Breeding for adaptation to drought and heat in cowpea

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Abstract

Accomplishments in breeding for adaptation to drought and heat are reviewed based upon work with the indeterminate grain legume species cowpea. Plant traits and some crop management methods are examined that influence adaptation to rainfed production in the drought-prone, semiarid tropical Sahelian zone of Africa. Drought escape, drought resistance, delayed-leaf-senescence, and varietal intercrops are examined. In addition, adaptation to the heat that can detrimentally impact irrigated production in the hot, subtropical arid zone of California is evaluated. Heat tolerance during reproductive development, electrolyte leakage, membrane thermostability, some aspects of crop management including date of sowing, and chilling tolerance during emergence including the beneficial effects of a dehydrin protein are considered. Methods for breeding cowpeas with adaptation to drought and heat are described that have been effective.
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1. Introduction

I will review accomplishments in breeding for adaptation to drought and heat with the indeterminate grain legume species cowpea (*Vigna unguiculata* L. Walp.). I mainly will discuss the work of a collaborative research program involving scientists in the USA and Africa. The history of our collaborative program is described in Hall et al. (2003). First I will consider adaptation to the droughts that can detrimentally impact rainfed production in the harsh, semiarid tropical Sahelian zone of Africa. I will then examine adaptation to the heat that can detrimentally impact irrigated production in the hot, subtropical arid zone of California. I will describe the breeding of adapted cowpea cultivars for these zones including effective methods for breeding for adaptation to drought and heat, and some aspects of crop management. I also will describe some approaches that have not yet been adopted by either crop improvement programs or farmers but appear to have some merit.

2. Breeding for adaptation to drought

Rainfed crops growing in the semiarid tropical Sahelian zone of Africa can be subjected to extremely

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dry and hot conditions. Since 1968, droughts have occurred on many years in the drier part of this zone which were so severe that local landraces and modern cultivars of drought hardy crops such as pearl millet, sorghum and peanut failed to produce significant quantities of grain. Also, virtually all cowpea landraces that had evolved over 100's of years in the Sahel did not produce significant quantities of grain in the years and locations with the most severe droughts due to the likely climate change since 1968. I will describe cultivars and crop management practices that have been developed that have enabled cowpeas to produce significant grain in most recent years in the Sahel.

2.1. Crop phenology and adaptation to drought

Initially we attempted to select plants with optimal numbers of days from sowing to first flowering and maturity, and appropriate plant habit. However, rainfall in the Sahel has been so variable and droughts have been so extreme that this approach only was partially successful. I now consider it necessary to breed two types of cultivars and recommend that farmers grow both types every year to enhance the chances that significant grain production will be achieved every year.

For about 30 years since 1968, there have been a series of droughts in the Sahel that have resulted in the growing season being considerably shorter than it was in the 50 years prior to 1968. Consequently, the first type of cultivar that we bred has a very short cycle from sowing to maturity. This was achieved by selecting plants that began flowering early and had synchronous flower production. They have an erect habit and produce their first floral buds on low main stem nodes and subsequent floral buds on the main stem and the first nodes on branches. We bred two of this type of cultivar. 'Ein El Gazal' (Elawad and Hall, 2002) and 'Melakh' (Cisse et al., 1997) are erect, begin flowering 30–35 days from sowing in the Sahel, and reach maturity within 55–64 days from sowing with the shortest cycles occurring with late-season drought. This type of cultivar should be sown at close spacing of about 50 cm between rows and 25 cm between seeds in the row. These erect plants exhibit less ground coverage than traditional Sahelian landraces that have a spreading habit and often have been sown at 100 cm × 100 cm

