3 Cowpea

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3.1 Introduction

3.1.1 Brief History: Origin and Distribution

Cowpea (Vigna unguiculata L. Walp.) (2n=2x=22) is a member of the Phaseoleae tribe of the Leguminosae family. Members of the Phaseoleae include many of the economically important warm season grain and oilseed legumes, such as soybean (Glycine max), common bean (Phaseolus vulgaris), and mungbean (Vigna radiata). The name cowpea probably originated from the fact that the plant was an important source of hay for cows in the southeastern United States and in other parts of the world. Some important local names for cowpea include “niebe,” “wake,” and “ewa” in much of West Africa and “caupi” in Brazil. In the United States, other names used to describe cowpeas include “southernpeas,” “blackeyed peas,” “field peas,” “pinkeyes,” and “crowders.” These names reflect traditional seed and market classes that developed over time in the southern United States.

Cowpea plays a critical role in the lives of millions of people in Africa and other parts of the developing world, where it is a major source of dietary protein that nutritionally complements staple low-protein cereal and tuber crops, and is a valuable and dependable commodity that produces income for farmers and traders (Singh, 2002; Langyintuo et al. 2003). Cowpea has considerable adaptation to high temperatures and drought compared to other crop species (Hall et al. 2002; Hall 2004). As much as 1000 kg ha⁻¹ of dry grain has been produced in a Sahelian environment with only 181 mm of rainfall and high evaporative demand (Hall and Patel 1985). Presently available cultivars of other crop species cannot produce significant quantities of grain under these conditions. The crop is more tolerant of low fertility, due to its high rates of nitrogen fixation (Elawad and Hall 1987), effective symbiosis with mycorrhizae (Kwapata and Hall 1985), and ability to better tolerate soils over a wide range of pH when compared to other popular grain legumes (Fery 1990). Dry grain yields above 7000 kg ha⁻¹ have been achieved in large field plots with guard rows in the southern San Joaquin Valley of California (Sanden 1993), where growers often obtain yields above 4000 kg ha⁻¹. Clearly, cowpea is both responsive to favorable growing conditions and capable of growing under drought, heat, and other abiotic stresses.

Cowpea most certainly evolved in Africa, as wild cowpeas only exist in Africa and Madagascar.
Interestingly, while West Africa appears to be the major center of diversity of cultivated forms of cowpea (Ng and Padulosi 1988) and was probably domesticated by farmers in this region (Ba et al. 2004), the center of diversity of wild Vigna species is southeastern Africa (Padulosi and Ng 1997). Some evidence that domestication occurred in northeastern Africa, based on studies of amplified fragment length polymorphism (AFLP) analysis, has also been presented (Coulibaly et al. 2002). The wild cowpea Vigna unguiculata ssp. unguiculata var. spontanea is the likely progenitor of cultivated cowpea (Pasquet 1999).

It is likely that the crop was first introduced to India during the Neolithic period, and therefore India appears to be a secondary center of genetic diversity (Pant et al. 1982). “Yardlong beans,” a unique cultivar group (Sesquipedalis) of cowpea that produces very long pods widely consumed in Asia as a fresh green or “snap” bean, apparently evolved in Asia and is rare in African landrace germplasm. Cowpea has been cultivated in southern Europe at least since the 8th century BC and perhaps since prehistoric times (Tosti and Negri 2002). Cowpea was introduced to the West Indies in the 16th century by the Spanish and was taken to the USA about 1700 (Pursglove 1968). Presumably it was introduced into South America at about the same time.

Web sites for the International Institute of Tropical Agriculture (www.IITA.org) and for the United States Agency of International Development (USAID)-funded Bean/Cowpea Collaborative Research Support Program (Bean/Cowpea CRSP) (www.isp.msu.edu/CRSP) are excellent references for general information about cowpea and current cowpea research.

### 3.1.2 Morphological and Phenological Characteristics

Cowpea is an herbaceous warm-season annual that is similar in appearance to common bean except that leaves are generally darker green, shinier, and less pubescent. Cowpeas also are generally more robust in appearance than common beans with better developed root systems and thicker stems and branches. Plant growth habit can be erect, semierect, prostrate (trailing), or climbing depending mostly on genotype, although photoperiod and growing conditions can also affect plant stature. Most cowpea accessions have indeterminate stem and branch apices. Early flowering cowpea genotypes can produce a crop of dry grain in 60 d, while longer season genotypes may require more than 150 d to mature depending on photoperiod. Flowers are borne on racemes on 15- to 40-mm peduncles that arise from the leaf axils. Two or three pods per peduncle are common, and often four or more pods are carried on a single peduncle if growing conditions are very favorable. The presence of these long peduncles is a distinguishing feature of cowpea, and this characteristic also facilitates hand harvesting.

Cultivated cowpea seed weighs between 8 and 32 mg and ranges from round to kidney shaped. Pods are cylindrical and may be curved or straight, with between 8 and 15 seeds per pod. The seed coat can be either smooth or wrinkled and of var...
ious colors including white, cream, green, buff, red, brown, and black (Fig. 1). Seed may also be speckled or patterned. Seeds of well-known cowpea types, such as “blackeye pea” and “pinkeye,” are white with a round irregular-shaped black or red pigmented area encircling the hilum, giving the seed the appearance of an eye.

Emergence is epigeal (similar to common bean and lupin), where the cotyledons emerge from the ground during germination. This type of emergence makes cowpea more susceptible to seedling injury, since the plant does not regenerate buds below the cotyledonary node. The open display of flowers in and above the canopy and the presence of extrafloral nectaries contribute to the attraction of insects. Cowpea primarily is self-pollinating, but outcrossing rates as high as 5% have been recorded and care needs to be taken to avoid outcrossing during the production of breeder and foundation seed, or unacceptable levels of “off-types” will result.

