days, whereas in well-watered environments the cycle length can be about 65 days. Optimal row spacing for early erect cowpeas is about 50 cm, with 33 cm between plants in the row. Traditionally, the spreading land races were sown at very wide spacings of about 100 × 100 cm. Reasons for the wide spacing included shortage of seed attributed to lack of methods for preventing weevil attacks during storage, and shortage of labor for hand sowing during the critical period after the first major rains when considerable sowing must be carried out in the Sahel. These problems have become less pronounced in Senegal because effective methods are now available for storing cowpea seed, and the crop is sown by horse-drawn sowing machines. After many years of testing on experiment stations and farmers fields, one of the 60-day cowpea lines (1-12-3 in Hall and Patel, 1985) was released as the cultivar Ein El Gazal for use in the Sahelian zone of the Sudan (Elawad and Hall, 2002).

In Senegal, a 60-day semierect cowpea cultivar has been developed, Melakh, by selecting for early flowering and high average grain yield in the Sahelian zone (Cisse et al., 1997). This cultivar also has resistance to cowpea aphid-borne mosaic potyvirus and partial resistance to bacterial blight (*Xanthomonas campestris* pv. *vignicola* (Burkholder) Dye), cowpea aphid (*Aphis craccivora* Koch), and flower thrip. Extremely early cultivars, such as Ein El Gazal and Melakh, can be severely damaged by drought at flowering (Thiaw et al., 1993). A semierect cultivar was bred in Senegal by empirical yield testing procedures, Mouride, that begins flowering a few days later and has greater resistance to midseason drought than Melakh (Cisse et al. 1995). This cultivar has resistance to cowpea aphid-borne mosaic virus, bacterial blight, cowpea storage weevil (*Callosobruchus maculatus* (F.)), and the parasitic weed *Striga gesnerioides* (Willd.) Vatke, and tolerance to heat. Because of variation in the timing of droughts and occurrence of biotic stresses, it has been recommended that farmers in the Sahelian zone of Senegal grow both Melakh and Mouride to increase the probability that at least one good crop is obtained.

Spreading cultivars of cowpea that are initially erect and then become prostrate can have substantial resistance to midseason droughts and other stresses. The earliest of the spreading cultivars have a cycle length of about 75 days and can be effective for producing both grain and hay in all but the

drier parts of the Sahelian zone. Varietal intercrops consisting of alternating rows of a spreading 75-day cultivar and an erect 60-day cultivar had higher and more stable yields of both grain and hay than the most productive sole crops, under the conditions of drought and infertile soil that are prevalent in the Sahelian zone (Thiaw et al., 1993).

The sensitivity of erect cowpeas to drought during pod development can be partially solved by incorporating a gene that confers delayed-leaf-senescence (DLS). Genotypes with DLS were able to recover after a midseason drought and produce a second flush of pods, whereas genotypes that did not have DLS senesced after producing the first flush of pods (Gwathmey and Hall, 1992). The DLS trait enables cowpea cultivars to more consistently produce two distinct flushes of pods. In fields where cowpeas have been grown for several years, most plants can die after producing the first flush of pods even with alternate year rotations. This premature death of cowpea is probably caused by the soil fungus *F. solani* f. sp. *phaseoli*. The DLS trait is associated with the maintenance of carbohydrate levels in roots and thus root health which, in some way, confers resistance to this pathogen. The DLS trait was effective in preventing the premature senescence of cowpea in several locations in California and in Bambey, Senegal (Hall et al., 1997b). At Bambey, Senegal, an early flowering cowpea line with the DLS trait began flowering in about 34 days and produced a first flush of pods and about 2000 kg/ha by 65 days, and then began flowering again at about 75 days and produced an additional 1000 kg/ha by about 100 days after sowing. Cultivars of this type have not yet been fully developed, but they could be well adapted to the wetter parts of the Sahelian zone and the dry parts of the Savanna zone where rainfall is 400–600 mm and there is a high probability of midseason droughts. In this environment, it would be necessary to harvest pods by hand throughout the growing season, which is the method currently used by farmers in much of sub-Saharan Africa. Genetic studies demonstrated that it is possible to breed cowpea lines that have early flowering, DLS, and heat tolerance at reproductive development, and that the DLS trait is highly heritable and appears to be conferred by a major gene (Ismail et al., 2000). Selection for DLS can be effective when carried out on a family basis with F₄ or later generations in field nurseries where the soil pathogen is present. When choosing families, it is important to select ones that have both DLS and a substantial first-flush pod load because plants with few pods exhibit a different type of DLS with no value. An example of the type of DLS that has no agronomic value is the male sterile plants with no pods that can be readily detected in breeding nurseries because of their green appearance at the end of the season when all of the other plants have produced many pods and have died.