spacing. 'Ein El Gazal' was evaluated in the Sahel as breeding line 1-12-3 over many years (Hall and Patel, 1985; Elawad and Hall, 2002). In 1981 at Louga, Senegal, 'Ein El Gazal' reached maturity 55 days from sowing and produced 1091 kg/ha of grain with a rainfall and total water supply of only 181 mm and hot conditions with an evaporative demand of 6 mm/day. In contrast, a set of local landraces had only just begun to produce pods at 55 days after sowing, and they produced very little grain during this year at Louga. In 1983 at El Obeid, Sudan with a rainfall of only 230 mm, 'Ein El Gazal' produced 500 kg/ha of grain while landraces with later flowering and longer cycles from sowing to maturity only produced 152 kg/ha. Early erect cultivars, such as 'Ein El Gazal' and 'Melakh', have performed well when the rainfall season was short but distinct due to their ability to escape late-season drought. Unfortunately, early erect cultivars have been damaged by mid-season droughts (Thiaw et al., 1993) due to the extremely detrimental effects of drought on pod set and pod-filling of erect synchronous-flowering varieties (Turk et al., 1980).

The second type of cultivar that we developed begins flowering later than either 'Ein El Gazal' or 'Melakh' and has a more spreading plant habit that provides it with more sequential rather than synchronous flowering and a medium cycle from sowing to maturity. 'Mouride' (Cisse et al., 1995) begins flowering in about 38 days and reaches maturity 70 days from sowing. Cultivars that are more spreading than 'Mouride' and reach maturity about 75 days from sowing also can be effective in the Sahel. The spreading cultivars should be sown in rows 50 cm apart with 50 cm between seeds within the row. In the Sahelian zone of Senegal, 'Mouride' has exhibited greater resistance to midseason drought but less ability to escape late-season drought than 'Melakh'. 'Mouride' also has greater yield potential, presumably due to its longer reproductive period than the early erect cultivars. 'Mouride' has produced about 3000 kg/ha at the wetter boundary of the Sahel with about 450 mm of rainfall compared with grain yields of about 2400 kg/ha for 'Melakh' and 'Ein El Gazal' under well-watered conditions (Hall and Patel, 1985).

'Mouride' and 'Melakh' have complementary performance and it is important to consider the cropping system that would be most effective if farmers are to grow both types of cultivars. Using other cultivars,

we have demonstrated that varietal intercrops can produce more grain and hay, and be more stable under dry Sahelian conditions with infertile soil than any of the sole crops of cowpea that were tested (Thiaw et al., 1993). The varietal intercrops we tested consisted of alternating rows of early erect and medium-cycle spreading cowpea cultivars. Some mechanisms for the beneficial effects of the varietal intercrops are as follows. In years when a mid-season drought occurs, the early erect cultivar becomes stunted and the medium-cycle spreading cultivar compensates by growing into the space that is made available and produces much of the grain and hay produced by the intercrop. In years when late-season drought occurs, the early erect cultivar produces abundant grain, while the medium-cycle spreading cultivar produces abundant hay but little grain. Farmers in the Sahel appreciate both the grain and the hay of cowpea, and are beginning to grow different types of cultivars (Hall et al., 2003), but, the concept of varietal intercropping has not yet been extended to them.

2.2. Drought resistance

'Mouride', 'Melakh' and 'Ein El Gazal' have substantial resistance to vegetative-stage drought. 'California Blackeye No. 5' ('CB5') is one of the parents of 'Ein El Gazal' (Elawad and Hall, 2002). In California, 'CB5' has exhibited the ability to survive a vegetative-stage drought that would have killed most other annual crop species, and to recover when re-watered and produce very high grain yields of about 4000 kg/ha that were similar to a weekly irrigated control treatment (Turk et al., 1980). The vegetative-stage drought had been imposed by sowing seed into a dry soil profile, providing a small amount of water with sprinklers to permit the seedlings to emerge, and then growing plants under hot sunny conditions for 43 days with no further irrigation or rain. In several years in the Sahel when severe vegetative-stage drought occurred, I observed that cowpea plants survived, while pearl millet and peanut plants that were growing in the same fields and had emerged at about the same time had died.

