Annals of Botany **109**: 1185–1200, 2012
doi:10.1093/aob/mcs048, available online at www.aob.oxfordjournals.org

ANNALS OF BOTANY
Founded 1887

The genetics of domestication of yardlong bean, *Vigna unguiculata* (L.) Walp. ssp. *unguiculata* cv.-gr. *sesquipedalis*

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Received: 9 December 2011 Returned for revision: 20 January 2012 Accepted: 3 February 2012 Published electronically: 14 March 2012

• *Background and Aims* The genetics of domestication of yardlong bean [*Vigna unguiculata* (L.) Walp. ssp. *unguiculata* cv.-gr. *sesquipedalis*] is of particular interest because the genome of this legume has experienced divergent domestication. Initially, cowpea was domesticated from wild cowpea in Africa; in Asia a vegetable form of cowpea, yardlong bean, subsequently evolved from cowpea. Information on the genetics of domestication-related traits would be useful for yardlong bean and cowpea breeding programmes, as well as comparative genome study among members of the genus *Vigna*. The objectives of this study were to identify quantitative trait loci (QTLs) for domestication-related traits in yardlong bean and compare them with previously reported QTLs in closely related *Vigna.*

• *Methods* Two linkage maps were developed from BC_1F_1 and F_2 populations from the cross between yardlong bean (*V. unguiculata* ssp. *unguiculata* cv.-gr. *sesquipedalis*) accession JP81610 and wild cowpea (*V. unguiculata* ssp. *unguiculata* var. *spontanea*) accession TVnu457. Using these linkage maps, QTLs for 24 domestication-related traits were analysed and mapped. QTLs were detected for traits related to seed, pod, stem and leaf.

• *Key Results* Most traits were controlled by between one and 11 QTLs. QTLs for domestication-related traits show co-location on several narrow genomic regions on almost all linkage groups (LGs), but especially on LGs 3, 7, 8 and 11. Major QTLs for sizes of seed, pod, stem and leaf were principally located on LG7. Pleiotropy or close linkage of genes for the traits is suggested in these chromosome regions.

• *Conclusions* This is the first report of QTLs for domestication-related traits in yardlong bean. The results provide a foundation for marker-assisted selection of domestication-related QTLs in yardlong bean and enhance understanding of domestication in the genus *Vigna.*

Key words: Cowpea, QTL analysis, domestication, *Vigna unguiculata*, evolution, yardlong bean.

INTRODUCTION

The Leguminosae genus *Vigna* is a pantropical genus comprising about 100 species mainly found in Africa and Asia (Maréchal *et al.*, 1978). Nine *Vigna* species have been domesticated, two of which were domesticated in Africa and seven were domesticated in Asia. The African *Vigna* consists of cowpea [*V. unguiculata* (L.) Walp.] and bambara groundnut [*V. subterranea* (L.) Verdc.] (Smartt, 1990). The Asian *Vigna* comprises mungbean [*V. radiata* (L.) Wilczek], blackgram [*V. mungo* (L.) Hepper], moth bean [*V. aconitifolia* (Jacq.) Maréchal], azuki bean [*V. angularis* (L.) Ohwi & Ohashi], rice bean [*V. umbellata* (Thunb.) Ohwi & Ohashi], jungli bean [*V. trilobata* (L.) Verdc.] and creole bean [*V. reflexo-pilosa* Hayata] (Tomooka *et al.*, 2002). All domesticated *Vigna* except creole bean have the chromosome number of $2n = 2x = 22$. These crops are adapted to various agroclimatic conditions and fit well into many cropping systems. Dry seeds, young pods and sprouts from these crops are consumed. Plant parts of the crops are used as fodder or hay for farm animals. Among these *Vigna* crops, cowpea is the most important in terms of planting area.

Yardlong bean [*Vigna unguiculata* (L.) Walp. ssp. *unguiculata* cv.-gr. *sesquipedalis*] is characterized by its very long (30–90 cm in length) pods with seeds usually 8–12 mm long. It is also known as asparagus bean, string bean, snake bean and sitao. Unlike other *Vigna* crops, which are grown primarily for seeds, yardlong bean is cultivated mainly for crisp and tender pods that are consumed both fresh and cooked. Yardlong bean is believed to have been domesticated from cultivated cowpea in Asia. It is widely grown as a vegetable in China, and South and South-East Asia.

Yardlong bean and cowpea differ phenotypically as a result of divergent selection during the evolution of the crop. The domestication syndrome is a suite of morphological and physiological traits that distinguish domesticated crops from their wild ancestors (Hammer, 1984). Domestication-related traits include changes in plant architecture (e.g. no branching in maize, determinate growth habit in beans), gigantism in the consumed plant organs (e.g. seed size in bean), reduced seed

dispersal (i.e. non-shattering or non-dehiscence in bean and rice) and loss of seed dormancy. Crop domestication is an accelerated evolutionary process that is the result of the synergistic effect of human (both intentional and unintentional selection) and natural selection. Plant scientists are interested in studying the genetic basis of crop domestication with an ultimate goal of identifying useful allele(s), gene(s) or genome region(s) that have not been exploited in the wild relatives of the cultivated crops and could have a positive impact on crop improvement. The search and localization for genes involved in crop domestication are performed by means of quantitative trait loci (QTL) analyses in many crops. Some genes for domestication have been cloned (Purugganan and Fuller, 2009; Izawa *et al.*, 2009). In addition, divergence within the primary gene pool of cowpea to a crop for seeds and pods outside the natural range of the wild relatives of cowpea can provide insight into crop evolution and agriculture. Unfortunately, there is a lack of archaeobotanical information on cowpea and particularly yardlong bean in Asia (but see Fuller and Harvey, 2006).

The genetics of domestication syndrome traits have been reported in a limited number of legume crops, including azuki bean, common bean, pea, soybean and rice bean. Among the nine cultivated *Vigna* species, comprehensive QTL mappings for domestication syndrome traits were reported for azuki bean (Kaga *et al.*, 2008) and rice bean (Isemura *et al.*, 2010), both of which are Asian *Vigna* crops. QTL analyses for domestication traits in cowpea and yardlong bean have recently been published (Andargie *et al.*, 2011; Xu *et al.*, 2011). However, these papers examined only two traits of domestication-related characters.

The genetics of domestication of yardlong bean is of particular interest because the genome of the bean has experienced divergent domestication from cowpea grown primarily for its seeds. Cowpea was domesticated from wild cowpea in Africa; in Asia, cultivated cowpea or its weedy relative was subsequently selected for the vegetable crop, yardlong bean. Information on the genetics of domestication-related traits would be useful for yardlong bean and cowpea breeding programmes, and for comparative genome studies among members of the genus *Vigna*.

The objectives of this study were to identify QTLs for domestication-related traits in yardlong bean and to compare them with previously reported QTLs in closely related *Vigna* species.

MATERIALS AND METHODS

Mapping populations

Mapping populations comprised F_2 and BC_1F_1 populations. They were derived from a cross between yardlong bean accession 'JP81610' and wild cowpea (*V. unguiculata* ssp. *unguiculata* var. *spontanea*) accession 'JP89083 = TVnu457'. JP81610 is a landrace from Sri Lanka, whereas JP89083 originated from Africa. Both accessions were obtained from the Gene Bank, National Institute of Agrobiological Sciences (NIAS), Tsukuba, Japan. Pollen of JP89083 was pollinated onto JP81610 to produce F_1 hybrid plants. An F_1 plant was self-pollinated to produce the F_2 population and, at the same time, another F_1 plant was crossed as female parent with JP81610 to develop the BC_1F_1 population. The F_2 population consisted of 188 plants, while the BC_1F_1 population consisted of 190 plants. The BC_1F_1 population was the same as that reported for linkage map construction by Kongjaimun *et al.* (2012).