Cowpea is a short day plant, and many cowpea accessions exhibit photoperiod sensitivity with respect to floral bud initiation and development, while others are day neutral (Ehlers and Hall 1996; Craufurd et al. 1997). For some genotypes, the degree of sensitivity to photoperiod (extent of delay in flowering) is modified by temperature (Wein and Summerfield 1980; Ehlers and Hall 1996). In West Africa, selection for differing degrees of photosensitivity or differences in juvenility has occurred in different climatic zones such that pod ripening coincides with the end of the rainy season in a given locale, regardless of planting date, which is often variable due to the variable onset of wet seasons (Steele and Mehra 1980). This attribute allows pods to escape damage from excessive moisture and pathogens. Photoperiod sensitivity, when appropriately deployed in a breeding program, can be valuable to ensure crop maturity after wet seasons or before drought or cold weather limits crop growth. However, it may constrain the direct usefulness of an otherwise desirable cultivar to a small area of adaptation or even to a specific season within this restricted area.

Cultivated cowpeas have been divided into five cultivar groups based mainly on pod and seed characteristics (Pursglove 1968; Pasquet 1999). Cultivar group Unguiculata is the largest and includes most medium- and large-seeded African grain and forage-type cowpeas. Cultivar group Melanophthal-
(650,000 mt) and Brazil (490,000 mt) (Singh et al. 2002). Estimates of cowpea grain production in Latin America and East and southern Africa, regions of the world that produce significant quantities of common beans [Phaseolus vulgaris (L.)], may be underestimates because cowpea grain is not always distinguished from common bean grain during collection of production statistics. Trade in dry cowpea grain and cowpea hay are important to the economy of West Africa in particular, with substantial quantities of cowpea grain being traded at the local and regional level (Singh 2002; Langyintuo et al. 2003). The large urban centers of coastal West Africa are huge markets for cowpea produced further inland where climates are drier and favorable to production of high-quality grain. The United States produces about 80,000 mt, in several southern states (Alabama, Arkansas, Georgia, Louisiana, Missouri, Tennessee) and in Texas and California (Fery 2002).

A long-term drought in the Sahelian zone of West Africa has caused many farmers in this part of Africa to shift more of their production to cowpea because of its drought tolerance (Duivenboorden et al. 2002). As a result of this shift in production and the adoption of new varieties and improved production systems, worldwide cowpea production has gone from an annual average of about 1.2 million mt during the decade of the 1970s to ca. 3.6 million mt per annum (during the five-year period spanning 1998 to 2003) according to the FAO (http://faostat.fao.org/faostat). Rapidly growing populations with high per-capita cowpea consumption in the West and Central African regions have fueled demand for cowpea grain during this period, and the trend is expected to continue.

3.1.4 Nutritional Composition

The nutritional content of cowpea grain is important because it is eaten in quantity by millions of people who otherwise have diets lacking in protein, minerals, and vitamins. The nutritional profile of cowpea grain is similar to that of other pulses, with a relatively low fat content and a total protein content that is two to four times greater than cereal and tuber crops. Like other pulses, the protein in cowpea grain is rich in the amino acids lysine and tryptophan, compared to cereal grains. However, it is deficient in methionine and cystine when compared to animal proteins. In a study of 100 cowpea breeding lines in the IITA collection, seed protein content ranged from 23 to 32% of seed weight (Nielson et al. 1993). Similarly, protein content of 12 West African and US cultivars ranged from 22 to 29%, with most accessions having protein content values between 22 and 24% (Hall et al. 2003). These results suggest that sufficient genetic variation exists to develop new cowpea cultivars with protein content of at least 30%. Cowpea grain is also a rich source of minerals and vitamins (Hall et al. 2003) and it has one of the highest levels of any food of folic acid, a crucial B vitamin that helps prevent spinal tube defects in unborn children (http://www.cdc.gov/doc.do/id/0900f3ec8000d558).

Cowpea can be used at all stages of growth as a vegetable crop, and the leaves contain significant nutritional value (Ahenkora et al. 1998; Nielson et al. 1993). The tender green leaves are an important food source in Africa and are prepared as a pot herb, like spinach. Immature green pods are used in the same way as snap beans, often being mixed with cooked dry cowpeas or with other foods. Nearly mature “fresh-shelled” cowpea grains are boiled as a fresh vegetable or may be canned or frozen. Dry mature seeds are also suitable for boiling and canning. In many areas of the world, cowpea foliage is an important source of high-quality hay for livestock feed (Tarawali et al. 2002).

In developed countries, cowpea is expected to become increasingly important as consumers seek interesting and healthy “new” foods and rediscover “traditional” foods that are low in fat, high in fiber, and that have other health benefits. Fat contents of 100 advanced breeding lines from IITA showed a range in fat contents from 1.4 to 2.7% (Nielson et al. 1993), while fiber content is about 6% (Bressani 1985). Besides being low in fat and high in fiber, the protein in grain legumes like cowpea has been shown to reduce low-density lipoproteins that are implicated in heart disease (Phillips et al. 2003). In addition, because grain legume starch is digested more slowly than starch from cereals and tubers, their consumption produces fewer abrupt changes in blood glucose levels following consumption (Phillips et al. 2003). Innovative and appealing processed-food products using dry cowpea grain, such as cowpea-fortified baked goods, extruded snack foods, and weaning foods, have been developed (Phillips et al. 2003). Protein isolates from cowpea grains have good functional properties, including
solubility, emulsifying and foaming activities (Rangel et al. 2004), and could be a substitute for soy protein isolates for persons (especially infants) with soy protein allergies.

Varieties of cowpea with a “persistent-green” grain have been developed by breeding programs in the USA that are a versatile product for frozen vegetable applications (Ehlers et al. 2002a). Persistent-green cowpea grains are green colored when dry but when soaked in water for several hours closely resemble fresh-shelled cowpea that can be used in frozen vegetable products to add color and variety. Because persistent-green cowpea grain can be harvested and stored dry until rehydration and freezing, it is a quite convenient and economical frozen vegetable compared to other frozen vegetable crops that require highly coordinated harvesting and processing operations and expensive long-term frozen storage.

3.1.5 Classical Genetics and Breeding

Significant long-term genetic improvement efforts of cowpea have taken place within national laboratories and universities in several West African countries, India, Brazil, and the USA, as well as at the International Institute of Tropical Agriculture (IITA), based in Ibadan, Nigeria. The accomplishments of some of these programs have been described recently (Ehlers et al. 2002a; Singh et al. 2002; Hall et al. 2003).