Local cultivars of peanut grown in the Sahelian and Savanna zones of West Africa, prior to the beginning of severe droughts in 1968, were prostrate

types with a 120-day cycle from sowing to harvest (Schilling and Misari, 1992). Since this time, erect earlier flowering cultivars have been bred for these zones that, in Senegal, are sown at close spacing using horse-drawn sowing machines. But the shortest cycle cultivars that have been developed still take 85–90 days from sowing to harvest (Subbarao et al., 1995), and are only well adapted to the wetter part of the Sahelian zone and the Savanna zone (Kahlfaoui, 1991). Genotypes with synchronous pod development and rapid partitioning of carbohydrate to pods may have improved adaptation to terminal droughts (Knauff and Wynne, 1995). Contrasting peanut genotypes have been compared with respect to their adaptation to hot, dry Sahelian conditions (Greenberg et al., 1992). Thirty-six genotypes were grown in five environments, where water supplies and temperature were varied by varying the sowing date and the irrigation treatments. Adaptation to hot dry Sahelian conditions was associated with below-average crop growth rates but much greater harvest index. Achieving a high harvest index also requires high levels of remobilization of carbon and nitrogen compounds to developing grain. Optimal rates and levels of remobilization are required, in that removal of nitrogen compounds from leaves leads to a reduction of their photosynthetic capacity (Sinclair and deWit, 1975). In addition, removal of carbohydrate from roots could result in decreases in nitrogen fixation (Subbarao et al., 1995) and increased sensitivity to soil organisms that cause premature senescence (Gwathmey et al., 1992b).

4.2 Drought Resistance

In some water-limited environments, there is no rain during the cropping season but considerable moisture is present in the soil during sowing. An example would be where grain legumes are grown after rice or after floodwaters have receded. Selecting for early appearance of mature pods can enhance the drought resistance of cowpea grown on stored soil moisture (Hall and Grantz, 1981). However, an optimal level of earliness must be sought because there can be an interaction between earliness and depth of rooting which can influence seasonal water extraction. For example, in pigeon pea (*Cajanus cajan* L. Millsp.), short-duration genotypes may develop shallow root systems of only 50-cm depth compared with long-duration genotypes that can develop 200-cm deep root systems (Subbarao et al., 1995). For cowpeas with similar cycle length, genotypic differences are present in the extent of rooting but it is not easy to screen for this trait. Typically, the evaluation of rooting characteristics has only been performed with a few cultivars when choosing parents for crosses or with a few promising advanced lines. However, a method has been developed that can evaluate rate of root growth of many cultivars or stable lines under field conditions (Robertson et al., 1985).

With this method, a herbicide is placed in a narrow horizontal band deep in the soil in-between rows of plants. Plants are scored daily for plant symptom responses as an indicator of the time taken for roots to grow and reach the herbicide. Using this technique, genotypic differences among cowpea accessions in rate of root development were detected (Hall and Patel, 1985) that were positively correlated with extent of soil water extraction (Robertson et al., 1985). A diverse set of peanut cultivars has been screened under field conditions by using this technique (Khalifaoui and Havard, 1993). Genotypic differences in days to appearance of herbicide symptoms were detected. Genotypes that exhibited symptoms earlier, and presumably had faster rates of root development, also had a longer cycle from sowing to maturity. It has been argued that increased root length density in deeper soil layers may be adaptive under water-limited conditions (Subbarao et al., 1995). However, studies comparing cowpea with pearl millet suggested that the micro-scale uniformity of root distribution may have a greater impact on the maintenance of plant water status than the overall density of the roots (Petrie and Hall, 1992a,b,c; Petrie et al., 1992).

Common beans have root systems that are less effective in extracting water stored deep in the soil than those of many cowpea accessions in fields with high bulk density soil at Riverside, CA. In many soils, more force is required to pull cowpea plants out of the ground than common beans. In general, an inadequate root system may be a weak link in the adaptation of many common bean cultivars. A unique study, in which root and shoot systems of contrasting common bean genotypes were separately evaluated using grafted plants, demonstrated that root characteristics can be much more important than shoot characteristics in conferring adaptation to drought (White and Castillo, 1989). Irrespective of their importance in drought adaptation, relatively little progress has been made in breeding for root traits because of the difficulty in screening large numbers of plants for these traits. For common beans, breeders can take advantage of an association which can be present between plant habit and rooting pattern (Kelly et al., 1999). The authors said that early flowering erect determinate cultivars tend to develop shallow root systems, erect indeterminate cultivars tend to have a more prominent tap root that can better exploit deep soil layers and can be effective with terminal droughts, and more prostrate indeterminate cultivars tend to have a more sprawling fibrous root system which can be effective under intermittent droughts.

