

## Registration of a Cowpea [*Vigna unguiculata* (L.) Walp.] Multiparent Advanced Generation Intercross (MAGIC) Population

Bao-Lam Huynh,\* Jeffrey D. Ehlers, Timothy J. Close, and Philip A. Roberts\*

### Abstract

The cowpea [*Vigna unguiculata* (L.) Walp] multiparent advanced generation intercross (MAGIC) population (Reg. No. MP-1, NSL 526803 MAP) consists of 305 recombinant inbred lines (RILs). The population was constructed from eight elite parents that are genetically diverse and carry combinations of abiotic and biotic stress resistance traits relevant to cowpea improvement in sub-Saharan Africa. The eight parents were intermated using structured crosses to ensure the population would have balanced representation from each of the founder parents, followed by seven rounds of single-seed descent. The resulting F<sub>8</sub> RILs each carry a mosaic of genome blocks contributed from all founders as revealed by high-resolution single nucleotide polymorphism genotyping. The RILs are diverse in agronomic traits, including flowering time, growth habit, maturity, yield potential, and seed characteristics across environments. Due to its broad genetic base, this cowpea MAGIC population will simplify and facilitate community-wide discovery of marker-trait associations and fine mapping for gene discovery.

COWPEA [*Vigna unguiculata* (L.) Walp] is native to Africa, where it provides a primary source of proteins that complements cereals in the diet (Ehlers and Hall, 1997; Kudre et al., 2013). However, in the Sudano-Sahel region of West Africa, typical smallholder farm cowpea yields are only 10 to 20% of known yield potential. Biotic stresses caused by insect pests and diseases caused by pathogens, parasitic weeds, and nematodes, as well as abiotic stresses from heat, drought, and low-fertility soils are primary constraints to cowpea grain production. Many of these problems also affect cowpea production in parts of southern Europe, Asia, Australia, Latin America, and the southern United States (Ehlers and Hall, 1997; Huynh et al., 2013). Multiparent advanced generation intercross (MAGIC) populations (Cavanagh et al., 2008) can help expedite the discovery of markers and genes and thus reduce the cost of this process and the cost of development of improved “stacked” cultivars. Such populations are developed by intermating multiple carefully chosen parents for several cycles followed by single-seed descent, resulting in recombinant inbred lines (RILs) each carrying a mosaic of genome blocks contributed by all founders. Development of MAGIC populations has been reported in a few other crops such as wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and chickpea (*Cicer arietinum* L.) due to their great potential for improving breeding populations and for dissecting genetic and genomic structure (Huang et al., 2015).

As part of the Tropical Legumes I Project (Generation Challenge Program of the Consultative Group for International Agricultural Research [CGIAR]), we initiated an eight-parent MAGIC population (Reg. No. MP-1, NSL 526803 MAP) for cowpea using founder parents that are highly diverse and that carry many key traits relevant to sub-Saharan Africa and other production regions. The population was then, in the ensuing years, developed, characterized, and genotyped with the 51,128-single nucleotide polymorphism (SNP) Illumina iSelect

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5585 Guilford Rd., Madison, WI 53711 USA

\*Corresponding author (baolam.huynh@ucr.edu;

philip.roberts@ucr.edu)

B.-L. Huynh and P.A. Roberts, Dep. of Nematology, Univ. of California, Riverside, CA 92521; J.D. Ehlers and T.J. Close, Dep. of Botany and Plant Sciences, Univ. of California, Riverside, CA 92521; J.D. Ehlers, current address: Bill and Melinda Gates Foundation, Seattle, WA 98102.

**Abbreviations:** CVARS, Coachella Valley Agricultural Research Station; IITA, International Institute of Tropical Agriculture; MAGIC, multiparent advanced generation intercross; RIL, recombinant inbred line; QTL, quantitative trait locus; SNP, single nucleotide polymorphism; UCR, University of California–Riverside.

BeadArray (Muñoz-Amatriaín et al., 2017) at University of California–Riverside (UCR), and seeds from  $F_8$  genotyped plants were increased for distribution.