Most cowpea breeders employ backcross, pedigree, or bulk breeding methods to handle segregating populations because cowpea is a self-pollinating species and varieties are pure lines. Grain yield and quality are primary breeding objectives of nearly all programs, but because losses to diseases and pests can be high, most programs are also concentrating on breeding for resistance to the major pests they face in their target environments. A comprehensive review of cowpea breeding that is still relevant was published in 1997 (Hall et al. 1997).

Sources of resistance to many viruses and fungal diseases have been identified, and screening techniques are well developed for many of these (Ehlers and Hall 1997). In general, good progress has been made using conventional techniques in breeding for resistance to the parasitic weeds *Striga gesneroides* (witchweed) and *Alectra vogelii*, root-knot nematodes, viruses, and fungal and bacterial diseases. Unfortunately, resistance to these pathogens and parasites is usually governed by single genes that are often only effective in a restricted region due to pathogen/parasite variability and may be overcome in a relatively short period of time. Marker-assisted selection (MAS) can be helpful in assembling more durable resistance by incorporating an array of resistance genes from other regions or defeated resistance genes, as discussed below.

Developing cultivars with sustainable resistance to insects is a key objective of breeding programs throughout the world for several reasons. Insect damage is the number one constraint for cowpea grain production in most cowpea-producing regions (Singh and van Emden 1979; Daoust et al. 1985). There is also concern that new and significantly more stringent restrictions on the use of some popular insecticides are forthcoming, and currently there is a lack of new alternative insect-control products registered for use on cowpea. The insecticides themselves, or the financial resources required to purchase them and the equipment required for proper application, are simply not available to the vast majority of farmers in Africa. In addition, there are concerns that the increased use of insecticides could cause major environmental and safety problems.

Breeding insect-resistant cowpeas would have a significant impact on food availability and nutritional status in many regions. Achieving this goal will not be easy, however, because of the number and diversity of pests that attack the crop and the nature of the pests. In many regions of the world, multiple pest resistance is needed to permit adequate grain production without the use of insecticides. This is because attacks by any one of the major pests can be devastating. For example, if cultivars were developed with a high level of resistance to flower thrips, capable of protecting their floral buds from damage, any resulting flowers and pods on these plants would likely be destroyed by pod bugs and pod borers. However, resistance to individual pests can reduce the number of sprays needed to obtain optimal yields and would generally increase yields without insect protection in regions where pest pressure is moderate, as in the case of the Sahel.

Screening methods have been developed for several major insect pests of cowpea (Ehlers and Hall 1997). However, despite the evaluation of hundreds to thousands of cowpea accessions, plants
with high levels of resistance to most notable significant pests have not been identified. The notable exceptions are resistance to cowpea aphid (*Aphis craccivora*) and leaf hoppers (*Empoasca* sp.). Recurrent selection is being used to combine low to moderate levels of resistance to flower thrips, pod bugs, and Maruca pod borer identified in several genotypes (Singh et al. 2002). However, progress in this area is being hampered by the low heritability of the traits based on the field screening methods used. Identification of molecular markers for insect resistance could facilitate transfer and pyramiding of the resistance genes.

### 3.1.6 Germplasm Collections

Cowpea germplasm is maintained in collections around the world with varying levels of accessibility and documentation. The largest collections are held by the IITA with more than 14,000 accessions. The collection can be accessed via an electronic database maintained through the CGIAR-SINGER system (http://singer.cgiar.org). The United States Department of Agriculture (USDA) maintains a collection with ca. 8,000 accessions. Access to this collection is through the USDA Germplasm Resources Information Network or GRIN system (www.ars-grin.gov). The University of California-Riverside has a collection with ca. 5000 accessions accessible on a Microsoft Access database. There is also a large collection of Mediterranean and African landraces (ca. 600 accessions) held at the Istituto di Genetica Vegetale at Bari, Italy (www.ba.cnr.it). Other centers maintaining seed of wild and cultivated cowpeas include the following: Agricultural University-Wageningen (Wageningen, The Netherlands), Botanical Research Institute (Pretoria, South Africa), Le Jardin Botanique National de Belgique (Meise, Belgium), International Plant Genetic Resources Institute (IPGRI) in Harare (Zimbabwe), Institut Français de la Recherché Scientifique pour le Développement en Coopération (ORSTOM; now IRD) in Montpellier (France), Empresa Brasileira de Pesquisa Agropecuária (EMBRAPA) in Goiana (Brazil), Zentralinstitut für Genetik und Kulturpflanzenforschung (GAT) in Gatersleben (Germany), and the National Bureau of Plant Genetic Resources in New Delhi (India).

In addition to the centers and facilities mentioned above, many national cowpea breeding programs in Africa (including programs in Botswana, Burkina Faso, Ghana, Kenya, Nigeria, and Senegal) also have substantial germplasm collections. The condition of some of these collections, which are important reserves of local diversity, could be improved with funding for germplasm maintenance and facility repair.

### 3.2 Molecular Phylogeny and Genome Organization

Cowpea (*Vigna unguiculata*) is one of several important cultivated species that constitute the genus *Vigna*. Other members include mungbean (*V. radiata*), adzuki bean (*V. angularis*), blackgram (*V. mungo*), and the bambara groundnut (*V. subteranea*). The genus was initially divided into several subgenera based upon morphological characteristics, extent of genetic hybridization/reproductive isolation, and geographic distribution of species (Marechal et al. 1978). The major groupings consist of the African subgenera *Vigna* and *Haydonia*, the Asian subgenus *Ceratotropis*, and the American subgenera *Sigmoidotropis* and *Lasiopron*. Under the scheme proposed by Marechal and his colleagues, cultivated cowpea was placed in the subgenus *Vigna*, whereas mungbean and blackgram were placed in the Asian subgenera.