Cowpea has exhibited substantial resistance to droughts occurring during the early vegetative stage. For example, cowpeas were subjected to a vegetative-stage drought that would have killed most other crop species, yet with rewatering, they recovered and produced very high grain yields (Turk et al., 1980). Seeds were sown into a soil that only had a small amount of water

in the upper profile to permit germination and emergence, and little available water in the rest of the soil profile. These plants did not receive rain or irrigation for 43 days under hot high evaporative demand conditions. After this period of drought, the plants were severely stunted, with leaf area being reduced by 74% and shoot dry matter being reduced by 63% compared with well-watered plants. These severely stunted plants were then irrigated optimally. Surprisingly, they produced grain yields of 3978/ha similar to those of control plants (3916 kg/ha) that had been optimally irrigated about every week since sowing. The cycle length from sowing to harvest was the same for both treatments (107 days). This study also demonstrated that grain yield of cowpea can be strongly influenced by photosynthesis that occurs after the initiation of flowering because the plants subjected to vegetative stage drought produced considerably less biomass prior to flowering but the same high grain yields as well-watered plants.

A rapid method in screening cowpeas for resistance to drought during the early vegetative state has been developed (Singh et al., 1999). This method consists of sowing seed at close spacing (10×5 cm) in a 12-cm deep layer of soil and sand, and watering daily until emergence of the first trifoliolate after which watering is stopped. Thereafter, the number of permanently wilted (dead) plants are counted on a daily basis and when all plants of susceptible control genotypes are dead, watering is resumed and the percentage of surviving plants is determined. Using this method, two different types of drought resistance were detected (Mai-Kodomi et al., 1999a). Type 1 resistant lines stopped growing and moisture was conserved in all plant tissues and plants stayed alive for at least 2 weeks. In Type 2 resistance, which appeared to be more effective in enhancing plant survival, trifoliate of resistant lines continued to grow slowly while unifoliate exhibited early senescence. Genetic studies indicated that the two types of drought resistance were conferred by different single dominant alleles that were closely linked or at the same locus (Mai-Kodomi et al., 1999b). Type 1 resistance appeared to be dominant over Type 2 resistance, and lines were not detected with both types of drought resistance. Because a shallow layer of soil is used, this screening method may detect shoot traits that enable plants to survive severe vegetative-stage droughts.

Drought during the vegetative stage can make cowpea (and common bean) more susceptible to ashy stem blight (*Macrophomina phaseolina* Tassi Goid) and lesser corn stalk borer (*Elasmopalpu lignosellus*). Host plant resistance to this disease and pest are not yet available in cowpea. Vegetative-stage drought can also strongly reduce biological nitrogen fixation (Elowad and Hall, 1987; Sinclair and Serraj, 1995).

The mechanisms whereby cowpea resists vegetative-stage drought may be related to the fact that leaf water potential does not decrease very much

even under extreme drought. The lowest leaf water potential recorded for cowpea is -18 bar (-1.8 MPa) (e.g., Turk and Hall, 1980; Hall and Schulze, 1980a), whereas peanut has developed leaf water potentials under drought as low as -82 bar (-8.2 MPa) (Turner et al., 2000). Several mechanisms may partially explain the extreme dehydration avoidance of cowpea. Cowpea has stomata that are very sensitive to soil drought, partially closing even before differences in leaf water potential are detected (Bates and Hall, 1981). In addition, the stomata of cowpea are very sensitive to humidity, partially closing in dry air in a manner that optimizes stomatal function with respect to the control of transpiration in relation to photosynthetic uptake of carbon dioxide (Hall and Schulze, 1980b), and acts to maintain high leaf water potential. When subjected to soil drought, leaflets of cowpea become paraheliotropic and orientated parallel to the sun's rays, which cause them to become cooler and thus transpire less (Shackel and Hall, 1979). In peanut, genetic differences have been observed in drought-induced leaflet folding responses but the differences are difficult to quantify (Knauff and Wynne, 1995). Predawn leaf water potential remained high in cowpea at about -8 bar (-0.8 MPa), with soil drought, that were killing pearl millet (*Pennisetum glaucum* L.R. Br.) and inducing it to have a predawn leaf water potential of -30 bar (-3.0 MPa) (Petrie and Hall, 1992a). The only explanation developed for this difference between species was that cowpea had a more effective root system because it was more uniform on a micro-scale level than pearl millet, which had a clumped root system with higher root length density (Petrie and Hall, 1992b,c; Petrie et al., 1992).