DNA extraction

Total genomic DNA of parents and F_2 and BC_1F_1 populations were extracted from fresh leaf tissue using the CTAB method (Lodhi *et al.*, 1994). DNA concentration was estimated and adjusted to 5 ng μL^{-1} for simple sequence repeat (SSR) analyses by comparing with a known concentration of standard λ-DNA on 1·5 % agarose gel.

Trait measurement

Twenty-four traits related to fitness and domestication were evaluated following Kaga *et al.* (2008) (Table 1). Of these, 21 were treated as quantitative traits and three, pod dehiscence, epicotyl colour and seed coat colour, were treated as qualitative traits. The F_2 population of 188 plants, together with ten plants of each parent, were grown in a net house at the experimental field of Kasetsart University, Kamphaeng Saen Campus, Nakhon Pathom, Thailand (13°48′N, 99°5′E) from October 2008 to February 2009. The BC_1F_1 population of 190 plants, together with ten plants of each parent, were grown in 20-cm-diameter pots in a vinyl greenhouse of the Gene Bank, National Institute of Agrobiological Sciences (NIAS), Tsukuba, Japan (36°2′N, 140°8′E) from May to August 2009.

In both F_2 and BC_1F_1 populations, seedling traits, i.e. primary leaf length (LFPL), primary leaf width (LFPW), epicotyl colour (ECC) and epicotyl length (ECL), were recorded when the first trifoliate leaf opened. Stem length (STL), stem thickness (STT) and branch number (BRN) were recorded when the tenth trifoliate leaf was fully developed. Whole stem length (STLW) was an additional trait evaluated only in the BC_1F_1 population (Table 1).

Seed-related traits were investigated using seeds and pods from both F_2 and BC_1F_1 plants. Seed coat permeability (SDP) as an index of seed dormancy was determined using ten unscarified seeds from each BC_1F_1 plant. The seeds were placed on filter paper, incubated at 25 °C for 7 d, and the number of seeds that imbibed water was counted daily. Seed dimensions, namely seed length (SDL), seed width (SDW) and seed thickness (SDT), were the averages of ten seeds. The 100-seed weight (SD100WT) was evaluated using intact seeds of each plant.

Pod traits, i.e. pod length (PDL), pod width (PDW), pod dehiscence (PDD) and number of twists along the length of dehisced pods (PDT) when kept at room temperature, were evaluated from ten pods of each plant. PDT was used as an index of pod structure. Pod dehiscence was scored as dehiscent or indehiscent on the basis of whether seeds shattered from pods or not.

The number of days from planting to first flowering (FLD) was recorded. Days to first mature pod (PDDM) was defined as the number of days from first flowering to harvesting of

TABLE 1. *Domestication-related traits examined in* F_2 *and* BC_1F_1 *populations of the cross between yardlong bean and wild cowpea (based on Kaga* et al.*, 2008: table 1)*

General attribute	Organ	Trait	Trait abbreviation	QTL/ gene	Evaluation method	Evaluated population
Seed dormancy	Seed	Seed coat permeability (%)	SDP	*Sdp*	Percentage of imbibed seeds at 25 °C in incubator (use 20 seeds)	$BC_1F_{1:2}/F_{2:3}$
Pod dehiscence	Pod	Number of twists (count)	PDT	*pdt*	Number of twists along the length of the shattered pod	BC_1F_1
		Pod dehiscence	PDD	*Pdd*	Dehiscence or indehiscence	F_2
Gigantism	Seed	100-seed weight (g)	SD100WT	*Sd100wt*	Weight of 100 seeds (use 100 seeds)	$BC_1F_{1:2}/F_{2:3}$
		Length (mm)	SDL	*Sdl*	Maximum distance from top to bottom of the seed (use 10 seeds)	$BC_1F_{1:2}/F_{2:3}$
		Width (mm)	SDW	*Sdw*	Maximum distance from hilum to its opposite side (use 10 seeds)	$BC_1F_{1:2}/F_{2:3}$
		Thickness (mm)	SDT	*Sdt*	Maximum distance between both sides of the hilum (use 10 seeds)	$BC_1F_{1:2}/F_{2:3}$
	Pod	Length (cm)	PDL	*Pdl*	Length of straight pod (use 10 pods)	BC_1F_1/F_2
		Width (mm)	PDW	*Pdw*	Maximum width (use 10 pods) measured after soaking in water to flatten the pod to measure	BC_1F_1/F_2
		Spacing between seeds (mm)	PDSBS*	*Pdsbs*	Spacing between seeds is calculated by formula: [(PDL*10) – (SDL*SDNPPD)]/SDNPPD	BC_1F_1/F_2
	Stem	Thickness (mm)	STT	*Stt*	Stem diameter under the primary leaf (measured at flowering stage)	BC_1F_1/F_2
	Leaf	Primary leaf length (cm)	LFPL	*Lfpl*	Distance from pulvinus to leaf tip	BC_1F_1/F_2
		Primary leaf width (cm)	LFPW	*Lfpw*	Maximum width	BC_1F_1/F_2
Plant type	Epicotyl	Length (cm)	ECL	*Ecl*	Length from cotyledon to primary leaf	BC_1F_1/F_2
	Stem	Length (up to 10th node) (cm)	STL10	*Stl10*	Length from node on primary leaf to node 10 of trifoliate leaf	BC_1F_1/F_2
		Length (whole)	STLW*	*Stlw*	Length from node on primary leaf to terminal shoot	BC_1F_1
	Branch	Number (count)	BRN	*Brn*	Number of branches on main stem from node 1 to node 10 of trifoliate leaf (measured at post maturity stage just before discarding)	BC_1F_1/F_2
Earliness	Flower	Days to first flower (day)	FLD	*Fld*	Number of days from planting to 1st flowering	BC_1F_1/F_2
	Pod	Days to maturity of 1st pod (day)	PDDM	*Pddm*	Number of days from 1st flowering to harvesting of 1st pod	BC_1F_1/F_2
Yield potential	Seed	Total weight (g)	SDTWT	*Sdtwt*	Total weight of harvested seeds	BC_1F_1/F_2
		Number of seeds per pod (seeds/pod)	SDNPPD	*Sdnppd*	Number of seeds per pod	BC_1F_1/F_2
	Pod	Total number (pod)	PDTN	*Pdtn*	Total number of harvested pods	BC_1F_1/F_2
Pigmentation	Epicotyl	Epicotyl colour	ECC	*Ecc*	Red or green	BC_1F_1/F_2
	Seed	Seed coat colour	SDC	*Sdc*	Black or brown	BC_1F_1/F_2

* Not included in Kaga *et al.* (2008).

the first mature pod. After harvesting all pods, total pod number (PDTN) and total seed weight (SDTWT) were measured in each plant. The number of seeds per pod (SDNPPD) was recorded using ten pods. Spacing between seeds (PDSBS) was evaluated with the formula: [(PDL*10) – (SDL*SDNPPD)]/SDNPPD using the data from ten pods. Seed colour from each plant was scored as black or brown.

