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Inheritance of 'domestication' traits in bambara groundnut (*Vigna subterranea* (L.) Verdc.)

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Abstract Controlled crosses in bambara groundnut were attempted between a range of thirty-six bambara groundnut landraces (thirty domesticated (*V. subterranea* var. subterranea) and six wild *(V. subterranea* var. *spontanea*)). Ten F_1 seed were produced. Of these, eight germinated producing F_2 populations. On seed set, four populations could be unambiguously confirmed as true crosses by F_3 seed coat colour. A single F_2 population, derived from a domesticated landrace from Botswana (DipC; female parent) crossed with a wild accession collected in Cameroon (VSSP11; male parent) was used to study a range of agronomic and domestication traits. These included; days to emergence, days to flowering, internode (fourth) length at harvest, number of stems per plant, leaf area, Specific Leaf Area (*SLA)*, Carbon Isotope Discrimination (*CID)*, 100 seed weight, testa colour and eye pattern around the hilum. On the basis of variation for internode length and stems per plant, 14 small F_3 families were selected and grown under field conditions to further investigate the genetic basis of the 'spreading' versus 'bunched' plant character, a major difference between wild and cultivated bambara groundnut. Results presented suggest that traits including leaf area, SLA, CID and 100 seed weight are controlled by several genes. In contrast, the variation for traits such as internode length, stems per plant, days to emergence and seed eye pattern around the hilum are likely to be under largely monogenic control. The results of this work are discussed in relation to the domestication of bambara groundnut.

Keywords Bambara groundnut · Domestication · Landraces · Plant breeding · Trait inheritance · *Vigna subterranea*

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Introduction

Bambara groundnut is an important food legume grown widely in semi-arid Africa and is closely related to cowpea (*Vigna unguiculata)* with which it shares much of its area of cultivation and origins of genetic diversity. In much of Africa, bambara groundnut is the third most important legume after groundnut (*Arachis hypogaea*) and cowpea (Sellschop 1962) and has a significant

advantage in that it is well adapted to prolonged periods of drought. The ability to produce a yield under conditions where groundnut, the South American equivalent widely introduced into Africa, may fail completely is important for food security (Linnemann and Azam-Ali 1993). It is nutritionally superior to other legumes and is the preferred food crop of many local people (Linnemann 1990; Brough and Azam-Ali 1992) being a rich source of protein (16–25%). Its seeds are of economic importance and command a high market price, with demand far outweighing supply in many areas (Coudert 1982). Drought tolerance, coupled to good resistance to pests (Obagwu 2003), adaptation to poor soils and nitrogen-fixing ability also make it a sustainable component of food security for Africa. In addition to its traditional and continuing importance in Africa, it is also being trialled for introduction into India, where similar problems, particularly with water availability, also exist (MS Basu pers. comm. and EU Framework Programme 6 'Bamlink'). The International Institute for Tropical Agriculture (IITA; Nairobi) holds the germplasm mandate for this crop, but CGIAR centres do not currently have a research mandate.

Bambara groundnut consists of two botanical forms; var. *spontanea* comprising the wild forms, which are restricted to an area from Nigeria to Sudan, with a centre of diversity around Cameroon, and var. *subterranea* comprising the cultivated forms, found in many parts of the tropics and particularly sub-Saharan Africa. The chromosome number in both wild and cultivated plants is $2n = 22$ (Frahm-Leliveld 1953).

In the absence of established varieties, farmers in Africa (largely marginal and subsistence) grow locally adapted landraces. The landraces are expected to consist of multiple inbred lines, as the species is believed to be cleistogamous. Evidence supporting this has come through the use of Amplified Fragment Length Polymorphism (AFLP) DNA markers (Massawe et. al. 2002; Ntundu et al. 2004). This mixture of adapted genotypes would be expected to result in an enhanced capacity to tolerate biotic and abiotic stress under low input agricultural systems and harsh environmental conditions (Zeven 1998) but it may also be a significant constraint to potential yields in higher input farming. Relatively high genetic identity between wild and domesticated forms suggests that wild bambara groundnut (*Vigna subterranea* var *spontanea*) is likely to be the true progenitor of cultivated types (Pasquet et al. 1999). Bambara groundnut is characterized by a higher genetic diversity in wild material than domesticated forms which makes the *spontanea* forms important potential sources of beneficial genes for bambara groundnut breeding and improvement (Pasquet et. al. 1999).