Differences are observed among grain legumes in the extent of drought-induced osmotic adjustment. Cowpea exhibits very little drought-induced osmotic adjustment (Shackel and Hall, 1983) compared with peanut (Turner et al., 2000). Values for cowpea were $0-4$ bar compared with $3-16$ bar for peanut. A diverse set of 100 cowpea accessions was screened under extreme soil drought and found to exhibit only small differences in leaf solute potential ranging from -11 to -13 bar, which were not significant (Shackel and Hall, 1983). Among the grain legumes, substantial osmotic adjustment has only been detected in chickpea (*Cicer arietinum* L.), peanut, and pigeon pea (Turner et al., 2000). It is not known whether selecting for enhanced osmotic adjustment can enhance the drought resistance of grain legumes, although a positive correlation was reported for a set of eight chickpea breeding lines between grain yield under water-limited field conditions and osmotic adjustment values for leaves measured in controlled environments (Morgan et al., 1991). A proposed mechanism whereby osmotic adjustment may enhance adaptation to drought is that osmotic adjustment in root cells could enhance their turgor pressure and thus may increase the growth rates of the roots (Hall, 2001).

4.3 Transpiration Efficiency

Selection for genotypic differences in transpiration efficiency (the ratio of net photosynthesis to transpiration) has been considered as an approach for enhancing crop resistance to drought, by using the following model for grain yield under water-limited conditions (Hall, 2001).

$$Y = \sum_{i=d}^{i=1} ET_i \times T_i/ET_i \times W_i \times CP_i \quad (5)$$

where Σ is the summation of daily values of $ET \times T/ET \times W \times CP$ over the period of days (d) when photosynthesis significantly contributes carbohydrate to developing grains, which often starts from an early flowering stage to the date when most grains are physiologically mature. According to the model, grain yield (Y in g m^{-2}) depends on the amount of evapotranspiration (ET in $\text{g}[\text{H}_2\text{O}] \text{ m}^{-2}$), the relative amount transpired (T/ET), the water-use efficiency (W in $\text{g}[\text{CH}_2\text{O}]/\text{g}[\text{H}_2\text{O}]^{-1}$, which is conceptually similar to transpiration efficiency, the ratio of photosynthesis to transpiration), and the proportion of carbohydrate partitioned to grain (CP , which is conceptually similar to HI). This model would provide a useful guide for selection if all of the components in the model were independent or associated positively. As will be seen, this is not the case because negative correlations have been observed among W , CP , and T , as it is determined by the extent of root growth, leaf area, and stomatal opening.

Direct measurement of transpiration efficiency takes considerable effort in that it may have to be measured many times during the season, and measurement of W is constrained by difficulties in measuring both T and below-ground biomass. A theory was developed which predicted that stable carbon isotope discrimination (Δ) can provide an indirect estimate of time-integrated internal carbon dioxide concentration (Farquhar et al., 1982). Consequently, the theory also predicts a negative association between Δ and time-integrated intrinsic transpiration efficiency (the ratio of net photosynthesis to leaf conductance to water vapor, P_n/g_w). This theory was shown to be effective, in that strong negative correlations have been observed between Δ and W in many cases (Hall et al., 1994a). This stimulated considerable research on the possible use of Δ as a selection criterion in plant breeding programs (Hall et al., 1994a). The association between crop performance and Δ has been reviewed for cowpea, common bean, and peanut (Condon and Hall, 1997).

In general, grain yield of cowpea cultivars has been positively associated with Δ (that is, negatively correlated with W) under well-irrigated and water-limited rainfed and stored soil-moisture conditions. When a set of diverse cowpea accessions was grown in different climatic zones, accessions adapted

to a specific zone tended to have high Δ when grown in this zone, but not when grown in other zones (Hall et al. 1994b). Genetic selection studies confirmed this positive association between grain yield and Δ (Hall et al. 1993, 1997b, Condon and Hall 1997). For well-watered conditions, these results may be partially explained by genotypic variation in stomatal conductance with higher stomatal conductance, resulting in lower transpiration efficiency (and thus lower W) and higher Δ but greater net photosynthesis, biomass production, and grain yield. For water-limited conditions, the positive correlations between grain yield and Δ are more difficult to explain. A possible explanation is that the genotypes with higher Δ had greater root growth, which enabled them to access more soil water and thus have greater ET and T . This would provide enhanced plant water status and higher stomatal conductance accounting for the higher Δ and the greater shoot biomass production and grain yield, although transpiration efficiency is low (and therefore W is low). An additional possibility is that the greater grain yields are caused by higher harvest index (and thus greater CP), and that the greater reproductive sink for carbohydrates is, in some way, causing the stomata to be more open through a regulation mechanism, thus causing Δ to be higher. This regulation mechanism could be present in both well-watered and droughted conditions, and a positive genetic correlation was observed between Δ and HI (Menéndez and Hall 1996). Therefore, selection in cowpea for high Δ may select plants with less conservative stomatal performance, i.e., plants whose stomata are more open for greater durations and this may indirectly reflect the fact that they have more effective root systems and/or greater partitioning of carbohydrate to grain.