SSR marker analysis

A genetic linkage map based on the F_2 population was constructed using framework SSR markers that were distributed throughout the BC_1F_1 genetic linkage map (Kongjaimun *et al.*, 2012). In total, 113 SSR markers, located at about 10-cM intervals on each linkage group of the BC_1F_1 genetic linkage map, were chosen to genotype the F_2 population. The polymorphic SSR markers consisted of 78 from cowpea, 26 from azuki bean and nine from mungbean.

The PCR reaction mixture and multiplex PCR were the same as those described by Kongjaimun *et al.* (2012). The PCR thermal cycling programmes for azuki bean, cowpea and mungbean SSRs were set as described by Wang *et al.* (2004). After amplification, allele size(s) of each primer pair was determined according to Kongjaimun *et al.* (2012).

Data analysis

Mean, standard deviation and broad-sense heritability were calculated, and the frequency distribution of phenotypes in the F_2 and BC_1F_1 populations were examined for each trait. The correlation coefficient (r) between traits was also calculated. The total number of seeds per plant was used as an index of seed productivity and treated as the dependent (y)

variable. As stem length, branch number, leaf size (the product of maximum length and width), 100-seed weight, pod length, total number of pods per plant and number of seeds per pod are possibly correlated to the total number of seeds, these traits were treated as the independent (x) variables.

Linkage map construction and QTL analysis

The linkage map of the F_2 population was constructed by JoinMap 4·0 (Van Ooijen, 2006). Chi-square analysis was performed for the goodness-of-fit to 1 : 2 : 1 segregation ratio of each marker at a probability (P) of 0·05, 0·01 and 0·001. A minimum LOD score of 3 and recombination frequency of 0·25 in the Kosambi mapping function (Kosambi, 1944) were used. Double crossovers between adjacent loci were confirmed manually. QTL analysis was conducted using the software package MultiQTL ver. 2·6 according to the procedures described by Kaga *et al.* (2008). The QTLs were named after Somta *et al.* (2006). Randomness of the genomic distribution of the QTLs was determined using chi-square tests (Isemura *et al.*, 2007). Randomness of the QTLs along a linkage group was tested using a Poisson distribution test (Somta *et al.*, 2006; Isemura *et al.*, 2007).

RESULTS

Linkage map construction

The BC_1F_1 map constructed by Kongjaimun *et al.* (2012) across 11 linkage groups (LGs) was used. The map consists of 226 SSR markers (165 from cowpea, 46 from azuki bean and 15 from mungbean) and spans a total distance of 852·4 cM. The F_2 map constructed here using 113 SSR markers (78 from cowpea, 26 from azuki bean and nine from mungbean) covering 977·1 cM with an average distance between the adjacent markers of 9·58 cM (Table 2). The length of the LGs ranged from 28·3 cM (LG11) to 140·4 cM (LG01) with a mean of 88·83 cM. The number of marker loci per LG varied from six (LG9) to 16 (LG1) with a mean of 10·27. The length of the F_2 map was equivalent to 114·6 % of the BC_1F_1 map. All of the LGs except LG11 had a length of 60 cM or longer. The largest gap of 41·3 cM was on LG9. Segregation distortion was observed at 48·7 % (55 of 113) of mapped markers ($P < 0·05$). The distorted markers were distributed on all LGs (Fig. 1). In most cases, on the same LG the distorted markers appeared to be clustered or close to one another. All the markers on LG11 and nine out of 11 (81·8 %) markers on LG7 showed distortion (Supplementary Data, Table S1). Orders and linkages of all the markers were the same in both linkage maps.

TABLE 2. *Number of markers and average distance between markers in each linkage group in the yardlong bean map estimated from the* F_2 *population*

Linkage group	Length (cM)	Average interval (cM)	No. of SSR markers			
			Total	Cowpea	Azuki bean	Mung bean
1	140·4	9·36	16	12	4	0
2	93·4	8·49	12	9	3	0
3	105·7	8·13	14	10	3	1
4	87·2	10·9	9	5	4	0
5	73·7	9·21	9	6	1	2
6	107·7	13·46	9	6	2	1
7	107·1	10·71	11	8	0	3
8	103·4	11·49	10	7	1	2
9	70·5	14·09	6	5	1	0
10	59·8	6·64	10	5	5	0
11	28·3	4·72	7	5	2	0
Total	977·1	9·58	113	78	26	9

Variation of domestication-related traits

The mean, range and standard deviation of traits in the parents, and F_2 and BC_1F_1 populations as well as their broad-sense heritabilities are shown in Tables 3 and 4. Means of the F_2 population generally fell between those of the parents for all traits except days to maturity of first pod and number of seeds per pod. Similarly, means of the BC_1F_1 population were between their parents for all traits except days to first flowering and number of seeds per pod. The parents were clearly different in all traits observed. The cultivated parent showed higher values than the wild parent for seed coat permeability, number of twists along the pod, stem length (1st to 10th nodes and the 1st node to terminal shoot) and the size of organs such as leaf, stem, seed and pod. A pronounced difference was observed for SD100WT, PDL, PDW, PDSBS, STL10 and PDTN. Regarding qualitative traits, the cultivated parent had a black seed coat and indehiscent pod whereas the wild parent had a black mottled over tan seed coat and pods were dehiscent. Both parents had green epicotyls.

The measured traits showed nearly a normal distribution in both populations (Supplementary Data, Figs S1 and S2). The mean percentage of imbibed seeds (SDP) for the F_2 population showed a biased distribution towards the cultivated parent. Clear transgressive segregation was observed in STT, PDSBS, ECL, STL10, STLW, BRN, FLD, PDDM, SDTWT, SDNPPD and PDTN in both the F_2 and the BC_1F_1 population.

Generally, the traits measured showed high broad-sense heritability (Tables 3 and 4). SDP, SDTWT, SDL, SDW, PDL, PDSBS and STL10 showed high heritability (>70 %) whereas STT, LFPL, LFPW, ECL, FLD and PDDM showed medium to low heritability (<70 %). SDT and PDW showed high heritability in only the BC_1F_1 population, while SDTWT, SDNPPD and PDTN showed high heritability in only the F_2 population.

There were significant positive correlations ($P < 0·05$) between related traits, such as between pod length and pod width, and between seed size-related traits and pod size-related traits (Supplementary Data, Tables S2 and S3). PDT and PDTN were negatively correlated with seed-related traits, STLW and earliness traits (FLD and PDDM).