## Methods

### Parentage

SuVita 2, also known as Gorom, a local landrace in Burkina Faso, is resistant to *Striga gesnerioides* (Willd.) Vatke (Ouedraogo et al., 2002) and *Macrophomina phaseolina* (Tassi) Goid (Muchero et al., 2011). ‘CB27’, a California blackeye cultivar bred by UCR (Ehlers et al., 2000), is heat tolerant (Lucas et al., 2013a) and highly resistant to root-knot nematodes (*Meloidogyne* spp.) (Huynh et al., 2016) and Fusarium wilt, caused by *Fusarium oxysporum* f. sp. *tracheiphilum* (E.F. Smith) Snyder & Hans. (Pottorff et al., 2012, 2014). IT93K-503-1, a breeding line from the International Institute of Tropical Agriculture (IITA) breeding nursery in Nigeria, is drought tolerant (Muchero et al., 2009), and resistant to root-knot nematodes (Huynh et al., 2016), *M. phaseolina* (Muchero et al., 2011), and Fusarium wilt (Pottorff et al., 2014). The other five parents (IT89KD-288, IT84S-2049, IT82E-18, IT00K-1263, and IT84S-2246) are also breeding lines from the IITA breeding program in Nigeria; they are known to carry different combinations of key traits including grain quality and resistance to root-knot nematodes, aphids (*Aphis craccivora* Koch), Striga, Fusarium wilt, viruses, and bacterial blight caused by *Xanthomonas axonopodis* pv. *vignicola* (Burkh.) Vauterin et al. (Table 1).

### Population Development and Evaluation

In spring 2010, initial crosses were made between four pairs of founder parents (IT89KD-288 × IT84S-2049, CB27 × IT82E-18, SuVita 2 × IT00K-1263, and IT84S-2246 × IT93K-503-1, designated as A × B, C × D, E × F, and G × H, respectively) to produce two-way  $F_1$ s. We confirmed the true two-way  $F_1$  plants by genotyping their  $F_2$  seed with 89 parent-unique SNPs using the kompetitive allele-specific polymerase chain reaction (KASP) assay (LGC Genomics Ltd.) (Semagn et al., 2014). In spring 2011, reciprocal

four-way crosses were then made between two pairs of the two-way  $F_1$ s to produce four-way  $F_1$ s. In fall 2011, 330 pair crosses were made between 330 four-way  $F_1$  plants of the pedigrees ABCD or CDAB and 330 four-way  $F_1$  plants of the other pedigrees EFGH or GHEF to produce 330 eight-way  $F_1$ s. Single seed descent without selection was then applied for each unique eight-way  $F_1$  until the  $F_8$  generation. A total of 365  $F_8$  RILs were generated from the 330 unique eight-way crosses. Among these, 29 crosses produced two or more  $F_8$  RILs, which are sister lines separated at earlier generations. These lines were maintained as temporary backup to help ensure the population size.

The eight parents and 365  $F_8$  single plants were genotyped with 51,128 SNPs using the Illumina iSelect BeadArray (Muñoz-Amatriaín et al., 2017). There were 36,346 SNPs that were polymorphic between the eight parents (68.26%). Among these, 11,848 SNPs were parent-unique, each of which can distinguish one parent from the other seven parents. Parent-unique SNPs indicated that 15 RILs lacked male-parent alleles at the two-way/four-way intercrosses and may have resulted from selfing during artificial pollination. Three RILs were found to carry nonparental alleles in that they were heterozygous at SNP loci that were monomorphic between the eight parents. Except for five RILs with more than 10% of heterozygosity, the rest of the population had a low level of heterozygosity, ranging from 0 to 3.33%. There were eight RILs, each showing very similar SNP genotypes (>99%) to another RIL, that were considered to be duplicates. After excluding lines with duplicates, selfing errors, nonparental alleles, and excess heterozygosity, a core set of 305 MAGIC RILs derived from 305 unique eight-way crosses was selected for registration (Supplement 1). For each RIL, seed from the genotyped  $F_8$  single plant was harvested and maintained as an original seed stock ( $F_{8,9}$ ). The  $F_{8,9}$  seed was then increased in bulk in greenhouses to make  $F_{8,10}$  seeds for distribution and phenotyping.