Bambara groundnut landraces have a compact well-developed tap root and many short lateral stems on which the leaves are borne. The leaves are trifoliate, the petiole is long, stiff and grooved, and the base is green or purple in colour. In contrast, wild forms have limited numbers of elongated lateral stems, no clear tap root, with pentafoliate leaves being reported (Swanevelder 1998). This leads to wild accessions adopting a 'spreading' rather than a 'compact' habit. Flowers in both wild and cultivated species are produced on hairy peduncles from the stem nodes. In domesticated landraces, this leads to a clustering of the pods at the base of the plant, while in wild forms, pods form along the length of the elongated stems. Upon fertilisation, the peduncle elongates to bring the fertilised ovary to or below the soil surface, in a similar way to groundnut. However, unlike groundnut, darkness is not a prerequisite for pod formation. Instead, the apical end of the peduncle, which bears the ovary with the fertilised ovules, expands into a pod close to or just below the soil surface. The pods are spherical or oval in shape and may contain only one seed, although pods with two seeds are also common in some landraces (Rassel 1960; Pasquet and Fotso 1997). Mature pods are indehiscent and range from cream/yellow to reddish or dark brown in colour (Massawe et. al. 2004). A major difference between wild and cultivated forms is seed size, with wild seeds generally small (9–11 mm) while domesticated seeds are larger (11–15 mm), although there is also considerable variation between landraces. Hepper (1963) also reported that the germination of the cultivated form is more rapid than that of the wild form (typically 15 days compared to 31 days or longer), and that the rate of germination is more uniform in the cultivated form, being erratic in the wild form.

Both of these features are likely to represent selections to facilitate cropping of the species and important steps in the domestication process. Flowering in both var *spontanea* and var *subterranea* starts 30–35 days after emergence and may continue until the end of the plant's life. However, at least in the cultivated forms examined by Linnemann and Azam-Ali (1993) and Linnemann (1994), the swelling of fruit (i.e. pod filling) requires a minimum photoperiod of 12 h. The photoperiodic requirements of wild forms of bambara groundnut for pod filling has not been reported in the literature.

The domestication of a crop involves two major steps; the initial development of altered plant architecture and 'harvestability' traits (to recruit the wild ancestor into a 'landrace' form compatible with farming) and the subsequent development of specific cultivars (i.e. *cultivated varieties*) of known genotype from landrace progenitors. In this paper, we report work to examine the genetic basis of a number of the first class of domestication traits in bambara groundnut (*V. subterranea* (L) Verdc.). We also report the results of the first ever successful controlled crosses, i.e. the second requirement to fully domesticate a species as a modern crop. Despite the potential of bambara groundnut as a crop, the lack of artificial pollination has prevented the final step in domestication being achieved. This has prevented the establishment of plant breeding programmes based on hybridisation and selection.

In the present study the inheritance of a number of plant morphology traits were examined in F_1 hybrids and a segregating F_2 population obtained from a cross between a wild and a domesticated bambara groundnut. The importance of such developments to permit the full exploitation of this key underutilised African legume is discussed.

Materials and methods

Plant material

Thirty bambara groundnut landraces from different areas of Africa, together with six wild accessions from Cameroon, were grown and artificial cross-pollination attempted in different combinations (Basu et al. 2003; Massawe et. al. 2004). Eight mature F_1 seeds were germinated, grown and allowed to self-pollinate to produce F_2 seed. A further two F_1 seeds failed to germinate. Fidelity was assessed by examining the F_2 seed-coat colour with four of the eight population confirmed as derived from true crosses. One of these confirmed F_2 populations generated was a wide cross, derived by hybridising a bambara groundnut landrace (DipC; a cream seeded type collected at Diphiri, Botswana) with a wild accession (VSSP11; collected from North Western Cameroon). This was selected for further study. F_2 plants from this cross were established in a glasshouse of the Tropical Crops Research Unit (TCRU), University of Nottingham, Sutton Bonington Campus, during 2002–2003. Of one hundred and forty-seven F_2 seed, 100 individual F_2 plants were trait recorded and further allowed to self-pollinate, producing F_3 seeds.