For common bean under water-limited rainfed conditions on a deep fertile soil, White et al. (1990) observed positive associations between Δ and both shoot biomass production and grain yield for 9 out of 10 common bean cultivars that were tested. This result is consistent with the positive genotypic association reported for stomatal conductance and Δ in another set of common bean cultivars (Ehleringer, 1990). However, when White et al. (1990) studied the same 10 common bean cultivars in another water-limited rainfed environment with a shallow root zone due to an acid subsoil that restricted root penetration, there was no association among Δ and shoot biomass production or grain yield. However, Δ was positively associated with root length density, which substantially varied among the common bean cultivars. Consequently, a possible explanation for the genotypic differences in Δ and grain yield is that, at the site where deep rooting was possible, genotypes with greater root length densities could have had greater access to water and therefore suffered smaller water deficits, which could have resulted in greater stomatal conductance (and therefore greater Δ), greater biomass, and greater grain yield. At the site where root depth was restricted, Δ and root length

density were again positively correlated but the highest grain yields were associated with intermediate values of Δ . In this case, it is possible that genotypes with very low root length density suffered from water deficits and had very low stomatal conductance (and therefore very low Δ), and grew slowly such that they had low yields. In contrast, genotypes with very high root length density initially had high stomatal conductance (and thus high Δ), rapid growth, and rapid water use, but depleted moisture in the shallow soil profile and became severely stressed during reproductive development such that CP was reduced, and they also produced small grain yields (White, 1993). These hypotheses have not been rigorously tested. However, it would appear that genotypic differences in root growth are an important component of drought resistance in common bean and can strongly influence the relations among Δ , edaphic conditions, and grain yield.

In peanut, the genotypic association between Δ and biomass production appears to be different from either cowpea or common bean. For peanut, the relationship between Δ and biomass production almost invariably has been found to be negative (Wright et al., 1993). There has been a positive association between transpiration efficiency (and thus W) and crop growth rate under both well-watered and water-limited conditions. Much of the genotypic variation for Δ arises from variation in photosynthetic capacity and the amount of rubisco per unit leaf area and not in stomatal conductance (Nageswara Rao et al., 1995). In addition, there does not appear to have been a trade-off between genotypic variation in photosynthetic capacity and leaf area growth rate. Specific leaf area (SLA = leaf area per unit dry weight) is easier to measure than Δ , and a strong positive association was observed between SLA and Δ (Nageswara Rao and Wright, 1994). Unfortunately, attempts to breed improved peanut cultivars by indirectly selecting for increased transpiration efficiency have been impeded by positive associations between harvest index (and thus CP) and either Δ or SLA (Wright et al., 1993). These associations have been found in studies with diverse peanut cultivars and also in populations from crosses involving parents with high and low Δ values. As a consequence of the association, there was no increase in pod yield with selection for lower Δ , despite large increases in biomass production. If the linkage between high transpiration efficiency and low harvest index proves to be unbreakable (this association was also observed in several other species including cowpea), the high biomass production associated with high transpiration efficiency should still be advantageous in production systems where fodder yield for animal production and pod yield for human consumption are both important.

In general, adaptation to water-limited environments requires that many traits be optimized: days to first flowering, cycle length, rooting rate and depth, transpiration efficiency, and harvest index. Where levels of several

traits are not optimal, cultivars with improved adaptation may be developed by simultaneous selection for these traits so that they approach optimal levels. Days to first flowering, cycle length and harvest index can be effectively selected, but instead of selecting for root traits or transpiration efficiency, it may be more practically effective to select advanced lines based on their grain yield in the target production environment.

5 ADAPTATION TO INFERTILE SOILS

In many countries, grain legumes are often grown in infertile soils with major deficiencies of nitrogen and phosphate. Consequently, the biological fixation of atmospheric nitrogen (BNF) by legumes in symbiosis with rhizobia and their enhanced uptake of soil phosphate (P) when associated with endomycorrhizal fungi are critical aspects of their adaptation. The enhancement of soil fertility also benefits subsequent crops in the rotation. The extent to which BNF and P acquisition by grain legumes can be enhanced by breeding is examined.