The development and use of biochemical-based analytical techniques and molecular-marker technologies, such as analysis of restriction fragment length polymorphisms (RFLPs), random amplified polymorphic DNAs (RAPDs) (Williams et al. 1990), amplified fragment length polymorphisms (AFLPs) (Vos et al. 1995), minisatellites (Sonnante et al. 1994), and simple sequence repeats (SSRs) (Akkaya et al. 1992, 1995), have greatly facilitated the analysis of the structure of plant genomes and their evolution. This in turn has contributed significantly to our current understanding of cowpea genome organization. Using RFLP analysis, Fatokun et al. (1993a) analyzed 18 *Vigna* species including five of the subgenus *Ceratotropis* in order to determine the taxonomic relationship between the subgenus *Ceratotropis* and other subgenera. These investigators showed that a high level of genetic variation exists within the genus, with a remarkably higher amount of variation associated with *Vigna* species from Africa relative to those from Asia. Their data...
supported the taxonomic separation of the Asian and Africa genera as proposed by Marechal et al. (1978) and underscored the previously held viewpoint that Africa is the likely center of diversity for Vigna. In general, the placement of species and subspecies based upon molecular taxonomic procedures by Fatokun et al. (1993 a) substantiated prior classifications based on classical taxonomic criteria, such as morphological and reproductive traits.

Genetic variation in the subgenus Ceratotropis was subsequently reinvestigated by using RAPD analysis (Kaga et al. 1996 a). Examining the extent of polymorphism in 23 accessions of five species within the subgenus Ceratotropis, these investigators identified ca. 404 amplified fragments capable of providing comparative information. Based on the degree of polymorphism at these informative loci, these investigators were able to separate the accessions into two main groups differing by ca. 70% at the molecular level. Within each of the main groups, the accessions could be further divided into five subgroups whose composition were in complete agreement with their taxonomic species classifications.

Sonnante et al. (1996) examined isozyme variation between V. unguiculata and other species in the subgenus Vigna and showed that V. unguiculata was more closely related to V. vexillata, a member of the subgenus Plectotropis, than to any other species belonging to section Vigna. This is not surprising since V. vexillata is thought to be the intermediate species between African and Asian Vigna species. Vaillancourt and Weeden (1996) reached a similar conclusion about the relatedness of these species. Based on an analysis of variation in chloroplast DNA structure (Vaillancourt and Weeden 1992) and isozyme polymorphisms (Vaillancourt et al. 1993), it was suggested that V. vexillata and V. reticulata were the closest relatives of V. unguiculata. While the close relationship between V. unguiculata and V. vexillata proposed by Vaillancourt and Weeden (1996) is consistent with previous observations (Marechal et al. 1978), V. reticulata was placed in a different cluster based upon RFLP analysis (Fatokun et al. 1993 a).

Polymorphisms in 21 different enzyme systems were used by Pasquet (1999) to evaluate the relationship between 199 accessions of wild and cultivated cowpea differing in breeding system and growth characteristic (i.e., annual vs. perennial growth habit). Based on these allozyme data, perennial subspecies of cowpea (spp. unguiculata var. unguiculata) were shown to form a coherent group closely related to annual forms (spp. unguiculata var. spontanea). Among the ten subspecies studied, V. unguiculata var. spontanea and ssp. pubescens were the closest taxa to cultivated cowpea. Most recently, Ajibade et al. (2000) used inter simple sequence repeat (ISSR) DNA polymorphism analysis to study the genetic relationships among 18 Vigna species. They showed that closely related species within each subgenus clustered together [e.g., V. umbellata and V. angularis (subgenus Ceratotropis), V. adenantha and V. caracalla (subgenus Sigmoidotropis), and V. luteola and V. ambacensis (subgenus Vigna)], Cultivated cowpea grouped closely with the wild subspecies of V. unguiculata, and the entire species was separated from its most closely allied species V. triphilla and V. reticulata. ISSR polymorphism analysis split Vigna into groupings that differed in their composition from previous classifications. For example, the subgenus Vigna was split into three lineages, with V. unguiculata/reticulata/friesorum forming one group, V. luteola/ambacensis forming a second, and V. subterranea being far from the other two. Ceratotropis split into two sections, with three species (V. radiata, V. mungo, and V. aconitifolia) in one section and two species (V. angularis and V. umbellata) in a second section. While such groupings had been suggested previously (Marechal et al. 1978; Fatokun et al. 1993 a; Vaillancourt and Weeden 1996), it should be noted that ISSR analysis was not as effective at resolving genetic distance relationships at the subgeneric level as it was at resolving relationships at the species level and below. Therefore, the authors note that their conclusions regarding subgeneric classifications should be taken with some caution. Thus, there is still considerable need to develop appropriate strategies and molecular techniques to resolve exact taxonomic relationships among members of this important genus.

Repetitive DNA sequences have been shown to represent a substantial fraction of the nuclear genome of all higher plant species and to account for much of the variation in genomic DNA content observed among species (Flavell et al. 1994). Many of the repeat sequences found in plant genomes appear to have originated through the activity of transposable elements (transposons) that either move by first forming an RNA intermediate [i.e., retrotransposons (Boeke et al. 1985)] or by direct
DNA transposition intermediates [i.e., transposons (Federoff 1989)]. To gain insight into the genomic organization and evolution of species within Vigna, Galasso et al. (1997) examined the genomic organization and distribution of Ty1-copia type retrotransposons in seven different species and subspecies of Vigna and several related leguminous plants. Gel blot analysis of genomic DNA from V. unguiculata, V. luteola, V. oblongifolia, V. ambacensis, and V. vexillata probed with radioactively labeled probes to the reverse transcriptase gene amplified from V. unguiculata subsp. unguiculata, V. unguiculata subsp. dekindtania, V. luteola, and V. vexillata showed variable hybridization patterns and intensities generally correlating with their previously defined taxonomic position. Fluorescence in situ hybridization analysis of the distribution of the Ty1-copia type sequences showed that these elements represented a major fraction of the cowpea genome and were dispersed relatively uniformly over all of the chromosomes. Little or no hybridization was found associated with centromeric, subtelomeric, and nucleolar organizing regions of the chromosomes, indicating that these portions of the genome may not be suitable sites for transposition. Comparisons of retrotransposon structural similarity between Vigna and other genera of legumes generally supported the subdivision of the tribes Phaseoleae and Vicieae, with greater homology being seen between members of the Cicereae and Phaseoleae than Cicer species and those from the Vicieae (Galasso et al. 1997).