F_3 families were selected on the basis of spreading versus bunched habit in the F_2, were grown in the field in Swaziland (26 30 S, 31 30 E) under non-limiting water conditions and were scored for a range of morphological traits.

The TCRU growth conditions

Each of the five TCRU glasshouses has a total cropping area of 32 m^2 divided into two plots within which stands of up to 400 plants can be grown under uniform conditions of soil, atmospheric moisture and air temperature. The soil within each plot is separated by a 1.25 m deep butyl liner from the external water table surrounding the glasshouses. The F_2 plants were grown at a constant 12 h photoperiod and 28°C temperature with an amplitude of ±5°C (33–23°C, day and night, respectively) under non-limiting soil moisture conditions provided by trickle seep hoses attached to an irrigation system.

Traits recorded

Days to emergence was recorded as the number of days from sowing to two (fully-expanded) leaves. *Days to flowering* was recorded from the time of emergence to first flowering. *Internode length* was

measured as the average length of the fourth internode of three stems in each individual F_2 plant and was recorded at harvest. Based on the number of leaflets in a compound leaf of bambara groundnut, two primary types were identified: *trifoliate leaf*: a three-leaflet structure occurring in all landraces and *pentafoliate leaf*: a five-leaflet structure found in combination with trifoliate and 'dented' leaves and characterising the wild accession 'VSSP11'. Leaf area (cm^2), based on the average leaf area of 10 leaves per F_2 plant grown under the uniform conditions of the TCRU glasshouse and measured using a Leaf Area Meter (Licor 3000, Licor, USA). Specific Leaf Area (SLA; $cm^2\ g^{-1}$) was calculated from leaf area divided by dry weight average of the 10 leaves collected from each F_2 plant (oven dried at 70°C for two days). The dried leaves were then finely ground using a motor grinder to pass material through a sieve of 300 mesh for CID (Carbon Isotope Discrimination) analysis of leaf $\Delta^{13}C$ (Farquhar et al. 1984; Condon et al. 2004). The $\Delta^{13}C$ was determined in dried leaf powder using Isotope Ratio Mass Spectrometer (IRMS), at the National Facility, Department of Crop Physiology, University of Agricultural Sciences, Bangalore, India. The IRMS was interfaced with an elemental analyser through a continuous flow device to determine the stable isotope ratios on a continuous flow basis. Carbon isotope fractionation values were computed in relation to Pee Dee belemnite (PDB) standards and expressed as per mil (%O) (Ehleringer and Osmond 1989). *Testa colour* and *hilum pattern* were recorded within two months of harvest and were divided into three subgroups described in the 'Descriptors for Bambara Groundnut' (IPGRI and IITA 2000). *100-seed weight* (g) was calculated from seed samples taken within two months of harvest (at 12% moisture content, after oven-drying for 2 weeks at 35°C).

Trait analysis

Traits were examined for consistency with a Normal distribution (using an Anderson Darling Normality test) and discontinuous distributions were tested against specific hypotheses using a χ^2 test. Correlations between traits were examined by Pearson Product Moment Correlation (Stephens 1974; Snedecor and Cochran 1989).

Results

The F_1 hybrids

A total of eight F_1 seed were followed into the F_2 generation, to try to confirm hybrid status through the use of seed coat colour in the subsequent generation (it being a maternal character). Four of these could be unambiguously 'confirmed' as hybrids (see Table 1) and a further four were 'inconclusive'. Another two F_1 seed failed to germinate. The DipC × VSSP11 cross was chosen for further analysis, as it represented a cross between a cultivated landrace and a wild collection. All crosses between domesticated plant types (including 'inconclusive' ones) gave the bunched, short internode length plant types, as expected.

The successful hybridisation between 'DipC', a cultivated, non-spreading/bunched type and 'VSSP11' a wild, spreading type, resulted in a spreading type F_1 hybrid, with more leaves, pods and seeds than 'VSSP11' (see Fig. 1). This argues for at least partial dominance of the 'spreading' habit over the 'compact' plant habit.

Plant traits

Days to emergence recorded in the F_2 population showed a non-normal distribution pattern (Anderson Darling Normality test (AD); $P = 0.00$). Sixty-seven plants emerged before 30 days, with the remaining twenty-four plants emerging between 35 days and 67 days. The overall pattern would be consistent with a single dominant gene for rapid emergence (3:1 segregation, $\chi^2 = 0.06 < 3.84$; 1 df). However, substructure was also observed within the late emergence class, which suggests other genes may have minor effects.