The initial phenotyping experiments for basic agronomic traits are described in Huynh et al. (2018). The MAGIC RILs and parents were screened for photoperiod sensitivity under long-day conditions during summer, from June (14.5 h) to

**Table 1. Cowpea multiparent advanced generation intercross (MAGIC) founder parents and their traits relevant to sub-Saharan Africa and other production areas.**

Name	Source†	Resistance/tolerance trait	Agronomic trait
IT89KD-288	IITA	Root-knot nematode resistant	High yielding under drought in Burkina Faso and Nigeria; brown-eye seed; photoperiod sensitive
IT84S-2049	IITA	Resistant to aphid, bacterial blight, viruses, root-knot nematode	High yielding under drought in Burkina Faso; brown-eye seed; erect growth habit
CB27	UCR	Heat tolerant, resistant to root-knot nematode, Fusarium wilt, and foliar thrips	High yielding under drought in Mozambique; large black-eye seed; photoperiod insensitive; erect growth habit; early maturing
IT82E-18	IITA	Broadly adapted, resistant to root-knot nematode	High yielding under drought in Mozambique; early maturing, light-brown seed; photoperiod insensitive
SuVita 2	INERA	Drought tolerant, resistant to Striga, foliar thrips and <i>Macrophomina</i> disease	High yielding under drought in Senegal, Burkina Faso and Mozambique; large dark-brown seed
IT00K-1263	IITA	Resistant to Striga, aphid, fusarium wilt, root-knot nematode	High yielding under drought in Mozambique and Nigeria; dark-brown seed; stay-green under drought
IT84S-2246	IITA	Resistant to aphid, bacterial blight, viruses, root-knot nematode	High yielding under drought in Burkina Faso and Mozambique; dark-brown seed
IT93K-503-1	IITA	Drought tolerant, resistant to nematodes, Fusarium wilt, and <i>Macrophomina</i>	High yielding under drought in Senegal; brown-eye seed; stay-green under drought

† IITA = International Institute of Tropical Agriculture, Nigeria; UCR = University of California–Riverside, Riverside, CA; INERA = Institut de l’Environnement et des Recherches Agricole, Burkina Faso.

September (12.8 h), at the UCR Citrus Experiment Station, CA (33.97° N, 117.34° W). In 2015, each MAGIC RIL and parent was planted in a single row (0.76 m wide and 5.5 m long) at a density of 12 seeds m<sup>-1</sup> using a tractor-mounted planter. The field was watered to capacity before and after planting until maturity using furrow irrigation. In 2016, the experiment was repeated but under restricted irrigation; the field was watered to capacity before planting, and then irrigation was withheld until the end of trial. For each line in both trials, days to flowering was determined when 50% of plants in the plot had flowered.

The population was also screened under short-day conditions during autumn, from September (12.8 h) to December (9.9 h), at the UCR Coachella Valley Agricultural Research Station, CA (CVARS, 33.52° N, 116.15° W). In 2015, the MAGIC RILs and parents were grown together in separate blocks with contrasting watering regimes (full and restricted irrigation). In each block, each line was planted in a single row (0.76 m long and 3.7 m long) at a density of 12 seeds m<sup>-1</sup> using a tractor-mounted planter. The field was watered to capacity before and after planting using subsurface drip-irrigation. After 2 wk when the seedlings were well established, the irrigation was withheld in the restricted-irrigation block until maturity, whereas in the full-irrigation block the rows were watered to capacity up to 100 d after planting. In 2016, the experiment was repeated in an adjacent field site using the same design and conditions as applied in 2015. For each line in both trials, days to flowering was determined when 50% of plants in the plot had flowered. Plant growth habit was measured at 40 d after planting using a visual rating scale from 1 to 6 based on the angles formed between primary branches and the main stem, where 1 = acute erect, branches form angles less than 45° with the main stem; 2 = erect, branching angles between 45° and 90° with the main stem; 3 = semi-erect, branches perpendicular to the main stem but not touching the ground; 4 = intermediate, lower branches touching the ground; 5 = semiprostrate, lower branches flat on the ground but the main stem standing upright; and 6 = prostrate, the entire plant flat and spreading on the ground. At maturity, the plants in each plot were cut at the lower stems and machine-threshed for measurement of plot yield and 100-seed weight.