Mechanisms for the resistance to vegetative-stage drought of cowpea compared with the other species have been studied. When these species were subjected to drought as seedlings growing in shallow soil in boxes, cowpeas survived 8–12 days longer than either pearl millet or sorghum or peanut (Singh and Matsui, 2002). The authors hypothesized that the resistance mechanism may reside in the plant shoot. Under severe droughts, cowpea exhibits greater dehydration avoidance and maintains leaf water potentials above -1.8 MPa, while pearl millet, sorghum and peanut can develop leaf water potentials as negative as -4 to -9 MPa under these conditions. Petrie and Hall (1992) found that pearl millet developed more negative leaf water potentials than cowpea, even at predawn with plants of the two species growing in the same pot. Petrie et al. (1992) hypothesized that these species differences in leaf water potential may be due to pearl millet having a root system that is less effective on a micro-scale in taking up water during soil drying, even though it has more roots than cowpea. They argued that the numerous high-density clumps of roots in pearl millet would develop internal dry soil layers, such that they would only take up water at the ends of the roots. In contrast, cowpea has a more uniform root system and was hypothesized as using more of the root surface and thus being more effective in taking up water from drying soil than pearl millet. These hypotheses were consistent with results from simulation modeling, but have not been adequately tested. Apparently, the reasons for the high level of vegetative-stage drought resistance in some cowpea cultivars are controversial and largely unknown.

We probably incorporated resistance to vegetative-stage drought into 'Ein El Gazal', 'Mouride' and 'Melakh' by chance, either through the choice of parents, such as CB5, or through our selections based on yield trials in the Sahel. This indicates that many cowpeas may have substantial resistance to vegetative-stage drought. A simple screening technique has been developed that uses visual observations of young plants subjected to drought and recovery while growing in shallow soil in boxes, which may be useful for selecting cowpea genotypes with the ability to survive vegetative-stage drought (Singh et al., 1999; Singh and Matsui, 2002). A large number of cowpea breeding lines (190) were screened using the box method and most of them (148) exhibited substantial survival of vegetative-stage drought, even though they had not been selected for this trait (Singh and Matsui, 2002). The research on improving drought resistance by Singh and Matsui (2002) provides a promising avenue for approaching this difficult problem; however, additional

information is needed on the extent of genetic variation, mechanisms and types of resistance to vegetative-stage drought present in cowpea cultivars and accessions.

In general, cowpeas are very sensitive to drought during pod set and pod filling (Turk et al., 1980). A delayed-leaf-senescence (DLS) trait has been discovered in cowpea that conferred some resistance to reproductive-stage drought in erect cowpea cultivars. The DLS trait enabled them to recover after the drought and produce a larger second flush of pods that compensated for the low yield by the first flush of pods (Gwathmey and Hall, 1992). The DLS trait appears to be conferred by a single gene and may involve resistance to premature death caused by *Fusarium solani* f. sp. *phaseoli* (Burke) Synd. & Hans., type A, which probably is widely distributed (Ismail et al., 2000). In Senegal, an early erect DLS cultivar began flowering in about 35 days and produced about 2000 kg/ha of grain by 60 days, followed by a second flush of pods with the potential to produce an additional 1000 kg/ha by 100 days from sowing (Hall et al., 2003). Farm families in Africa typically harvest cowpea pods by hand and do not uproot plants such that they can make multiple harvests with individual crops. An early erect DLS cultivar might be adapted to locations in the wetter boundary of the Sahelian zone or the wetter Savanna zone where there is sufficient rainfall in most years to support a cropping season of at least 100 days but a tendency for mid-season droughts to occur.