Days to flowering, *internode length* and *stems per plant* all showed non-normal distributions (AD; $P = 0.000$; $P = 0.022$; $P = 0.000$, respectively). Grouping *stems per plant* into three probable classes suggested by the trait distribution

Table 1 Assessment of hybrid status using the seed coat colour

	Parents of hybrid		Seed coat colour				Hybrid status
	Male parent	Female parent	Male parent	Female parent	F_1	F_2	
1	KabCa4	Dod R	Cream	Red	Red	Red	Inconclusive
2	AHM 968	Tiga Nicaru	Light brown	Cream	No germination	–	–
3	Dod R	SB 4-2	Red	Cream	Cream	Cream	Inconclusive
4	Dod R	OM1	Red	Cream with black winged eye	Cream with black winged eye	Cream with black winged eye	Inconclusive
5	AHM 753	SB4-2	Red	Cream	Cream	Cream	Inconclusive
6	VSSP11	DipC	Light brown with dark brown spots	Cream	Cream	Dark purple	Confirmed
7	Ramayana	SB4-2	Black	Cream	Cream	Black	Confirmed
8	Ramayana	Namibia black	Black	Black	No Germination	–	–
9	DipC	Swazi red	Cream	Red	Red	Dark purple	Confirmed
10	Ramayana	Uniswa cream	Black	Cream	Cream	Black	Confirmed

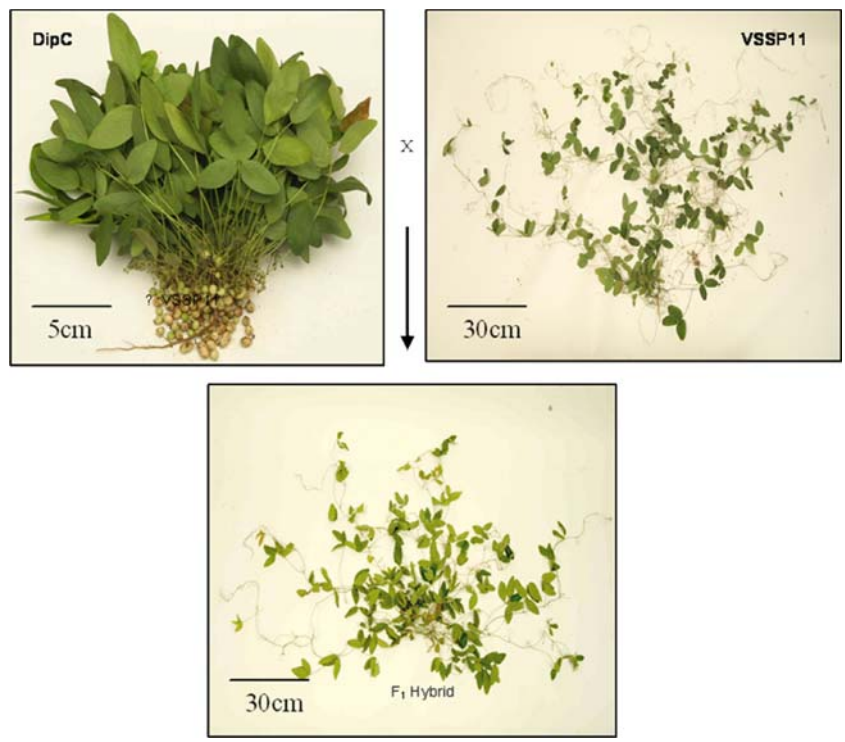

Fig. 1 DipC female parent (var subterranea) × VSSP11 male parent (var spontanea) and the derived F1 hybrid

and parental phenotypes (fewer than 8 stems/plant; 9 to14 stems/plant; 15 or more stems/plant) a possible 1:2:1 segregation pattern was observed, consistent with a χ^2 test ($P = 0.03 < 5.99$; 2 df). The results suggest a largely co-dominant control of this trait in the present cross. The bimodal distribution of *internode length* (Fig 2a) is also suggestive of a single gene with long internodes