## Characteristics

Phylogenetic analysis based on 11,848 parent-unique SNPs showed a high diversity among the eight-way RILs relative to their eight parents (Supplement 2). The F<sub>8</sub> lines were also highly diverse in morphological traits, including growth habit, flower color, flowering time, leaf shape, and seed characteristics (size, shape, color, and texture) (Fig. 1).

Variation in agronomic traits expressed in the parents and MAGIC RILs is detailed in Table 2. The flowering time varied widely in the population under both long-day and short-day conditions, and there were significant correlations ( $r = 0.63$ ,  $P < 0.001$ ) between the two environments. Under the long-day condition, the population started flowering as early as 42 d after planting, but there were many lines with flowering delayed more than 2 mo after planting. In contrast,

under the short-day condition, the population started flowering as early as 33 d after planting and completed flowering within another month (57 d). Among the parents, CB27 (35–38 and 42–45 d) was the earliest to flower, while IT89KD-288 (45–47 and 86–90 d) was the most delayed in both environments (CVARS and UCR Citrus Experiment Station, respectively).

None of the parents or MAGIC RILs showed prostrate or semiprostrate growth habit. The majority of MAGIC RILs had the plant type ranging from semi-erect to erect under both watering conditions. There were significant but moderate correlations in the growth habit scores between full and restricted irrigation ( $r = 0.53$ ,  $P < 0.001$ ), with only 39% of the lines showing similar growth habit between the two environments. Among the parents, CB27 and IT84S-2049 maintained their growth habit under both conditions and were classified as acute-erect and erect, respectively. The other six parents had a semi-erect growth type under full irrigation but grew erectly under the restricted irrigation conditions (Table 1).

Maturity varied considerably in the MAGIC population grown at CVARS in 2015 and 2016, with significant correlations ( $r = 0.53$ ,  $P < 0.001$ ) existing in the phenotypic ranking between the two watering conditions (normal and restricted irrigation). Transgressive segregation was also observed (Table 1). Some lines were fully mature as early as 63 d after planting, while others were still green and kept producing pods 90 d after planting under restricted irrigation, including four of the parents (IT84S-2049, IT82E-18, IT00K-1263, IT93K-503-1) and 142 MAGIC RILs (47% of the population) (Table 1 and Fig. 1c).

Plot yield and seed size also varied considerably under both full irrigation and restricted irrigation conditions at CVARS in 2015 and 2016. There were significant ( $P < 0.001$ ) correlations in these traits between the two environments, with seed size appearing more stable in the phenotypic ranking ( $r = 0.76$ ) than yield ( $r = 0.30$ ). About 75% of lines developed larger seeds under water stress compared with full irrigation (Table 1). This was probably due to source–sink relationship associated with seed and pod abortion under restricted irrigation. Transgressive segregation was observed for both traits. Many lines yielded much higher than all parents under water stress. Among the parents, CB27 consistently had the highest yield and seed size across the two environments.

## Conclusions

The broad genetic base and wide phenotypic variation with transgressive segregation combined with high-density SNP genotyping make this cowpea MAGIC population a unique genetic resource for improving breeding populations, trait discovery, and quantitative trait loci (QTL) mapping. The QTL detected in the MAGIC population combined with existing knowledge of biparental mapping and QTL haplotypes in the parents (Huynh et al., 2015, 2016; Lucas et al., 2013a, 2013b; Muchero et al., 2011; Pottorff et al., 2014) can be applied to develop novel combinations of QTLs through intercrossing the best MAGIC RILs, providing super trait-donor lines for use in breeding programs.