QTLs for domestication-related traits

The results of the QTL analysis for each trait in each population are shown in Table 5. Only QTLs with $P \leq 0·05$ were considered. In total, 153 QTLs were identified for the 21 traits. One to 11 QTLs were detected for each trait except

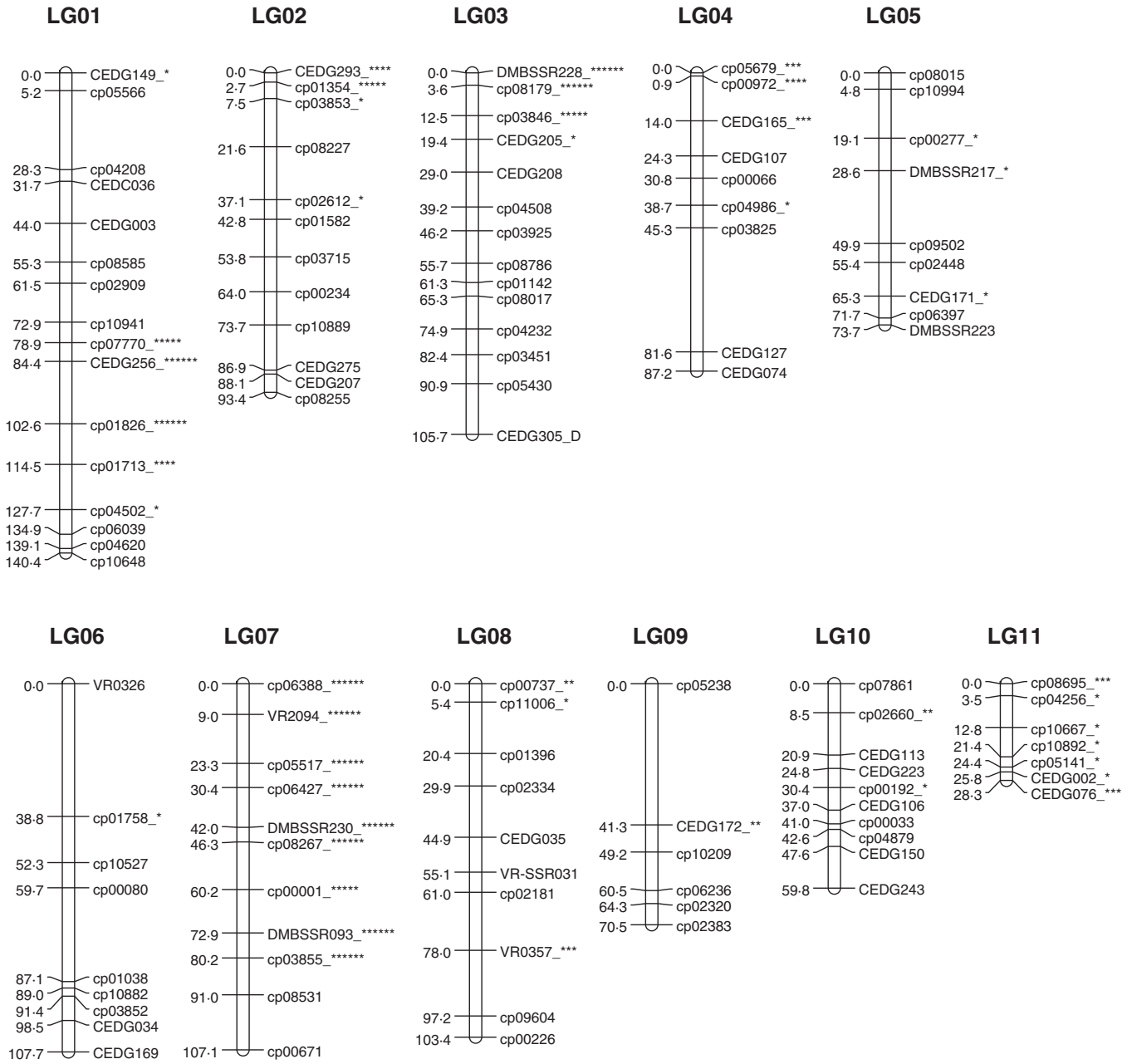

FIG. 1. A genetic linkage map of yardlong bean based on SSR markers. This map was constructed from 188 F_2 individuals of *V. unguiculata* ssp. *unguiculata* cv.-gr. *sesquipedalis* × *V. unguiculata* ssp. *unguiculata* var. *spontanea*. Map distances (cM) are shown on the left side and marker names on the right side of the linkage groups. 'cp-' and 'CED-' represent the SSR marker loci from cowpea and azuki bean, respectively, and 'DMBSSR-', 'VR-' and 'VR-SSR-' represent the SSR marker loci from mungbean. Asterisks indicate significant segregation distortion at the *5, **1 and ***0·1 % significance levels, respectively.

for BRN and SDTWT in the BC_1F_1 population, from which no significant QTL was detected.

Seed coat permeability (SDP). One key trait in domestication is reduction or loss of seed dormancy, which enables uniform germination. Like several cereal and legume crops, domestication of cowpea/yardlong bean has resulted in reduced seed dormancy. SDP in yardlong bean and wild cowpea were 100 and 0 %, respectively. Six QTLs were detected on LGs 1, 2, 4, 7, 8 and 11, where all alleles, except *Sdp7·1*–, of the yardlong bean parent increase the percentage of permeable seeds. The QTL located on LG1 had the largest effect on phenotypic variance explained (Table 5).

Pod dehiscence (PDT and PDD). Loss of pod dehiscence in legume crops is advantageous for harvesting seeds but reducing seed dispersal in wild species. Pod dehiscence can be characterized as a qualitative or quantitative trait based on visual score (PDD; dehiscent vs. indehiscent) or number of twists along the shattered pod (PDT).

The qualitative nature of dehiscence was examined only in the F_2 population (Table 3) and the progenies segregated for

TABLE 3. *Mean, standard deviation, minimum, maximum and heritability values of parents, and* F_2 *or* $F_{2:3}$ *populations derived from the cross between cultivated yardlong bean and wild cowpea*

		Cultivated yardlong bean, JP81610				Wild cowpea, TVnu457				F_2 or $F_{2:3}$				
Trait	Units	Mean	s.d.	Min.	Max.	Mean	s.d.	Min.	Max.	Mean	s.d.	Min.	Max.	Heritability (%)
SDP	(%)	100·0	0·0	100·0	100·0	0·0	0·0	0·0	0·0	78·2	36·5	0·0	100·0	100·0
PDD	–	Indehiscence				Dehiscence				Dehiscence : indehiscence*				
SD100WT	g	19·4	1·4	16·6	20·9	2·5	0·2	2·2	2·7	5·7	1·9	2·0	16·1	72·6
SDL	mm	11·9	0·4	11·3	12·5	3·9	0·2	3·6	4·1	7·2	1·1	4·3	9·9	92·5
SDW	mm	3·7	0·2	3·3	4·0	2·0	0·1	1·8	2·2	2·7	0·3	0·8	3·8	81·0
SDT	mm	6·2	0·2	5·9	6·5	2·7	0·3	2·4	3·9	4·0	0·5	2·6	5·8	65·7
PDL	cm	78·1	3·1	72·9	84·0	9·9	0·4	8·8	10·4	21·3	5·8	10·2	41·3	85·7
PDW	mm	11·5	0·8	10·0	13·0	0·5	0·0	0·4	0·5	0·7	0·1	0·5	1·0	49·9
PDSBS	mm	26·6	1·8	23·8	30·8	1·9	0·2	1·6	2·2	9·9	3·7	2·1	26·3	87·8
STT	mm	15·3	2·0	11·2	18·4	9·7	1·8	6·3	11·9	13·4	2·0	7·4	18·8	15·1
LFPL	cm	7·6	0·7	6·5	8·8	2·9	0·4	2·2	3·4	4·7	0·6	2·4	6·1	18·0
LFPW	cm	5·2	0·5	4·5	6·0	1·6	0·2	1·2	2·0	2·9	0·4	1·9	3·7	2·6
ECL	cm	6·6	0·9	5·0	8·0	4·2	0·5	3·2	5·0	5·2	1·1	2·5	8·5	62·2
STL10	cm	120·8	9·5	105·0	134·3	30·0	9·5	16·0	46·0	68·3	19·9	30·0	118·5	77·1
FLD	day	55·1	3·5	50·0	62·0	43·9	5·9	37·0	62·0	43·9	4·3	37·0	58·0	0
PDDM	day	18·6	4·1	15·0	28·0	14·6	3·3	9·0	19·0	20·6	2·2	15·0	29·0	0
SDTWT	g	209·0	55·5	115·0	307·5	94·9	23·3	54·3	131·8	161·1	99·8	12·9	631·1	81·8
SDNPPD	count	20·3	0·7	19·1	21·6	17·3	0·6	15·9	17·9	12·8	3·0	7·0	20·3	95·7
PDTN	count	128·5	20·3	59·0	130·0	504·8	131·9	248·0	701·0	461·9	248·6	15·0	1609·0	85·6
ECC	–	Green				Green				Green				
SDC	–	Black				Brown				Brown : black†				