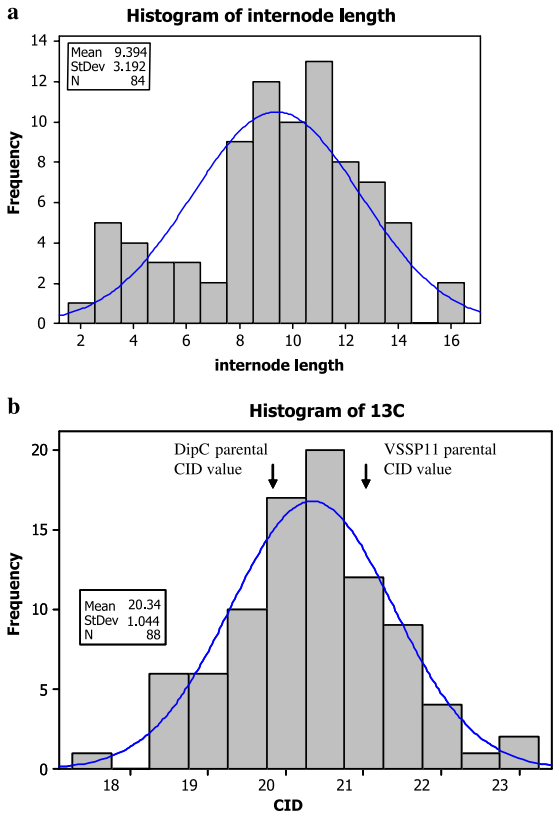

Fig. 2 (**a**) Trait distribution of *internode length* (cm) in the F_2 population. (**b**) Trait distribution of CID, showing transgressive segregation in the progeny

being dominant (internode <8 cm, internode >8 cm; $\chi^2 = 0.564 < 3.84$; 1 df) which would also be consistent with the observed dominance of long internodes in the F_1 plant.

The expression of *pentafoliate* and/or dented leaves was observed clearly in 52 plants, whereas the expression of only *trifoliate* leaves was observed clearly in 39 plants. The hypothesis of single gene control for leaf morphology can be tentatively rejected ($\chi^2 = 4.58 > 3.84$; 1 df).

Leaf area, *SLA* and *CID* showed normal distributions in the F_2 population (AD: $P = 0.347, 0.237$ and 0.638 respectively). *CID* also showed significant transgressive segregation (Fig 2b).

Seed characters

Wide variation for *100-seed weight* (10–80 g) was observed in the F_2 population, with consistent seed size within individual F_2 plants. This trait appeared normally distributed (AD: $P = 0.064$). The F_2 seeds had a non-parental phenotype for *testa colour*. The segregation of this trait was studied in the F_3 generation of seeds obtained by self-fertilization of the F_2 plants (as the trait is maternally inherited). In the 90 F_2 plants studied for *testa colour*, 23 plants had cream testa, 58 had dark purple testa, and only nine plants had a light brown testa with dark brown spots. The hypothesis that this trait segregates in a 1:2:1 ratio indicative of co-dominance was rejected on the basis of χ^2 test value ($\chi^2 = 11.86 > 5.99$; 2 df). The hilum *eye pattern* associated with the landrace 'DipC', was absent in the wild accession 'VSSP11' and also in the F_2 seeds derived from the cross between them. A segregation ratio of 23: 67 (presence of eye: absence of eye) was observed in the F_3 generation of seeds consistent with a single recessive gene ($\chi^2 = 0.01 < 3.84$; 1 df).

Associations between traits

A series of Pearson's correlations were performed to better understand any associations and interactions among the traits studied in the cross. The most significant correlations are given in Table 2.

Days to emergence was negatively correlated to *SLA* and *CID* (–0.412, $P = 0.000$; –0.614, $P = 0.000$, respectively), with a positive correlation between *SLA* and *CID* (0.323, $P = 0.003$). *CID* was further correlated with 100 *seed weight*

Table 2 Significant Pearson Correlation between scored traits in the F_2 population

Trait A	Trait B	Correlation	Significance
Emergence	SLA	–0.412	0.000
	CID	–0.614	0.000
Days to flowering	Internode length	–0.359	0.001
	Leaf area	–0.414	0.000
	100 seed weight	–0.310	0.005
Internode length	Stems/plant	–0.262	0.012
	100 seed weight	0.318	0.003
Leaf area	100 seed weight	0.238	0.029
SLA	CID	0.323	0.003
CID	100 Seed weight	0.562	0.000

(0.562, $P = 0.000$). *Days to flowering* was negatively correlated to *internode length*, *leaf area* and 100 *seed weight* (–0.359, $P = 0.001$; –0.414, $P = 0.000$; –0.310, $P = 0.005$, respectively) with internode length negatively correlated to stems per plant (–0.262; $P = 0.012$) and positively correlated to 100 seed weight (0.318, $P = 0.003$).