Ba et al. (2004) used RAPD analysis to characterize genetic variation in domesticated cowpea and its wild progenitor, as well as their relationships. They included 26 domesticated accessions representing the five cultivar groups and 30 wild/weedy accessions, including accessions from West, East, and southern Africa. A total of 28 primers generated 202 RAPD bands. One hundred and eight bands were polymorphic among the domesticated compared to 181 among wild/weedy cowpea accessions. Wild accessions were more diverse in East Africa, which is the likely area of origin of V. unguiculata var. spontanea. V. unguiculata var. spontanea is thought to have spread westward and southward, with a loss of variability that is counterbalanced in southern Africa by introgressions with local perennial subspecies. Although the variability of domesticated cowpea was the highest ever recorded, cultivar groups were poorly resolved, and several results obtained with isozyme data were not confirmed here. However, primitive cultivars were more diverse than evolved cultivars, suggesting two consecutive bottlenecks within domesticated cowpea evolution. As with isozymes and AFLP markers, the RAPD data confirmed the single domestication hypothesis, the gap between wild and domesticated cowpea, and the widespread introgression phenomena between wild and domesticated cowpea. Therefore, these RAPD markers, which could have indicated a narrow center of origin, demonstrated that there is a widely distributed cowpea crop-weed complex all over Africa, as do some isozyme (Pasquet 1999), cpDNA (Pasquet, unpubl. obs.), and AFLP (Coulibaly et al. 2002) markers. Taking into account that there appears to have been a single domestication event, the genetic similarity of some of these wild accessions to the domesticated group would be the result of postdomestication gene flow between wild and domesticated forms due to their sympatric distribution.

3.3 Genetic Maps

The first attempt to generate a comprehensive linkage map for cowpea was by Fatokun et al. (1993b), who used polymorphisms detected by 87 random genomic DNA fragments, 5 cDNAs, and RAPDs to generate a map consisting of ten linkage groups (LGs) spanning 680 cM. Improvement on this initial map was made by Menéndez et al. (1997), who were able to develop a linkage map for V. unguiculata consisting of 181 loci falling into 12 LGs. The resolution of the map was to ca. 6.4 cM between loci. Similarly, Menancio-Hautea et al. (1993a,b) used RFLP analysis to construct a genome map of mungbean (V. radiata). The map consisted of 172 markers placed into 11 linkage groups and provided 1570 cM coverage with an average distance of 9 cM between loci. It is worth noting that even at these early stages of genome comparison, significant colinearity was recognized to exist between the cowpea and mungbean genomes (Menancio-Hautea et al. 1993b). A total of 132 markers (108 RAPDs, 19 RFLPs, and 5 morphological markers) have been mapped in azuki bean using an interspecific population generated from a cross of V. angularis×V. nakashimae (Kaga et al. 1996b). Comparison of the linkage map of azuki bean with those of
mungbean and cowpea using 20 RFLP markers indicated that, as might be expected, the three genomes share many linkage blocks in common.

Li et al. (1999) used DNA amplification fingerprinting (DAF) and AFLP analysis to identify additional molecular markers segregating in the F₈ recombinant inbred population derived from a cross between IT84S-2049 and 524B (Menéndez et al. 1997). These researchers screened 400 randomly generated DAF decamers and 128 AFLP primer combinations and were able to place 57 DAF and 90 AFLP markers to the existing cowpea genetic map. In addition, a map of the wild relative of cowpea _V. vexillata_ has also been generated (Ogundiwin et al. 2000).

Building on the earlier version of the map developed by Menéndez et al. (1997), Ouédraogo et al. (2002 a) published what is the most current and complete map of _V. unguiculata_ (http://pubs.nrc-cnrc.gc.ca/cgi-bin/rp/rp2_absf/gen_g01-102_45_nsf_gen1-02). This map was established in the recombinant inbred population IT84S-2049×524B developed by Tony Hall at the University of California-Riverside. IT84S-2049 is an advanced breeding line that was developed at IITA in Nigeria for multiple disease and pest resistance and has resistance to several races of blackeye cowpea mosaic virus (B1CMV) and to virulent root-knot nematodes in California (Menéndez et al. 1997). Line 524B is a

![Fig. 2. Current genetic linkage map of cowpea. Shown are the 11 LGs comprising the genetic linkage map of cowpea as published by Ouédraogo et al. (2002 a). Above each LG is the length in centimorgans (cM) and number of markers comprising the LG. Distances (in cM) between adjacent markers are indicated to the left. Markers associated with LGs determined by Menéndez et al. (1997) are color coded in order to show their distribution on the current map. Markers linked to _Striga_ resistance are given in red and marked by an asterisk. Loci for biological resistance/tolerance loci and resistance gene analogs (RGAs) are boxed in red. Markers that could not be placed with a LOD 3 score are listed under the LG they have the greatest affinity to. Unlinked markers are AAC-CTA-3, Parthcnap, AAC-CTT-10, ACA-CTA-7, ACG-CAA-10, AGG-CAT-1, R25, AAG-CTT-9.](image-url)
blackeye cowpea that shows resistance to Fusarium wilt and was derived from a cross between cultivars CB5 and CB3, which encompasses the genetic variability that was available in cowpea cultivars in California (Kelly et al. 2003).

The current map of cowpea consists of 11 LGs spanning a total of 2670 cM, with an average distance of ca. 6 cM between markers (Fig. 2). It includes 242 AFLP and 18 disease or pest-resistance-related markers (Ouédraogo et al. 2002a), plus 133 RAPD, 39 RFLP, and 25 AFLP markers from the original map of Menéndez et al. (1997), for a total of 441 markers, of which 432 were assigned to a LG. Among these marker loci, genes for a number of biochemical and phenotypic traits have been located on this map. These include C, a general color factor, and P, for purple pod color, on LG4 (according to the numbering system of Ouédraogo et al. (2002a), LGs on the bean and cowpea maps have been numbered independently; thus, LGs with the same number on the two maps probably refer to nonsyntenic groups), a 35-kDa dehydrin protein, implicated in chilling tolerance during emergence (LG2; Ismail et al. 1999), and markers for resistance to *Striga gesnerioides* races 1 and 3 (LG1 and LG6), cowpea mosaic virus (CPMV) and cowpea severe mosaic virus (CPSMV) (two distinct loci on LG2), southern bean mosaic virus (SBMV) (LG6), Fusarium wilt (LG3), and root-knot nematodes (gene *Rk*; *NemR* on LG1) (Ouédraogo et al. 2002a). Candidate resistance genes (termed resistance gene analogs or RGAs) were also placed by RFLP analysis in various locations on the integrated cowpea map, including LG2, LG3, LG5, and LG9. Nevertheless, none of the RGA loci cosegregated with disease resistance phenotypes, suggesting that additional mapping for both RGAs and phenotypic disease resistance traits should be pur-
sued in cowpea. Table 2 lists the various agronomic and disease resistance trait loci that have now been placed on the cowpea genetic map.