* = 111:77 (ratio = 9 : 7, $\chi^2 = 0{\cdot}60$, $P = 0{\cdot}44$).
† = 33:155 (ratio = 3 : 13, $\chi^2 = 0{\cdot}18$, $P = 0{\cdot}67$).

TABLE 4. *The mean, standard deviation, minimum, maximum and heritability values of parents, and the* BC_1F_1 *or* $BC_1F_{1:2}$ *populations derived from the cross between cultivated yardlong bean and wild cowpea*

		Cultivated yardlong bean, JP81610				Wild cowpea, TVnu457				BC_1F_1 or $BC_1F_{1:2}$				
Trait	Units	Mean	s.d.	Min.	Max.	Mean	s.d.	Min.	Max.	Mean	s.d.	Min.	Max.	Heritability (%)
SDP	(%)	97·7	2·7	93·0	100·0	0·0	0·0	0·0	0·0	46·9	31·4	0·0	100·0	99·6
PDT	count	0·0	0·0	0·0	0·0	6·2	0·3	5·8	6·6	3·4	4·6	0·0	13·0	99·9
SD100WT	g	17·5	1·4	14·4	19·6	2·4	0·2	1·8	2·6	10·5	1·9	6·4	18·7	71·4
SDL	mm	11·2	0·4	10·5	11·9	3·6	0·1	3·5	3·9	8·9	0·8	4·6	10·7	85·2
SDW	mm	6·3	0·2	5·9	6·7	2·5	0·1	2·3	2·6	5·0	0·4	3·9	5·9	78·1
SDT	mm	4·1	0·2	3·9	4·4	1·8	0·1	1·7	1·9	3·4	0·2	2·7	4·1	72·1
PDL	cm	64·4	5·7	56·8	73·9	8·5	0·3	8·0	9·0	31·6	7·8	15·1	57·1	73·1
PDW	mm	1·3	0·1	1·2	1·4	0·5	0·0	0·5	0·5	0·9	0·1	0·7	1·3	88·2
PDSBS	mm	30·0	3·5	25·1	38·1	3·1	0·7	2·1	4·0	17·4	6·7	4·4	40·2	86·1
STT	mm	7·4	1·1	5·7	9·1	5·4	1·0	4·2	6·8	6·0	1·1	3·9	8·5	0
LFPL	cm	8·0	0·7	7·2	9·3	3·4	0·3	2·9	4·0	5·9	0·5	4·3	7·5	6·3
LFPW	cm	5·5	0·3	5·0	5·9	1·8	0·3	1·2	2·2	3·7	0·3	2·8	4·5	13·9
ECL	cm	4·2	0·4	3·6	5·0	2·2	0·4	1·7	3·0	3·3	0·6	2·0	5·7	65·8
STL10	cm	177·8	14·1	157·0	195·5	63·6	6·3	53·0	73·0	142·4	32·9	61·0	219·5	89·0
STLW	cm	154·8	23·8	121·0	195·0	21·6	14·6	11·0	48·0	99·5	45·4	17·0	220·0	81·1
BRN	count	2·7	1·6	1·0	6·0	7·1	0·9	6·0	9·0	3·8	1·8	0·0	9·0	45·8
FLD	day	57·6	2·7	55·0	64·0	56·8	4·4	50·0	66·0	56·0	4·4	47·0	67·0	29·5
PDDM	day	18·4	1·5	16·0	21·0	12·3	0·9	11·0	14·0	15·9	1·7	7·0	24·0	47·2
SDTWT	g	15·4	5·1	10·9	28·0	12·8	4·2	7·0	22·4	15·7	5·5	4·6	31·5	27·8
SDNPPD	count	15·7	2·2	11·6	19·8	12·9	1·1	11·3	14·3	12·5	3·2	5·1	19·5	69·7
PDTN	count	6·7	2·2	3·0	10·0	89·3	21·6	47·0	119·0	17·3	8·1	2·0	50·0	0
ECC	–	Green				Green				Green				
SDC	–	Black				Brown				Black				

PDD in the ratio 111 dehiscent to 77 indehiscent plants. The segregation ratio was 9 : 7 ($\chi^2 = 0{\cdot}60$, $P = 0{\cdot}44$), indicating that duplicated recessive genes control pod indehiscence.

The quantitative nature of pod dehiscence was investigated only in the BC_1F_1 population (Table 4). Yardlong bean JP81610 showed no pod twisting in contrast to wild cowpea

TABLE 5. *QTLs detected in the* $BC_1F_{1:2}$, F_2 *and* $F_{2:3}$ *populations derived from the cross between cultivated yardlong bean and wild cowpea*