Overall, the correlations are as expected, with phenological (i.e. developmental) traits (*days to emergence* and *days to flowering*), having significant negative effects on morphological (i.e. growth) traits (*internode length*, *leaf area*, 100 *seed weight*). An exception to this is the negative relationship between *internode length* and *stems per plant* which could be the result of limited growth resources available to the plant during development.

Investigating the relationship between stems per plant and internode length in the F3 generation

The 'spreading' habit compared with the 'bunch-type' is a major difference between wild material and most cultivated material. To try to understand the basis for this trait further, 14 F_2 plants were selected for differences in the above traits and six seeds grown from the F_3 generation for each plant (Fig 3 and Table 2). While the limited numbers that could be grown make detailed analysis unfeasible for traits within F_3 families, initial scoring within and across families was used to provide an indication for trait inheritance.

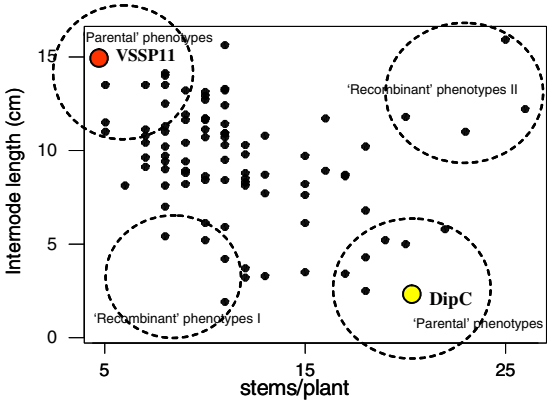

Fig. 3 Plot of *internode length* against *stems per plant* and identification of possible lines for field planting in Swaziland as small F_3 families

In the F_2, a significant negative correlation was observed between *internode length* and *stems per plant* (–0.262; $P = 0.012$). However, as Fig. 3 shows and as is detailed in Table 2, there were plants which showed potentially recombinant morphotypes; Recombinant I – high *internode length*, high *stems per plant*- and Recombinant II – low *internode length*, low *stems per plant*. Examining F_3 families from the non-recombinant forms suggested that the negative correlation observed within the F_2 between *internode length* and *stems per plant* was maintained in the F_3 family means (–0.356; ns), However, for the recombinant families, the correlation between *internode length* and *stems per plants* was no longer present, in contrast to the F_2 results (0.08; ns). This could be indicative of genetic linkage between the two traits. Days to emergence was also seen to segregate within families and between families, For example; $F_3(52)$ and $F_3(54)$ both showed consistent, rapid, emergence (25.3 and 22.7 days average; 14–26 and 20–27 days range, respectively) some showed mixed emergence dates - $F_3(15)$(32.5 days average; 15 to 52 days range) and one family showed consistently late emergence – F_2 (20)(49.6 days average, 47 days–51 days range). Taken across all F_3 families, individual emergence times confirmed the trend seen in the original F_2, with a 3:1 segregation for early to late ($\chi^2 = 0.025$; ns; 1 df). Erratic seed emergence is undesirable in a crop and is usually lost during domestication. This would support the division observed in the F_2 and argue for a strong genetic control of this trait. The development of a spreading, high stem number morphology could also potentially be of interest for plant breeding in bambara groundnut and provides an interesting parallel with cultivated forms of peanut (*Archis hypogaea*) in which more primitive alternate branched forms (runner and spreading bunch) and more recent sequential branched forms (erect bunch) provide contrasting agronomic options for different environments. Semi-bunch types are already held within germplasm collections, but fully spreading material is associated with wild accessions, yet may become important in breeding programmes for harsh environments (Table 3).