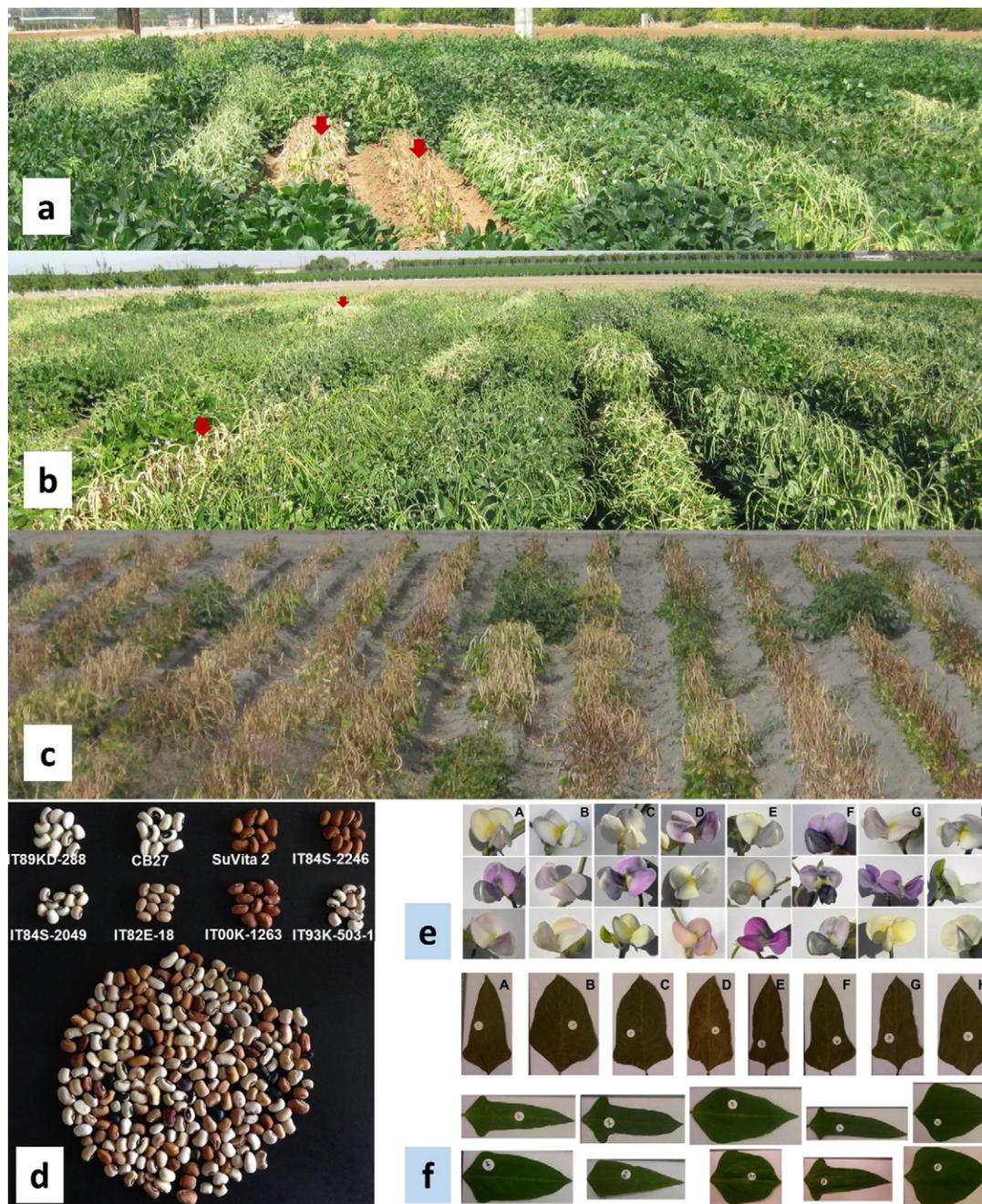


Fig. 1. Morphological variation in the cowpea multiparent advanced generation intercross (MAGIC) population. Plant appearance at 65 d after planting under (a) long-day conditions at the University of California–Riverside Citrus Experiment Station in 2015 and (b) short-day conditions at the University of California–Riverside Coachella Valley Agricultural Research Station (CVARS) in 2016, both under full irrigation; (c) variation in maturity under restricted irrigation at CVARS in 2015; (d) seed appearance, (e) flower color, and (f) leaf shape of parents (top panel) and a representation of MAGIC  $F_8$  recombinant inbred lines (RILs). In lower part of 1d, each seed is from a different  $F_8$  RIL. In (a) and (b), red arrows indicate examples of lines that matured earlier than other lines. In (e) and (f), parent codes are: A, IT89KD-288; B, IT84S-2049; C, CB27; D, IT82E-18; E, Suvita-2; F, IT00K-1263; G, IT84S-2246; H, IT93K-503-1.

## Availability

Seeds of the MAGIC core set (305  $F_{8,9}$  RILs) and the eight founder parents have been deposited at the IITA germplasm repository, Ibadan, Nigeria, for propagation followed by worldwide distribution on request. In addition, seeds of the RILs and parents have been deposited at the USDA-ARS National Center for Genetic Resources Preservation, Fort Collins, CO, where they will be available for research purposes after five years. Original seed stocks for every generation of the MAGIC development including the  $F_8$  RILs and

parents are being archived and conserved at the UCR cowpea gene bank. Information on marker genotyping, genetic map positions, genomewide recombination rate within the MAGIC population, and QTL mapping for basic agronomy traits can be obtained from the concurrent publication (Huynh et al., 2018). Should these resources contribute to further research or germplasm development, we request that their origin and development at the University of California–Riverside be acknowledged by citing both Huynh et al. (2018) and this registration article.