5.1 Biological Nitrogen Fixation

The circumstances where inoculation of seed with selected strains of rhizobia can enhance BNF are considered. Typically, inoculant use is recommended when the legume crop is to be planted on a soil where this species has not been grown before and levels of effective native rhizobia are too low. Cowpea and peanut can exhibit effective symbiosis with a broad range of rhizobia and inoculation is not often necessary. In contrast, common bean can benefit from inoculation with rhizobia in some circumstances. Care is needed in choosing inoculants, however, in that some commercial inoculants have low quality (Date, 2000). Where effective inoculation technologies have been developed, the use of rhizobial inoculants in common bean production and research can be worthwhile. Cases where the use of inoculants has been effective with common bean are reviewed by Graham and Vance (2000).

Under well-watered conditions, cowpea has the potential for substantial BNF. In a 95-day growing season, cowpea has produced 3 ton/ha of grain and 4.7 ton/ha of hay while relying mainly on BNF for nitrogen (Elowad and Hall 1987), indicating the potential to fix about 200 kg/ha of atmospheric nitrogen. In California, no grain yield responses of cowpea to inoculation have been reported and the crop often is grown without applying nitrogen fertilizer or manure (Hall and Frate, 1996). In contrast, common bean often has exhibited low levels of BNF, while peanut is intermediate for this trait

(Hardason et al., 1993). In the United States, inoculants are rarely applied to common beans and substantial nitrogen fertilizer is usually applied. In many areas of the world, nitrogen fertilizer is applied to peanuts (Knauff and Wynne, 1995).

Substantial genotypic variation for BNF is present in common bean (Hardason et al., 1993). Bliss (1993) has bred genetic lines of common bean that have sufficient BNF to support grain yields of 1000–2000 kg/ha in infertile soils. Five of these lines (Bliss et al., 1989) and one common bean cultivar with high BNF (Henson et al., 1993) have been released. BNF appears to be a quantitatively inherited trait in common bean, and family rather than single-plant selection has been practiced (Bliss, 1993). With advanced lines, BNF can be assessed indirectly based on plant performance in field conditions on low N soils (Bliss, 1993). Selection for grain yield or grain nitrogen may be effective but in some conditions, it may be useful to select for total shoot dry matter or total shoot nitrogen as well (Elizondo Barron et al., 1999). For parents used in crosses and selected advanced lines, it is useful to determine the proportion of nitrogen in the plants because of BNF. This can be estimated based on the proportion of nitrogen in xylem sap that is ureides and thus was formed by BNF for some legumes, including common bean (Herridge and Rose, 2000) and cowpea (Elowad et al., 1987; Elowad and Hall, 1987), but not peanut.

BNF is extremely sensitive to drought with greater reductions occurring than the levels observed for photosynthesis and carbohydrate accumulation rate (Serraj et al., 1999). Sinclair and Serraj (1995) determined the ratio of the sensitivities to drought of BNF and transpiration (stomatal conductance) of nine grain legume species. Some species that transport BNF products as ureides (including cowpea) had BNF that was more drought-sensitive than transpiration. In contrast for species that transport BNF products as amides (including peanut), BNF had less sensitivity to drought than transpiration. For common bean, the study was somewhat inconclusive in that it transports BNF products as ureides and tends to have low BNF, but in this study, its BNF was less sensitive to drought than transpiration. Subsequent studies confirmed that the BNF of common bean can be less sensitive to drought than its transpiration, although it produces some ureides (Serraj and Sinclair, 1998). Serraj et al. (1999) provided a hypothesis to explain the sensitivity of BNF to drought in species such as soybean and cowpea. They argue that feedback by high concentrations of BNF products, such as ureides, may be responsible for drought-induced reductions in BNF. They also proposed that genetic variation existing in soybean may provide an opportunity to overcome this problem through plant breeding.

Generally, plants engaged in symbiotic nitrogen fixation have a higher requirement for phosphate than those that rely on inorganic nitrogen (Gra-

ham and Vance, 2000). Consequently, genotypes with enhanced P acquisition in P-deficient soil may also have enhanced BNF.