3.4 Transgenic Cowpea

Until recently cowpea remained one of the last major grain legume species for which an efficient genetic transformation/regeneration system had not been developed (Van Le et al. 2002; Avenido et al. 2004; Popelka et al. 2004), despite substantial efforts for more than ten years by several groups of researchers (Machuka 2002; Machuka et al. 2002). Ikea et al. (2003) reported the successful genetic transformation of cowpea using the particle-gun bombardment of shoot meristems. They were able to isolate several plants in the T3 generation that showed strong expression of the transgene “bar” that confers resistance to the herbicide Basta, but these studies were inconclusive. An efficient and stable cowpea transformation/regeneration system has been developed recently (Popelka et al. 2006), so that transgenic cowpea is now a reality.

Transgenic approaches should be undertaken to develop varieties of cowpeas with strong resistance to insect pests. Insect-resistant cowpeas would dramatically increase cowpea productivity in many developing countries and reduce costs, safety hazards, and environmental risks in virtually all cowpea-producing countries. Traditional plant breeding has made only limited progress in breeding for resistance to the major insect pests of cowpea and “new genes” are apparently needed to protect cowpea. The development and successful deployment of transgenic cultivars with genes conferring resistance to insects will be a major achievement.

The best current options for developing insect resistant cowpeas is to employ Bt technology against the Maruca pod borer (Maruca testulalis) and the alpha-amylase inhibitor gene from common bean that provides effective control of cowpea weevil (Callosobruchus maculatus) (T.J. Higgins, personal communication, 2004). The soybean cysteine protease inhibitor soyacystatin N (scN) and alpha-amylase inhibitor (alphaAI) from wheat have synergistic effects against the cowpea weevil in artificial seed systems and are also potential genes that could be used to develop cowpea cultivars with resistance to this pest (Amirhusin et al. 2004).

Several different Cry1Ab, Cry1C, and CryIIA proteins that are produced by different forms of Bt genes are toxic to Maruca pod borer (L.E.N. Jackai, unpbl. data) and using these Bt genes in cowpea is considered a high priority for transformation (L.L. Murdock, personal communication, 2004). Genes producing plant lectins and plant proteinaceous inhibitors (PIs) of insect proteinases (serine, cysteine, aspartic, and metalloproteinases) are also considered potential candidates for gene transfer for resistance to Maruca pod borer (Machuka 2002).

3.5 Marker-Assisted Cowpea Breeding

Marker-assisted selection (MAS) is a tool to more efficiently assemble alleles of interest into an improved cultivar (Charcosset and Moreau 2004) and thereby increase the overall efficiency and effectiveness of crop improvement programs. Prior to applying MAS a realistic assessment of the cost-benefit ratio in comparison with phenotypic assays performed in the field, greenhouse, or laboratory needs to be conducted (Dekkers and Hospital 2002; Dreher et al. 2003). The expected economic return of MAS compared with phenotypic assessment decreases with the cost of genotyping (Moreau et al. 2000). In general, traits that are difficult or expensive to measure using phenotypic assays are good candidates for MAS. In some cases, MAS can allow smaller populations to be used, reduce the number of generations needed to reach a goal, or increase the accuracy of evaluations (Sharma et al. 2002). MAS offers the only practical method to combine multiple resistance genes into one cultivar when the genes mask the expression of one another, yet when together provide more durable resistance (Kelly et al. 2003). Other advantages of MAS are that a single technology can handle selection of diverse types of traits (e.g., pest resistance and grain quality parameters) and that cultivars developed through the use of MAS are not subjected to negative stereotyping as transgenic cultivars (Dubcovsky 2004). Also, selection of traits conferring resistance to quarantined pests can be conducted using MAS, eliminating the need for transfer of quarantined pests and assessment of resistance in expensive quarantine facilities.

MAS has yet to be implemented in cowpea, but some of the groundwork has been laid for its de-
### Table 1. Races of *Striga gesnerioides* parasitic on cowpea in West Africa and differential responses of host cultivars and breeding lines

<table>
<thead>
<tr>
<th>Cowpea Cultivar</th>
<th>Race 1 (Burkina Faso, Mali)</th>
<th>Race 2 (Mali)</th>
<th>Race 3 (Niger, Nigeria)</th>
<th>Race 4 (Benin)</th>
<th>Race 5 (Cameroon, West Africa)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IT93K-693-2</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>B301</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Suvita 2 (Gorom)</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
<td>S</td>
</tr>
<tr>
<td>IT81D-994</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
<td>S</td>
</tr>
<tr>
<td>IT82D-849</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Tvu 14676</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>S</td>
<td>R</td>
</tr>
<tr>
<td>Tvx 3236</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
</tr>
<tr>
<td>IT84S-2246</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
</tr>
<tr>
<td>IT84S-2049</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
<td>S</td>
</tr>
</tbody>
</table>

*Adapted from Lane et al. (1996, 1997)*

### Table 2. Agronomic, growth habit, and disease and pest resistance trait loci currently placed on the cowpea genetic map of Ouédraogo et al. (2002) and other traits mapped to probable nonanalogous linkage groups