2.3. Pest and disease resistance

Farmers are not likely to adopt a new cultivar simply because it has improved adaptation to drought. In addition, farmers are concerned about the damage they readily see that is caused to cowpea by several pests and diseases that are prevalent in the Sahelian zone (Hall et al., 1997). Both 'Mouride' and 'Melakh' have resistance to the seed-borne diseases caused by bacterial blight (*Xanthomonas campestris* pv*vignicola* Burkholder) Dye and cowpea aphid-borne mosaic virus. 'Mouride' also has resistance to cowpea weevil (*Callosobruchus maculatus* Fabricius) and the parastic weed *Striga gesnerioides* Willd. Vatke. In contrast, 'Melakh' has resistance to cowpea aphid (*Aphis craccivora* Koch) and flower thrip (*Megalurothrips sjostedti* Trybom). The fact that these two cultivars have resistance to different pests also supports the recommendation that farmers should grow both cultivars, since seasonal pest patterns often are not known at sowing time. Ideally one should breed cultivars that are adapted to drought and resistant to all of the major pests and diseases that can occur in the target production zone, but this is not easy and will take several more years to accomplish for the Sahel.

2.4. Performance testing

Relative yield of potential new cultivars compared with current cultivars is an important measure of what has been achieved by incorporating traits that improve adaptation to drought and resistance to pests and diseases. Relative yield provides a measure of the relative efficiency of the cultivar in terms of the returns in grain per unit of land or other inputs when the new cultivar has similar input requirements as the old cultivars. This often is the case when cowpeas are grown in both the Sahel and California, since they usually are not provided with either fertilizer or manure.

Advanced cowpea breeding lines were evaluated in multiple locations on experiment stations and farmers fields in the Sahelian zone of Senegal and Sudan over several years (Cisse et al., 1995, 1997; Elawad and Hall, 2002). Performance testing of this type is critical for ensuring that selected cultivars are adequately robust in relation to the highly variable environments that they will experience when grown on farmers fields under the harsh rainfed conditions that occur in semiarid zones such as the Sahel. On-farm trials also provided an opportunity to obtain feedback from farm families concerning traits in the various lines they did and did not appreciate, and especially their opinions on grain quality as perceived by both looking at and consuming the grain in local dishes. Grain quality is an extremely important trait for buyers and consumers that is difficult for breeders to assess and has a major impact on the extent of adoption by farmers.

3. Breeding for adaptation to heat

The hot arid subtropical zone in the San Joaquin Valley of California where cowpea is grown under irrigation has a cool spring followed by a very hot summer. Cowpea often is sown in May and then is subjected to hot weather during flowering and pod set in

July and August (Hall and Frate, 1996). Studies have been conducted with cowpea plants subjected to higher night temperatures during flowering using enclosures in field conditions (Nielsen and Hall, 1985a,b), and with almost isogenic pairs of heat-resistant and heat-susceptible lines grown in field environments with contrasting temperatures (Ismail and Hall, 1998). These studies showed that increases in night temperature caused 4–14% decreases in both pod set and grain yield for each °C above a threshold of 16 °C. The main mechanism for these effects on cowpea is that high temperatures occurring in the late night during flowering can cause pollen sterility and indehiscence of anthers (Hall, 1992, 1993). For cowpea, the heat-stress problem mainly has been solved by breeding, however, crop management also can be important in some cases.

3.1. Crop phenology and adaptation to heat

In principle, early sown cowpeas that flower early could escape the high night temperatures that occur in July and August in the San Joaquin Valley of California. However, current cowpea cultivars cannot be sown too early in spring because they are sensitive to chilling and require a minimum soil temperature greater than 18 °C if they are to emerge adequately (Ismail et al., 1997). Also, the cool night temperatures of spring cause cowpeas to develop slowly and the earliest flowering cowpea cultivars take about 60 days from sowing to first flowering in cool conditions. Some progress has been made in breeding cowpeas with chilling tolerance during emergence. An additive model was proposed by Ismail et al. (1997), whereby chilling tolerance during emergence is conferred by the presence of a specific dehydrin protein in the seed (positive single gene nuclear effect) and the extent of electrolyte leakage from seed (negative maternal effect) as a measure of membrane thermostability. Tests with backcross materials and molecular genetic (Ismail et al., 1999) and inheritance studies (Ismail and Hall, 2002) supported the hypothesis that the dehydrin protein confers an increment of chilling tolerance under single nuclear gene inheritance. They also showed that the dehydrin protein effect is independent of the electrolyte-leakage effect, which was shown to be nuclear rather than cytoplasmic (Ismail et al., 1999).