5.2 Phosphorus-Deficient Soils and Mycorrhizal Roots

In many—if not most—field conditions, the roots of cowpea and other grain legumes are mycorrhizal beginning about 3 weeks after germination because of associations with specific fungi. Vesicles and arbuscules resulting from this association are present in root cortical cells, and the hyphae of the fungi extend into the soil. In infertile soils, mycorrhizal cowpea plants can take up more P, zinc, and copper than nonmycorrhizal cowpea plants and produce more biomass and grain in either well-watered or water-limited conditions (de Faria, 1984; Kwapata and Hall, 1985). With optimal irrigation, mycorrhizal infection was inhibited by 80–91% when cowpea plants were grown under high levels of soil P, but with moderate levels of soil drought, normal levels of infection occurred at high soil P, despite high P concentrations in the plants (de Faria, 1984; Kwapata and Hall, 1985). Mycorrhizal infection did not influence biomass production or grain yield of plants grown with both high soil P and moderate soil drought. The mycorrhizal cowpea root system may be very effective in accessing soil P. In California field conditions, cowpea has shown no response to P fertilization in very low P soils where cotton (*Gossypium hirsutum* L.) and maize (*Zea mays* L.) showed substantial yield responses to P fertilization (Hall and Frate, 1996). Common bean is similar to cowpea in that mycorrhizal infection has resulted in improved acquisition of P and enhanced shoot growth in low soil P conditions, but little effect in high P soils (Lynch et al., 1991).

The initial and major response of common bean (Lynch et al., 1991) and cowpea (de Faria, 1984) to P deficiency is that plants produce fewer leaves and less leaf area. The net photosynthesis per unit leaf area does decrease, but at a much lower rate than the total leaf area. Low soil P availability is considered the greatest soil constraint to common bean production; consequently, substantial effort has been devoted to breeding common bean cultivars with improved productivity in low P soils (Lynch et al., 1998). Emphasis has been placed on enhancing the efficiency whereby common bean acquires soil P. Genetic variation in the ability to acquire soil P is present and was independent of mycorrhizal and soil-type effects (Yan et al., 1995a,b). Several mechanisms influencing soil P acquisition have been studied. Three Andean common bean genotypes exhibited greater extraction of P from calcium phosphates in artificial medium than three Mesoamerican genotypes (Yan et al., 1996). In low soil phosphorus conditions, one of these Andean genotypes acidified the rhizosphere more than the other five genotypes. It should

be noted that this mechanism may be more important in high pH soils or where plants have been fertilized with rock phosphate. Many low P soils have low pH and in this situation other types of root exudates may enhance P acquisition (Lynch et al., 1998). Root architecture is important in P acquisition because of the relative immobility of P in the soil. The proportion of the root system that explores the region where soil P is highest, which is often the upper part of the soil profile, may be important. Genotypic differences have been detected in this trait under low soil P conditions (Lynch et al., 1998). A trade-off is involved, however, in that a root system that mainly explores the upper soil profile would not be adaptive in water-limited conditions where substantial water is available deep in the soil. A common bean genotype that is efficient in acquiring soil P also had a greater tendency to produce adventitious roots under low soil phosphorus conditions than a less efficient genotype (Lynch et al., 1998). The efficient genotype also produced more root hairs under low soil phosphorus than an inefficient genotype (Lynch et al., 1998). An additional complication is that root traits should complement mycorrhizal hyphae traits with respect to their abilities to access soil P in different parts of the rhizosphere (Koide, 2000).

Direct selection for root traits is usually difficult. Indirect selection for root traits using molecular markers could enhance the efficiency of breeding for improvements in phosphorus acquisition and some molecular markers for root traits have been detected (Lynch et al., 1998). The growth pouch technique of Omwega et al. (1988) was used to screen cowpea accessions for differences in root hairs. Cowpea genotypes have been detected (Melakh and IT82E-18) that produce more and longer root hairs under low soil P conditions than other cowpea genotypes using the growth pouch technique (J.D. Ehlers and W.C. Matthews, unpublished, 2001). The growth pouch technique for detecting differences in root hair production is very efficient in that thousands of plants can be screened in a few weeks and the screen is nondestructive in that selected plants can be removed from the pouches and grown to produce seed.

Some common bean breeding programs have selected for traits thought to confer enhanced performance in low P soils, but, according to Lynch et al. (1998), these programs have yet to produce genotypes with superior performance in low P soils than check cultivars. Papers describing genetic differences among peanut that may be relevant to performance in low P soils have been reviewed by Knauff and Wynne (1995).

Breeding for infertile soils needs to be integrated with other components of a comprehensive breeding program. An efficient way to partially accomplish this objective is to conduct at least some performance trials in fields in the target production environment with infertile soils. These trials

can be expensive because of the substantial soil variability that inflates the error term, requiring many replications of both plots and experiments if reliable predictions are to be obtained from the results of such trials.