		$BC_1F_{1:2}$						$F_{2:3}$						
Trait	QTL name	LG	LOD	*P*	Loci (cM)	PVE (%)	Additive effect	LG	LOD	*P*	Loci (cM)	PVE (%)	Additive effect	Dominant effect
SDP	*Sdp1·1* +	1	27·3	0·0009	90·2	41·1	8·1	1						
	Sdp2·1 +	2	4·3	0·0009	2·2	4·3	2·6	2						
	Sdp4·1 +	4	2·2	0·0112	46·9	2·9	2·1	4				NI		
	Sdp7·1–	7	1·9	0·0300	30·8	1·9	–1·7	7						
	Sdp8·1 +	8	3·1	0·0019	82·8	3·0	2·2	8						
	Sdp11·1 +	11	4·9	0·0009	17·5	5·2	2·9	11						
PDT	*Pdt1·1*–	1	11·7	0·0009	93·4	11·8	–3·3	1				NI		
	Pdt4·1–	4	3·0	0·0009	24·5	2·6	–1·5	4						
	Pdt7·1–	7	30·1	0·0009	9·3	47·6	–6·5	7						
	Pdt9·1–	9	2·2	0·0084	58·1	1·9	–1·3	9						
SD100WT	*Sd100wt1·1* +	1	17·2	0·0009	116·2	11·0	1·3	1	18·9	0·0009	89·0	16·8	1·1	–0·5
	Sd100wt2·1 +	2	8·4	0·0009	2·9	4·6	0·8	2	4·7	0·0009	45·7	3·6	0·5	0·3
	Sd100wt3·1 +	3	12·4	0·0009	0·6	7·1	1·0	3	16·4	0·0009	11·5	18·7	1·2	0·1
	Sd100wt4·1 +	4	10·6	0·0009	6·2	6·1	1·0	4	12·8	0·0009	24·3	8·9	0·7	0·4
	Sd100wt5·1 +	5	5·7	0·0009	64·9	2·9	0·7	5						
	Sd100wt6·1 +	6	5·1	0·0009	38·7	5·2	0·9	6						
	Sd100wt7·1 +	7	31·2	0·0009	22·9	24·6	1·9	7	11·9	0·0009	51·6	13·1	1·0	0·3
	Sd100wt8·1 +	8	9·5	0·0009	21·6	5·5	0·9	8	14·1	0·0009	23·7	11·4	0·9	0·0
	Sd100wt10·1 +	10	8·0	0·0009	28·9	4·3	0·8	10	4·4	0·0009	5·8	2·6	0·4	0·2
	Sd100wt11·1–	11	11·8	0·0009	31·9	7·6	–1·1	11						
SDL	*Sdl1·1* +	1	12·6	0·0009	89·8	10·4	0·5	1	29·4	0·0009	94·9	20·8	0·7	–0·1
	Sdl2·1 +	2	6·4	0·0009	56·5	4·8	0·4	2	8·0	0·0009	47·7	2·8	0·2	0·2
	Sdl3·1 +	3	8·8	0·0009	18·5	7·2	0·4	3	25·0	0·0009	8·6	18·8	0·7	0·3
	Sdl4·1 +	4	16·0	0·0009	35·0	13·5	0·6	4	21·9	0·0009	24·3	7·5	0·4	0·1
	Sdl5·1 +	5	3·8	0·0009	15·9	2·7	0·3	5	5·9	0·0009	49·9	1·6	0·2	0·0
	Sdl6·1 +	6	2·4	0·0075	34·5	2·1	0·2	6	4·9	0·0009	7·3	1·7	0·2	0·2
	Sdl7·1 +	7	13·6	0·0009	23·4	13·5	0·6	7	41·8	0·0009	46·3	26·5	0·7	0·5
	Sdl8·1 +	8	12·7	0·0009	56·2	9·8	0·5	8	22·6	0·0009	23·9	9·1	0·5	0·0
	Sdl11·1–	11	11·9	0·0009	34·4	9·3	–0·5	11						
SDW	*Sdw1·1* +	1	22·1	0·0009	93·2	18·4	0·3	1	3·2	0·0047	114·5	4·1	0·1	0·0
	Sdw2·1 +	2	11·1	0·0009	15·6	8·2	0·2	2						
	Sdw3·1 +	3	19·6	0·0009	16·8	17·2	0·3	3	3·1	0·0094	25·8	4·2	0·1	0·1
	Sdw4·1 +	4	4·8	0·0009	4·7	3·3	0·1	4	6·6	0·0009	58·3	11·7	0·2	0·0
	Sdw6·1 +	6	2·5	0·0075	61·2	1·6	0·1	6						
	Sdw7·1 +	7	22·9	0·0009	21·6	20·9	0·4	7	5·3	0·0009	63·4	18·5	0·2	0·2
	Sdw8·1 +	8	6·7	0·0009	20·3	4·6	0·2	8	8·2	0·0009	29·9	8·8	0·1	0·0
	Sdw10·1 +	10						10	8·7	0·0009	23·3	10·0	0·2	0·0
SDT	*Sdt1·1* +	1	6·8	0·0009	123·9	6·4	0·1	1	12·6	0·0009	120·3	11·3	0·2	–0·1
	Sdt2·1 +	2						2	9·0	0·0009	70·7	7·5	0·2	0·1
	Sdt3·1 +	3	11·8	0·0009	0·0	10·5	0·2	3	21·4	0·0009	16·4	26·4	0·3	0·1
	Sdt4·1 +	4	8·7	0·0009	3·8	7·7	0·1	4	5·5	0·0009	38·7	3·8	0·1	0·0
	Sdt6·1 +	6	4·2	0·0009	39·4	5·3	0·1	6	5·6	0·0009	91·4	3·9	0·1	0·0
	Sdt7·1 +	7	8·5	0·0009	39·4	7·5	0·1	7	14·2	0·0009	43·0	15·2	0·3	0·1
	Sdt8·1 +	8	10·1	0·0009	20·4	9·5	0·1	8	12·1	0·0009	29·7	7·8	0·2	0·1
	Sdt9·1 +	9	2·6	0·0009	51·4	2·1	0·1	9						
	Sdt10·1 +	10	14·0	0·0009	38·6	13·8	0·2	10						
	Sdt11·1–	11	4·9	0·0009	29·2	4·2	–0·1	11						
PDL	*Pdl1·1* +	1	21·9	0·0009	81·3	12·1	5·4	1	22·3	0·0009	86·5	14·3	3·1	–1·2
	Pdl2·1 +	2	2·2	0·0112	45·6	0·9	1·5	2						