Table 3 Individual F_2 plant data used to select small F_3 families for growth in Swaziland

Parental class	F2 plant number	Internode length (cm)	Stems per plant
'DipC'	79	5	20
	92	5.2	19
'VSSP11'	2	13.5	7
	16	11.5	5
	39	13.5	5
	80	12.5	8
	98	13.5	8
'Recombinant I'	44	1.9	11
	52	4.2	11
	95	5.4	8
'Recombinant II'	20	12.2	26
	41	11.8	20
	93	15.9	25
	94	11	23

Discussion

The adaptation of a wild progenitor to a useful 'crop' involves a number of developmental and phenological changes which facilitate farming. These include; limited seed dormancy, even emergence, modified/compact plant architecture, non-shattering seed and free-freshing grain (Harlan 1992; see Salamini et al. 2002). In addition to domestication changes *per se*, domesticated crop species are also likely to need to be adapted to local conditions, through such adaptive genes as vernalisation requirement and photoperiod-sensitivity (see Paterson 2002).

The development of a number of controlled crosses in bambara groundnut and the detailed examination of an initial wild × cultivated bambara groundnut cross and subsequent F_2 and F_3 material is an important step in beginning to understand the genetic basis of the domestication events in this species, as well as to facilitate the other major aspect of full domestication of a crop species – plant breeding programmes based on controlled crossing events.

In maize, it is clear that relatively few gene changes are needed to permit this domestication process. A controlled cross between teosinte and maize allowed analysis of the subsequent F_2 population and suggested that only five genomic regions were involved in changes needed to 'convert' teosinte to maize (Doebley et al. 1990). A similar situation has been described by Peng et al. (2002) for Durum wheats, where 7 'Domestication Syndrome Factors' were identified.

Our initial investigation into bambara groundnut domestication suggests that the major morphological difference between *spontanea* and *subterranea* types (spreading or compact plant habit) is under the control of a relatively limited numbers of genes. The major components of this habit, *internode length* and *stems per plant*, both show segregation patterns in the F_2 population which are consistent with monogenic inheritance in this cross. For *stems per plant* a single gene co-dominant for stem number, and for *internode length* a single gene dominant for long internodes, could be postulated to explain the majority of the variation present. Examining the F_2 population and selected F_3 families suggests that recombinant forms (Recombinants I + II) were also formed in the F_2. In the small F_3 families, a negative correlation (although not statistically significant) between these traits was observed in the DipC and VSSP11 ('parental') types, as observed in the F_2. However, this negative correlation was no longer observed in the Recombinant I + II F_3 families, suggesting that the coupling between these two main determinants of 'landrace' versus 'wild' morphology can be broken and a potentially significant range of spreading material developed into domesticated varieties, as had been achieved in *Archis hypogaea*.

The postulation that *days to emergence* could be largely controlled by a single gene dominant for early emergence, as was observed in the F_2 and F_3 generations, may also be a reflection of how cultivated landraces have lost their ability to stagger seed emergence – a trait which is essential to establishing a seed bank for wild species survival, but clearly detrimental to commercial cultivation.

Leaf area, *SLA*, *CID* and *100* seed weight were clearly multigenic. That there is significant transgressive segregation for *CID* is interesting, although it may also be a reflection of significant morphological variation within this cross, rather than a true indicator of useful differences in water use efficiency for breeding programmes.

Conclusions

The first controlled crosses and the first intraspecific hybrid between a wild and cultivated bambara groundnut accession were developed under the scope of the present study. Many contrasting traits in plant morphology and agronomic traits were studied for the first time leading to a better understanding of the number of genes controlling these traits, their inheritance and segregation. This gives a key insight into how this species was domesticated and perhaps more importantly, the ease with which new genes could be introduced into cultivated material. As has been discovered for other species where such studies have been possible, such as maize and wheat, the basic changes in plant morphology between domesticated and wild progenitors are often controlled by a limited number of genes. Here, the switch between the spreading wild type and the bunch type is likely to be largely under the control of two genes, with variation in *internode length* being the most important.

Good water-use efficiency and tolerance to periods of drought will be essential to future farming in many countries. The development of a method of controlled crossing is key to the production of varieties of bambara groundnut. Such genetic improvement from landraces to varieties will ensure that bambara groundnut plays an enhanced role in sustainable farming in Africa, with the potential for introduction into India and even Europe.

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