<table>
<thead>
<tr>
<th>Trait</th>
<th>Locus designation</th>
<th>Linkage group/reference map</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pod pigmentation</td>
<td>P</td>
<td>LG1; (LG1-Menéndez et al. 1997)</td>
</tr>
<tr>
<td>Resistance to <em>Striga gesnerioides</em>-Race 1</td>
<td>Rsg2-1</td>
<td>LG1</td>
</tr>
<tr>
<td>Resistance to <em>Striga gesnerioides</em>-Race 3</td>
<td>Rsg4-3, Rsg1-1</td>
<td>LG1</td>
</tr>
<tr>
<td>Root-knot nematode (<em>Meloidogyne incognita</em>) resistance</td>
<td>Rk</td>
<td>LG1</td>
</tr>
<tr>
<td>Nodes to 1st Flower (D1301a)</td>
<td>NTF</td>
<td>LG2; (LG2-Menéndez et al. 1997)</td>
</tr>
<tr>
<td>Dehydrin protein</td>
<td>Dhy</td>
<td>LG2; (LG7-Menéndez et al. 1997)</td>
</tr>
<tr>
<td>Resistance to cowpea mosaic virus</td>
<td>CPMV</td>
<td>LG2</td>
</tr>
<tr>
<td>Resistance gene analog (pathogen unknown)</td>
<td>RGA-438</td>
<td>LG2</td>
</tr>
<tr>
<td>Resistance gene analog (pathogen unknown)</td>
<td>RGA-468</td>
<td>LG2</td>
</tr>
<tr>
<td>Resistance gene analog (pathogen unknown)</td>
<td>RGA-490</td>
<td>LG2</td>
</tr>
<tr>
<td>Resistance to <em>Fusarium oxysporum</em></td>
<td>FusR</td>
<td>LG3</td>
</tr>
<tr>
<td>Cowpea severe mosaic virus resistance</td>
<td>CPSMV (ims)</td>
<td>LG3</td>
</tr>
<tr>
<td>Cowpea mosaic virus resistance</td>
<td>CPMV</td>
<td>LG3</td>
</tr>
<tr>
<td>Resistance gene analog (pathogen unknown)</td>
<td>RLRR3-4B</td>
<td>LG3</td>
</tr>
<tr>
<td>General flower color factor</td>
<td>C</td>
<td>LG4; (LG1-Menéndez et al. 1997)</td>
</tr>
<tr>
<td>Seed weight (OB6a)</td>
<td>SW</td>
<td>LG5; (LG5-Menéndez et al. 1997)</td>
</tr>
<tr>
<td>Resistance gene analog (pathogen unknown)</td>
<td>RGA-434</td>
<td>LG5</td>
</tr>
<tr>
<td>Resistance to southern bean mosaic virus</td>
<td>SBMV (sbc-1,2)</td>
<td>LG6</td>
</tr>
<tr>
<td>Resistance to <em>Striga gesnerioides</em>-Race 1</td>
<td>Rsg3-1, Rsg-994</td>
<td>LG6</td>
</tr>
<tr>
<td>Resistance to blackeye cowpea mosaic virus</td>
<td>BICMV</td>
<td>LG8</td>
</tr>
<tr>
<td>Resistance gene analogs (pathogen unknown)</td>
<td>RLRR3-4T</td>
<td>LG9</td>
</tr>
</tbody>
</table>

**Traits mapped in other populations with probably nonanalogous linkage groups to map of Ouédraogo et al. 2002**

- Resistance to cowpea aphid (*Aphid craccivora*) *Rac1* (LG1-Menéndez et al. 1997)
- 50% Flowering *50%FL* (LG7-Fatokun et al. 1993)
- Seed weight *SW* (LG7-Fatokun et al. 1993)
- Plant height *HT* (LG7-Fatokun et al. 1993)
- Pod number per plant *PodN* (LG9-Fatokun et al. 1993)

*Adapted from genetic maps and data of Ouédraogo et al. (2002) and Menéndez et al. (1997) that used the same genetic population. There is insufficient marker data to integrate LGs of the maps of Fatokun et al. (1993) and data from Myers et al. (1996) with the map of Ouédraogo et al. (2002)*
velopment (Kelly et al. 2003). A genetic map has been constructed (Ouédraogo et al. 2002 a) and loci controlling important pest and disease resistance genes and agronomic traits have been placed on the map (Section 3). In addition, markers closely linked to some resistance factors whose function has yet to be fully defined have been identified (Gowda et al. 2002). Many of these traits are controlled by single genes and therefore are potentially good candidates for MAS. Currently, no quantitative trait loci (QTLs) with linked markers have been identified for use in selecting for more complex traits such as grain yield.

At least five distinct races of the parasitic weed Striga gesnerioides have been identified within the cowpea-growing regions of West Africa (Lane et al. 1996, 1997) based on the differential response of various cowpea genotypes (cultivars and breeding lines) carrying specific resistance genes (Table 1). Similarly, “resistance-breaking” strains of the root-knot nematode Meloidogyne incognita, cowpea aphid (Aphis craccivora), cowpea weevil (Callosobruchis maculatus), and Fusarium wilt (Fusarium oxysporum f. sp. tracheiphilum) have been recognized in specific cowpea production areas. Markers for genes conferring resistance to the various strains of these pests would allow efficient development of varieties with resistance that is more broadly effective using MAS.

Currently, useful markers in cowpea for implementation of MAS are only available for some of the Striga resistance genes, and these are the first candidates for broad application in cowpea breeding programs (Fig. 3). Ouédraogo et al. (2001, 2002 b) found three AFLP markers linked to Rsg2-1, a gene that confers resistance to Striga Race 1.
(SG1) present in Burkina Faso, and six AFLP markers linked to gene \( Rsg4-3 \), a gene that provides resistance to Striga Race 3 (SG3) from Nigeria. Two of the AFLP markers were associated with both \( Rsg2-1 \) and \( Rsg4-3 \). Ouédraogo et al. (2002a) were able to convert one of these markers to a SCAR (sequence-characterized amplified region) that has proven to be an effective and remarkably reliable marker for resistance to Striga SG1 and SG3 conferred by \( Rsg2-1 \) and \( Rsg4-3 \). This SCAR marker, designated 61R (E-ACT/M-CAA), detects a single polymorphic band linked to SG1 and SG3 resistance in the resistant cultivars B301, IT82D-849, and Tvu 14676 and is being tested for use in breeding trials. Recently, two AFLP markers were identified that are closely linked to \( Rsg1-1 \), a gene that also confers resistance to SG3 in Nigeria (Boukar et al. 2004). One of the AFLP markers, designated E-ACT/M-CAC\(_{15} \) and determined to be 4.8 cm from \( Rsg1-1 \), was converted to a SCAR marker for ease of use in breeding programs (Boukar et al. 2004).