Continued

TABLE 5. *Continued*

		$BC_1F_{1:2}$						$F_{2:3}$						
Trait	QTL name	LG	LOD	*P*	Loci (cM)	PVE (%)	Additive effect	LG	LOD	*P*	Loci (cM)	PVE (%)	Additive effect	Dominant effect
	Pdl3·1 +	3	13·0	0·0009	1·8	6·6	4·0	3	22·8	0·0009	15·1	19·9	3·6	1·8
	Pdl4·1 +	4	6·2	0·0009	33·2	2·9	2·7	4	2·4	0·0280	38·7	0·9	0·7	0·7
	Pdl5·1 +	5	9·6	0·0009	64·9	4·5	3·3	5	7·0	0·0009	49·9	3·1	1·5	0·0
	Pdl7·1 +	7	42·4	0·0009	26·5	31·0	8·7	7	31·6	0·0009	33·9	26·9	4·4	0·1
	Pdl8·1 +	8	15·7	0·0009	20·4	8·5	4·6	8	12·3	0·0009	23·6	6·9	2·1	0·9
	Pdl9·1–	9	3·0	0·0019	29·6	1·3	−1·8	9						
	Pdl11·1 +	11	23·0	0·0009	39·0	14·4	5·9	11	22·6	0·0009	24·4	10·4	1·7	−3·1
PDW	*Pdw1·1* +	1	17·8	0·0009	111·0	12·1	0·1	1	14·7	0·0009	105·8	10·7	0·0	0·0
	Pdw2·1 +	2						2	5·5	0·0009	39·6	3·1	0·0	0·0
	Pdw3·1 +	3	16·7	0·0009	1·9	10·6	0·1	3	29·7	0·0009	14·2	31·1	0·1	0·0
	Pdw4·1 +	4	11·0	0·0009	23·5	6·4	0·1	4	12·1	0·0009	24·2	7·3	0·0	0·0
	Pdw6·1 +	6	1·7	0·0290	73·4	1·0	0·0	6						
	Pdw7·1 +	7	35·1	0·0009	23·2	31·2	0·1	7	15·5	0·0009	42·9	11·0	0·0	0·0
	Pdw8·1 +	8	20·3	0·0009	24·9	14·0	0·1	8	21·1	0·0009	24·6	16·4	0·1	0·0
	Pdw11·1 +	11	5·9	0·0009	32·1	3·5	0·0	11	3·3	0·0009	24·4	1·5	0·0	0·0
PDSBS	*Pdsbs1·1* +	1	17·3	0·0009	75·5	11·2	4·6	1	14·5	0·0009	64·0	8·8	1·2	−1·6
	Pdsbs2·1 +	2						2	9·2	0·0009	64·0	5·1	1·2	0·6
	Pdsbs3·1 +	3	6·3	0·0009	3·3	3·5	2·6	3	21·4	0·0009	12·9	21·6	2·4	1·1
	Pdsbs4·1 +	4	6·2	0·0009	37·8	4·3	2·9	4	11·0	0·0009	0·5	5·2	1·1	0·9
	Pdsbs5·1 +	5						5	8·8	0·0009	71·7	4·5	1·2	0·0
	Pdsbs7·1 +	7	30·4	0·0009	34·2	25·0	6·9	7	6·2	0·0009	9·0	5·1	1·2	0·2
	Pdsbs8·1 +	8	8·1	0·0009	9·6	5·4	3·2	8	16·2	0·0009	13·5	14·4	2·0	−0·9
	Pdsbs9·1 +	9						9	7·7	0·0009	66·5	4·5	1·1	−0·4
	Pdsbs11·1–	11	31·4	0·0009	32·3	28·4	−7·4	11	17·4	0·0009	18·1	10·8	−1·1	2·0
STT	*Stt1·1*–	1	4·0	0·0019	87·5	7·6	−0·6	1						
	Stt2·1 +	2	1·7	0·0465	75·1	3·1	0·4	2	3·1	0·0102	86·9	4·3	0·6	0·1
	Stt3·1 +	3	2·8	0·0056	78·1	5·2	0·5	3	6·4	0·0009	83·2	9·9	0·9	0·2
	Stt4·1 +	4						4	4·1	0·0019	30·8	5·9	0·7	0·0
	Stt6·1 +	6	1·8	0·0262	23·6	3·0	0·4	6	3·7	0·0028	56·0	5·8	0·6	0·5
	Stt7·1 +	7						7	5·8	0·0009	42·0	13·0	1·0	0·4
	Stt9·1–	9	2·0	0·0112	19·5	4·6	−0·5	9						
	Stt10·1–	10	2·2	0·0112	63·2	3·7	−0·4	10						
	Stt11·1–	11	2·3	0·0065	35·5	4·1	−0·4	11	4·7	0·0009	23·8	6·6	0·7	−0·4
LFPL	*Lfpl3·1* +	3	2·0	0·0234	29·7	3·2	0·2	3						
	Lfpl6·1 +	6	2·0	0·0168	79·5	3·1	0·2	6						
	Lfpl7·1 +	7	10·9	0·0009	28·7	20·9	0·5	7						
	Lfpl8·1 +	8	1·7	0·0475	62·4	2·5	0·2	8						
	Lfpl11·1 +	11	4·9	0·0009	0·0	8·2	0·3	11	3·9	0·0009	21·4	10·0	0·3	0·1
LFPW	*Lfpw1·1* + –	1	3·1	0·0019	101·5	4·8	0·1	1	6·1	0·0009	6·7	9·7	−0·2	0·0
	Lfpw2·1 +	2						2	5·5	0·0009	53·8	7·6	0·1	−0·1
	Lfpw3·1 +	3	3·8	0·0009	26·6	5·9	0·2	3	6·0	0·0009	89·3	9·6	0·2	0·0
	Lfpw6·1–	6	2·9	0·0009	8·6	5·0	−0·1	6						
	Lfpw7·1 +	7	7·3	0·0009	28·6	13·1	0·2	7	3·0	0·0112	0·0	5·4	0·1	0·0
	Lfpw8·1 +	8	2·6	0·0084	79·4	4·4	0·1	8						
	Lfpw9·1–	9	1·8	0·0215	38·9	2·7	−0·1	9	3·8	0·0009	41·3	6·8	−0·1	0·0
	Lfpw11·1 +	11	1·4	0·0393	5·7	2·3	0·1	11	5·6	0·0009	20·2	9·5	0·2	0·0
ECL	*Ecl2·1*–	2	2·0	0·0206	25·6	1·9	−0·2	2						
	Ecl4·1 +	4	6·1	0·0009	42·2	8·3	0·4	4						
	Ecl6·1–	6	6·8	0·0009	34·9	9·9	−0·4	6						
	Ecl7·1 +	7	3·1	0·0009	41·0	3·0	0·2	7						
	Ecl9·1–	9	6·1	0·0009	33·2	6·9	−0·3	9	2·3	0·0178	49·7	5·2	−0·3	0·2