Single seeds of cowpea can be screened for the presence of the dehydrin protein using an immunoblot as-

say of a chip taken from a cotyledon in a manner that does not harm the germination of the seed (Ismail et al., 1999). Several cowpea accessions were discovered to have this dehydrin protein in their seed that could be used as parents (Ismail and Hall, 2002). Consequently, this trait can be readily bred into cultivars. Surprisingly, only three out of 61 US cowpea cultivars, which had been developed in subtropical zones where soils can be cool at sowing, contained the dehydrin protein (Ismail and Hall, 2002).

3.2. Heat tolerance during reproductive development

A method for breeding cowpeas with heat tolerance during reproductive development has been developed (Hall, 1992, 1993) that was used to breed 'California Blackeye No. 27' ('CB27') (Ehlers et al., 2000). 'CB27' is both tolerant to heat during reproductive development and heat resistant in that it produces more grain yield than other cowpea cultivars in hot field environments (Ismail and Hall, 1998). Breeding for heat tolerance, involved subjecting progeny to very high night temperatures and long days in either field or glasshouse conditions, which only could be done in the summer, and selecting plants with the ability to abundantly produce flowers and set pods (Hall, 1992, 1993). Long days must be used because under short days the detrimental effects of heat on reproductive development of cowpea are either much smaller or may not occur (Ehlers and Hall, 1998). In the F_2 generation, plants were selected that abundantly produced flowers and set pods. This virtually fixed the recessive gene that provides tolerance to heat-induced suppression of floral bud development (Hall, 1993). Tolerance to heat during pod set was more difficult to incorporate because, even though it appeared to mainly involve a single dominant gene, the realized heritability was low at about 0.26 (Marfo and Hall, 1992) and it is likely that inheritance also depends on some minor genes (Hall, 1993). Fixing a high level of heat tolerance during pod set has taken several generations of family selection, followed by single-plant selection in these families, that only could be conducted in the summer in places where night temperatures were very hot and days were long.

A more rapid method for breeding for heat tolerance during reproductive development recently has been developed based on the observation that heat tolerance

during pod set might be associated with slow electrolyte leakage from leaf discs subjected to heat stress and thus membrane thermostability (Ismail and Hall, 1998). This latter study was conducted with sets of cowpea lines that had differences in heat tolerance but different genetic backgrounds. Genetic selection experiments now have been conducted using a pair of these lines as parents that have shown there is a close relationship between heat tolerance during pod set and slow electrolyte leakage from leaf discs subjected to heat stress (Thiaw and Hall, 2004). The protocol used consisted of taking leaf discs from recently expanded leaves and subjecting them to $46\,^{\circ}$C in aerated distilled water and determining the % electrolyte leakage into the water after 6 h. Lines divergently selected for leaf-electrolyte-leakage under heat stress also differed with respect to heat tolerance during pod set with low leakage being associated with high pod set. Lines divergently selected for heat tolerance during pod set also differed in leaf-electrolyte-leakage with high pod-set lines also having low electrolyte leakage from leaf discs.

Realized heritability of leaf-electrolyte-leakage under heat stress was 0.28–0.34 and the genetic correlation between this trait and pod set was −0.36. This gives an indirect realized heritability when using slow electrolyte leakage to select for high pod set of only 0.10–0.12, which is smaller than the realized heritability for direct selection for pod set of 0.26 obtained by Marfo and Hall (1992). However, genotypic differences in electrolyte leakage of leaf discs under heat stress were detected with plants grown in a range of environments (Thiaw, 2003). Genotypic differences were most readily detected with plants grown at moderate temperatures and long days, but they were also detected in hot conditions and short days which indicates that this selection technique may be effective with plants growing in both off-season and summer nurseries. This would permit more generations of selection for heat tolerance in each year.