6 FUTURE DIRECTIONS FOR PLANT BREEDING

As more information is gained, it is likely that improved ideotypes will be developed for grain legume cultivars which will exhibit superior performance in specific target production zones. I am using a broad definition of an ideotype as being a plan of the phenotype of a cultivar that will perform optimally in a specific set of climatic, soil, biotic, and sociocultural conditions (Hall, 2001). Incorporating all of the traits defined by these improved ideotypes will be difficult even when the inheritance of many of the individual traits is known. Direct selection can be particularly difficult for traits that are difficult to screen, such as many of the root traits. Moreover, direct selection is not very effective for incorporating multiple traits. Indirect marker-assisted selection, with emphasis on molecular markers, has the potential to substantially increase the efficiency of breeding to incorporate multiple traits and traits which are difficult to screen. Prior to developing marker-assisted selection procedure, it is useful to have a high-density genetic-linkage map. Considerable progress has been made in this area with common bean (Gepts, 1999), and some progress has been made with cowpea (Ouedraogo et al., 2002). Common bean breeders are already using DNA marker-assisted selection (Kelly and Miklas, 1999).

Grain legume breeders should consider possible climate changes when developing breeding strategies (Hall and Ziska, 2000). Breeding for coordinated increases in both the reproductive sink and the photosynthetic source may be effective in increasing grain yield at the present time. However, increases are occurring in atmospheric $[\text{CO}_2]$ that could continue to make photosynthetic sources more effective per unit leaf area. Consequently, maintaining a balance between photosynthetic sources and reproductive sinks may require selecting plants for future environments that have even greater reproductive sinks. Breeding to enhance reproductive sinks will be particularly important for target production zones where stresses, such as high temperature, can cause greater damage to reproductive development than to the photosynthetic source. Breeding for heat tolerance during reproductive development has been effective (Hall, 1992, 1993). In cowpea, genes for heat tolerance during reproductive development enhance sink strength and harvest index (Ismail and Hall, 1998, 2000). Studies in elevated and current atmospheric $[\text{CO}_2]$ s suggest that heat-tolerance genes may enhance the grain yield response of cowpea to elevated $[\text{CO}_2]$ under both optimal and high tempera-

tures (Ahmed et al., 1993a; Hall and Allen, 1993). Selection for greater reproductive sink strength could indirectly enhance photosynthetic capacity and activity by minimizing the feedback effects that downregulate the photosynthetic system. Making full use of elevated $[\text{CO}_2]$ may also require selection to enhance those components of the photosynthetic system that limit photosynthesis per unit leaf area in these conditions.

Some radical approaches to grain legume breeding should be considered. Reproductive processes, especially production of pollen and pollination, are extremely sensitive to several stresses, such as chilling, high temperatures, and drought. The effects can be more severe than required to maintain a balance between photosynthetic source and sink, such that the seeds produced are adequately plump and viable. A potential solution to this problem is to develop cultivars that do not require pollination and other sexual processes while growing in farmers' fields. Cultivars with an appropriate type of apomixis would be able to produce viable seed from maternal tissue without requiring either meiosis of the embryo mother cell or pollen production and pollination of the embryo or endosperm. The advantages of cultivars with this type of apomixis are as follows.

1. Apomixis could confer resistance to stresses that damage pollination and other aspects of sexual production including chilling, heat, drought, and various insect pests (Hall et al., 1997a). Apomixis may also enhance grain yield in those grain legume species that may not have a completely effective pollination process, such as common bean (Ibarra-Perez et al., 1999).
2. Apomixis would fix hybridity in that F_1 hybrids would have true-breeding seeds. This would make possible the use of hybrid vigor, which would substantially increase yields of those grain legumes, such as cowpea (Hall et al., 1997a), that exhibit substantial heterosis for this trait. Farmers could reuse seed produced by apomictic hybrid cultivars in that the seed would retain its hybrid vigor. This would provide a significant advantage for the many poor farmers who grow grain legumes.
3. Seed production may be more effective in apomictic cultivars than with current grain legume cultivars, which are mainly self-pollinated but can exhibit a degree of cross-pollination that results in the production of genetically variable seed. Out-crossing can cause major problems in seed production of common bean (Ibarra-Perez et al., 1997) and cowpea.
4. Breeding programs would be accelerated by using apomictic lines because it would confer the ability to immediately fix superior heterozygous genotypes.

Sex would still be needed to permit the continual breeding of improved cultivars. This could be achieved by using facultative (switchable) apomixis systems, where the default state is apomictic. The sexual state would be switched on by the breeder by using specific chemical sprays or special environments. Several plant species have the genes needed for developing facultative apomictic breeding systems. Through genetic engineering, it may be possible to create and transfer the “cassette” of genes needed for facultative apomixis into grain legume cultivars (Jefferson, 1993). Grain legume cultivars with facultative apomixis could lead to a beneficial revolution in plant breeding, crop production, and the whole agricultural industry.

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