**Table 2. Variation in agronomic traits measured in the cowpea multiparent advanced generation intercross (MAGIC) population and the eight parents grown under different day and watering conditions at the University of California–Riverside Citrus Experiment Station (UCR-CES, long-day) and the University of California–Riverside Coachella Valley Agricultural Research Station (CVARS, short-day) in California during 2015–2016.**

Trait†	Watering condition	Founder parents										MAGIC RILs‡		
		IT89KD-288	IT845-2049	CB27	IT82E-18	Suvita-2	IT00K-1263	IT84S-2246	IT93K-503-1	Mean	Range	CV%		
Flowering time at UCR-CES (DAP)§	Full	86	56	42	52	70	63	57	70	61	42–88	19		
	Restricted	90	54	45	50	58	60	58	68	59	42–90	21		
Flowering time at CVARS (DAP)	Full	47	39	38	43	44	46	42	46	43	35–57	10		
	Restricted	45	36	35	43	44	44	42	47	42	33–57	11		
Growth habit at CVARS (score 1–6)¶	Full	3	2	1	3	3	3	3	4	2	1–4	30		
	Restricted	2	2	1	2	2	2	2	2	2	1–4	24		
Maturity at CVARS (DAP)	Full	85	78	89	85	85	89	85	89	87	65–120	13		
	Restricted	89	99	83	99	85	120	81	95	91	63–120	20		
Seed size at CVARS (g 100 seed <sup>-1</sup> )	Full	18	14	20	16	17	17	16	13	16	7–29	25		
	Restricted	23	18	22	20	20	17	19	15	18	8–35	25		
Yield at CVARS (kg ha <sup>-1</sup> )	Full	1790	1410	2151	1565	1108	1250	1310	1662	1312	5–2916	41		
	Restricted	519	463	653	476	426	283	514	441	449	20–1182	43		

† Phenotypic values are means of 2 yr of data, except for flowering time at UCR-CES which was measured once under full- and restricted irrigation in 2015 and 2016, respectively.

‡ RILs, recombinant inbred lines.

§ DAP, days after planting.

¶ Growth habit index, where 1 = acute erect; 2 = erect; 3 = semi-erect; 4 = intermediate; 5 = semiprostrate; and 6 = prostrate.

## Supplemental Material

Supplement 1: List of MAGIC parents and F<sub>8</sub> RILs with pedigrees.

Supplement 2: Phylogenetic relationships based on SNP genotyping.

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