The following strategy was proposed for rapid incorporation of heat tolerance during reproductive development into cowpea that combines direct and indirect selection for heat tolerance during pod set (Thiaw and Hall, 2004). During the summer with the F_2 generation, select single plants with abundant flower production and pod set in a field or glasshouse environment with very high night temperatures and long days. During the fall and winter with the F_3 and F_4 generations growing

in moderate-temperature glasshouses and short days, select single plants for low electrolyte leakage by leaf discs under heat stress. During the second summer, grow the F_5 generation in a field or glasshouse environment with very high night temperatures and long days. Select families for low leaf-electrolyte-leakage under heat stress during the vegetative stage, and then select individual plants within these families that have abundant flower production and pod set. In the F_6 and F_7 generations select single plants with slow electrolyte leakage of leaf discs under heat stress when growing in moderate-temperature glasshouses during the fall and winter when days are short. Finally, in the third summer, begin performance testing selected F_8 lines in hot long-day commercial production environments.

3.3. Interactions between heat tolerance during reproductive development and other traits

'CB27' and other genotypes we have bred with heat tolerance during reproductive development exhibit some dwarfing under hot and also moderate-temperature conditions (Ismail and Hall, 1998). Heat-tolerant genotypes were shorter due to shorter internodes, produced less vegetative shoot biomass and had greater harvest index (Ismail and Hall, 1998). The heat-tolerant genotypes produce much more grain than heat-sensitive genotypes under very hot conditions, i.e. they also are heat resistant. But, we were concerned that the dwarfing may reduce their value under moderate-temperature conditions, and the extent of hot weather during flowering varies from year to year. Semi-dwarf heat-resistant genotypes and cultivars were compared with standard-height heat-susceptible genotypes and cultivars under different row spacings in different moderate-temperature environments (Ismail and Hall, 2000). These and other studies indicated that the heat-resistant semi-dwarf lines can produce greater grain yield than standard-height lines under moderate temperatures, providing they are grown under narrow row spacing (51 cm) with soil conditions that promote moderate to vigorous early plant growth. The yield advantage was due to impaired production of pods by standard-height, but not semi-dwarf lines when competition for light was strong. In contrast, under wide row spacing (102 cm), poor soil conditions and moderate temperatures, the semi-dwarf heat-resistant lines are not as competitive with weeds and can produce less

grain than the standard-height lines, especially with ineffective weed management.

The heat-tolerance trait is associated with more rapid partitioning of carbohydrates to developing pods, under moderate or high temperatures, whereas the DLS trait is associated with the maintenance of greater carbohydrate reserves in stem bases and probably roots (Gwathmey et al., 1992). Consequently, we tested whether a negative interaction occurs between these traits (Ismail et al., 2000). We crossed a DLS heat-sensitive parent with a non-DLS heat-tolerant parent and bred four advanced populations with and without DLS and heat tolerance. These four populations were evaluated in moderate-temperature field environments where the soil organism (*F. solani*) for which the DLS trait confers resistance was present, and hot field and glasshouse environments where the soil organism was not present. We concluded from these studies that the DLS and heat-tolerance traits can be effectively combined. Genotypes with both traits exhibited beneficial effects on grain yield in two circumstances. The heat-tolerance trait enhanced pod set in hot environments, while the DLS trait enhanced plant survival when *F. solani* was present in the soil, and there were only small detrimental interactive effects due to the presence of both traits in the same genotype.

Heat-tolerance during reproductive development may depend on different membrane properties than chilling tolerance during emergence. Consequently, it could be hypothesized that it may not be possible to combine these traits. This does not appear to be the case in that we have bred lines that have both chilling tolerance during emergence and heat tolerance during reproductive development. An interaction may occur, however, that limits the extent to which these tolerances can be further developed in the same genotype.

Acknowledgments

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