Chida et al. (2000) obtained three RAPD markers flanking a gene conferring resistance to cucumber mosaic cucumovirus (\( Cry \) gene) that could be useful in MAS. Linkage analyses of these molecular markers showed that genetic distances of the markers CRGA5, D13/E14-350, WA3-850, and OPE3-500 to the \( Cry \) locus were 0.7, 5.2, 11.5, and 24.5 cm, respectively.

Insect resistance is a good candidate for MAS in cowpea because assessments of host plant resistance to insects are often difficult to conduct in the field or greenhouse. Most insect resistance factors in cowpea do not provide immunity to the pest and often have low heritability under field conditions. Field screenings that rely on natural insect infestations are subject to natural fluctuations in pest pressure. When such variability is combined with incomplete resistance, field screens can lead to misclassification and selection of lines lacking the strongest resistance. For example, this has been the case with screening cowpea breeding lines and accessions for resistance to aphids, Lygus bug (\( Lygus hesperus \)), and pod-sucking bugs (such as \( Nezara viridula \), Clavigralla tomentosicollis, Riptortus dentipes). In addition, colonies of insects may be difficult to rear without specialized facilities and trained entomologists to monitor the growth and uses. Such resources may not be available to cowpea breeding programs.

Resistance to the pod bug \( Clavigralla tomentosicollis \) has been identified in the wild cowpea (ssp. \( dekindtiana \)) germplasm line TVNu 151 (Koona et al. 2002). MAS could be used to introgress resistance factors from such wild cowpea into cultivated forms using a rapid backcrossing approach, based on simultaneous selection for the resistance genes (markers) and against markers associated with unwanted wild germplasm characteristics such as small seed size and seed shattering. Such an approach would require a substantial increase in the number of markers available in cowpea and the development of high-throughput markers such as SSR and SNP markers.

Implementation of MAS for resistance to root-knot nematodes (\( Meloidogyne \) spp.) in cowpea may be useful in some breeding programs. The genetic resistance to populations of these pests in the USA is well characterized (Roberts et al. 1996, 1997; Ehlers et al. 2002). At present, laboratory and field bioassays to assess resistance to root-knot nematodes in cowpea are effective and reasonably cost effective (Roberts et al. 1997; Ehlers et al. 2002b). However, \( Meloidogyne \) populations are highly variable in response to resistance genes and resistance phenotyping is difficult for breeders to undertake without the close collaboration of nematologists for maintenance of cultures, preparation of inocula, and screening protocols. Current work to develop PCR-based markers tightly linked to the \( Rk \) locus that has multiple resistance specificities to \( Meloidogyne \) populations should lead to more effective breeding for nematode resistance in cowpea (Roberts et al. 1996, 1997; Ehlers et al. 2002).

The application of MAS for improvement of agronomic traits controlled by QTLs is much more difficult. Expression of many quantitative traits (such as yield) reflects the influence of many (often interacting) developmental processes over a substantial period of time such as a full growing season. As noted earlier there has been little progress toward the development of markers linked to QTLs useful in the selection of agronomic characteristics in cowpea. Progress has been faster in other related legumes (such as \( Phaseolus \)), and it is possible that some of this information may be leveraged since there is a significant degree of synteny between the bean and cowpea genomes (Kelly et al. 2003).
3.6 Future Prospects for Crop Improvement

One of the major goals of cowpea programs is to combine resistances to numerous pests and diseases and other desirable traits such as those governing maturity, photoperiod sensitivity, plant type, and seed quality. Parental lines with many desirable traits, such as resistance to cowpea weevil, cowpea aphid, and the parasitic weeds *Alectra vogeli* and *Striga gesnerioides*, along with resistances to bacterial blight, CABMV, and other pathogens, exist in different advanced breeding lines developed by cowpea breeding programs around the world. One of the biggest current challenges is to incorporate all of these desirable traits into individual cultivars with acceptable grain quality and adaptation to targeted farming systems and environments. MAS could be an important tool to facilitate this effort.

Cowpea remains to a large extent an under-exploited crop where relatively large genetic gains can be made with only modest investments in both applied plant breeding and molecular genetics. Cowpea is grown mostly by poor farmers in developing countries and, as a consequence, has received relatively little attention from a research standpoint. Indeed, cowpea has been identified as an “orphan crop” that is recommended for increased public/donor support for biotechnology research (Naylor et al. 2004). A major challenge will be to apply the knowledge being gained from basic genomics research on “model species” such as Arabidopsis, rice (*Oryza sativa*), and *Medicago trunculata* to cowpea.

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References


Boeke JD, Garfinkel DJ, Styles CA, Fink GR (1985) Ty elements transpose through an RNA intermediate. Cell 40:491–500


Ehlers JD, Matthews WC, Hall AE, Roberts PA (2002b) Breeding and evaluation of cowpeas with high levels of broad-based resistance to root-knot nematodes. In: Fatokun CA, Tarawali SA, Singh BB, Kormawa PM, Tamo M (eds) Challenges and Opportunities for Enhancing Sustainable Cowpea Production. International Institute of Tropical Agriculture, Ibadan, Nigeria, pp 41–51


Ismail AM, Hall AE, Close TJ (1999) Allelic variation of a dehydrin gene cosegregates with chilling tolerance dur-


Menancio-Hautea D, Fatokun CA, Kumar L, Danesh D, Young ND (1993b) Comparative genome analysis of mung bean (Vigna radiata L. Wilczek) and cowpea (V. unguiculata L. Walpers) using RFLP mapping data. Theor Appl Genet 86:797–810

Menéndez CM, Hall AE, Gepts P (1997) A genetic linkage map of cowpea (Vigna unguiculata) developed from a cross between two inbred, domesticated lines. Theor Appl Genet 95:1210–1217


Ouedraogo JT, Tignegre J-B, Timko MP, Belzile FJ (2002b) AFLP markers linked to resistance against Striga gesnerioides race 1 in cowpea (Vigna unguiculata), Genome 45:787–793


Pant KC, Chandel KPS, Joshi BS (1982) Analysis of diversity in Indian cowpea genetic resources. SABRO J 14:103–111


Agricultural Sciences (JIRCAS). Sayce, Devon, UK, pp 313–325