	Ecl10·1 +	10	22·9	0·0009	63·2	28·7	0·7	10	3·2	0·0056	59·8	7·6	0·2	−0·6
STL10	*Stl101·1* +	1	2·8	0·0056	104·6	2·0	8·8	1						
	Stl102·1−	2	7·9	0·0009	56·9	6·3	−15·9	2						
	Stl103·1 +	3						3	7·5	0·0009	32·1	8·1	7·9	−1·5
	Stl104·1 +	4						4	4·7	0·0009	81·6	4·1	4·1	−5·4
	Stl105·1−	5	5·7	0·0009	54·7	4·2	−12·9	5	6·0	0·0009	67·2	5·5	−6·5	1·3
	Stl106·1−	6	9·5	0·0009	60·1	7·1	−16·8	6	7·9	0·0009	94·9	8·6	−7·3	5·2
	Stl107·1 +	7	14·6	0·0009	29·5	11·6	21·5	7	17·6	0·0009	36·9	19·7	10·5	−9·4
	Stl108·1−	8	2·8	0·0009	68·2	1·9	−8·7	8						
	Stl109·1−	9	4·0	0·0009	51·4	2·6	−10·2	9	4·6	0·0009	64·3	3·8	5·3	−1·7
	Stl1010·1 +	10	30·2	0·0009	59·5	33·9	36·7	10	16·1	0·0009	59·8	16·0	10·5	−5·3
	Stl1011·1 +	11	4·8	0·0009	5·7	3·4	11·6	11						
STLW	*Stlw1·1* +	1	4·2	0·0009	62·9	4·6	19·3					NI		
	Stlw2·1−	2	5·4	0·0009	51·0	6·4	−22·7							
	Stlw3·1−	3	2·1	0·0158	3·3	2·3	−13·6							
	Stlw5·1−	5	2·7	0·0056	35·7	2·9	−15·3							
	Stlw6·1−	6	6·0	0·0009	61·2	6·7	−23·3							
	Stlw8·1−	8	4·2	0·0009	39·0	4·6	−19·3							
	Stlw10·1 +	10	19·0	0·0009	59·9	28·6	48·1							
BRN					ND							NI		
FLD	*Fld1·1* +	1						1	3·7	0·0009	17·0	4·4	1·2	−0·8
	Fld2·1 +	2						2	15·7	0·0009	65·5	17·6	2·5	−0·6
	Fld4·1 + −	4	1·9	0·0177	3·1	2·6	1·4	4	3·7	0·0056	81·6	2·9	−1·0	−0·4
	Fld5·1−	5						5	7·8	0·0009	50·3	6·4	−0·6	2·0
	Fld6·1 +	6						6	4·8	0·0009	36·6	6·1	0·7	−1·9
	Fld7·1 +	7	5·3	0·0009	54·1	7·7	2·4	7	5·1	0·0009	98·7	6·9	1·6	−0·3
	Fld8·1 +	8	5·3	0·0009	36·1	7·9	2·4	8	5·1	0·0009	55·1	4·8	1·3	−0·4
	Fld9·1 +	9	2·7	0·0047	50·8	3·6	1·6	9	2·9	0·0065	0·0	2·3	0·6	1·0
	Fld10·1 +	10	3·0	0·0056	47·8	4·0	1·7	10	13·1	0·0009	39·2	15·6	1·7	−2·4
	Fld11·1−	11	11·4	0·0009	40·4	19·6	−3·8	11						
PDDM	*Pddm1·1*−	1						1	5·5	0·0009	28·3	9·2	−1·0	−0·4
	Pddm2·1 +	2						2	2·7	0·0206	78·3	5·5	0·8	−0·2
	Pddm3·1 +	3						3	4·4	0·0009	2·0	17·1	1·4	−0·1
	Pddm4·1 +	4	2·7	0·0009	52·9	6·6	0·9	4						
	Pddm6·1 +	6	2·5	0·0037	57·7	5·1	0·8	6						
	Pddm7·1 +	7	3·8	0·0009	59·7	7·9	1·0	7	2·8	0·0178	13·5	5·5	0·3	−1·0
SDTWT	*Sdtwt2·1* +	2			ND			2	3·2	0·0019	37·1	4·5	4·6	43·5
	Sdtwt4·1 +	4						4	2·7	0·0122	50·0	4·7	28·4	20·0
	Sdtwt5·1 +	5						5	2·8	0·0168	49·9	3·6	27·0	−10·2
	Sdtwt6·1 +	6						6	3·9	0·0028	52·3	5·1	9·4	45·0
	Sdtwt7·1 +	7						7	8·0	0·0009	48·5	23·1	64·5	39·9
	Sdtwt10·1−	10						10	4·1	0·0009	38·6	6·6	−22·5	42·9
SDNPPD	*Sdnppd7·1* +	7						7	10·6	0·0009	45·9	12·8	1·5	−0·4
	Sdnppd11·1 +	11	48·1	0·0009	36·5	70·1	5·4	11	31·6	0·0009	26·6	45·7	1·7	−3·2
PDTN	*Pdtn1·1*−	1	3·9	0·0009	91·6	5·7	−3·9	1						
	Pdtn2·1−	2						2	4·0	0·0028	73·7	1·8	−50·3	47·6
	Pdtn3·1−	3	3·3	0·0019	0·0	4·7	−3·5	3						
	Pdtn4·1−	4	2·4	0·0047	64·0	3·6	−3·1	4						
	Pdtn6·1 +	6						6	11·0	0·0009	10·6	57·1	270·1	−283·0
	Pdtn7·1− +	7	3·5	0·0009	28·0	5·2	−3·7	7	7·1	0·0009	50·2	8·1	69·6	149·3
	Pdtn8·1−	8	2·2	0·0178	70·1	3·2	−2·9	8	10·3	0·0009	10·2	6·7	−107·2	59·8
	Pdtn9·1−	9	1·8	0·0122	6·9	3·5	−3·0	9						
	Pdtn10·1−	10						10	3·9	0·0009	38·6	2·0	−57·9	33·9
	Pdtn11·1−	11	9·4	0·0009	35·8	15·6	−6·4	11	12·5	0·0009	3·5	6·8	−114·6	26·1

NI, not investigated; ND, no significant QTL detected.

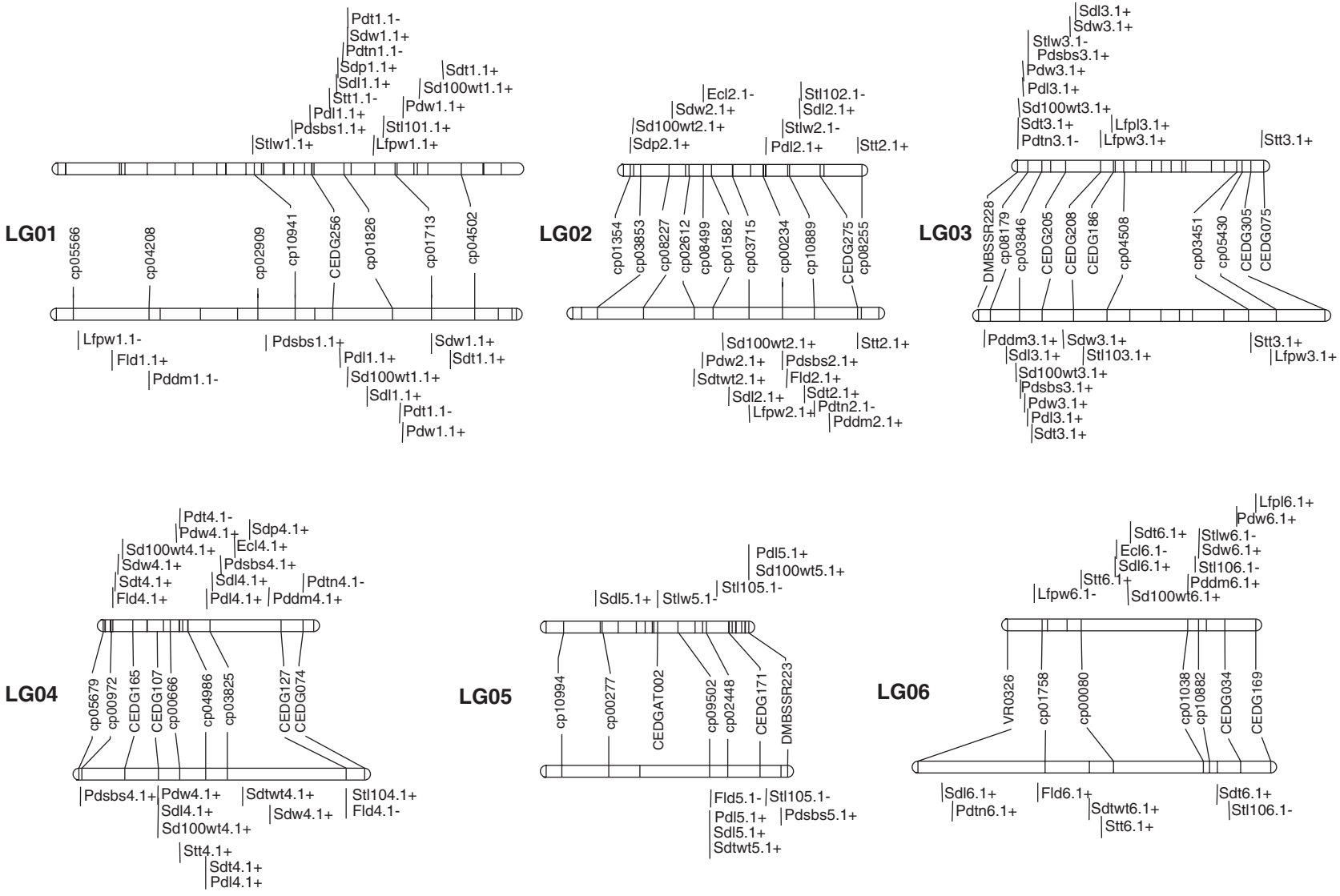

FIG. 2. QTLs detected on BC_1F_1 (upper) and F_2 (lower) populations from the cross between cultivated yardlong bean and wild cowpea. The effect of the cultivated parent is indicated after each QTL name. For explanation of trait abbreviations, see Table 1.

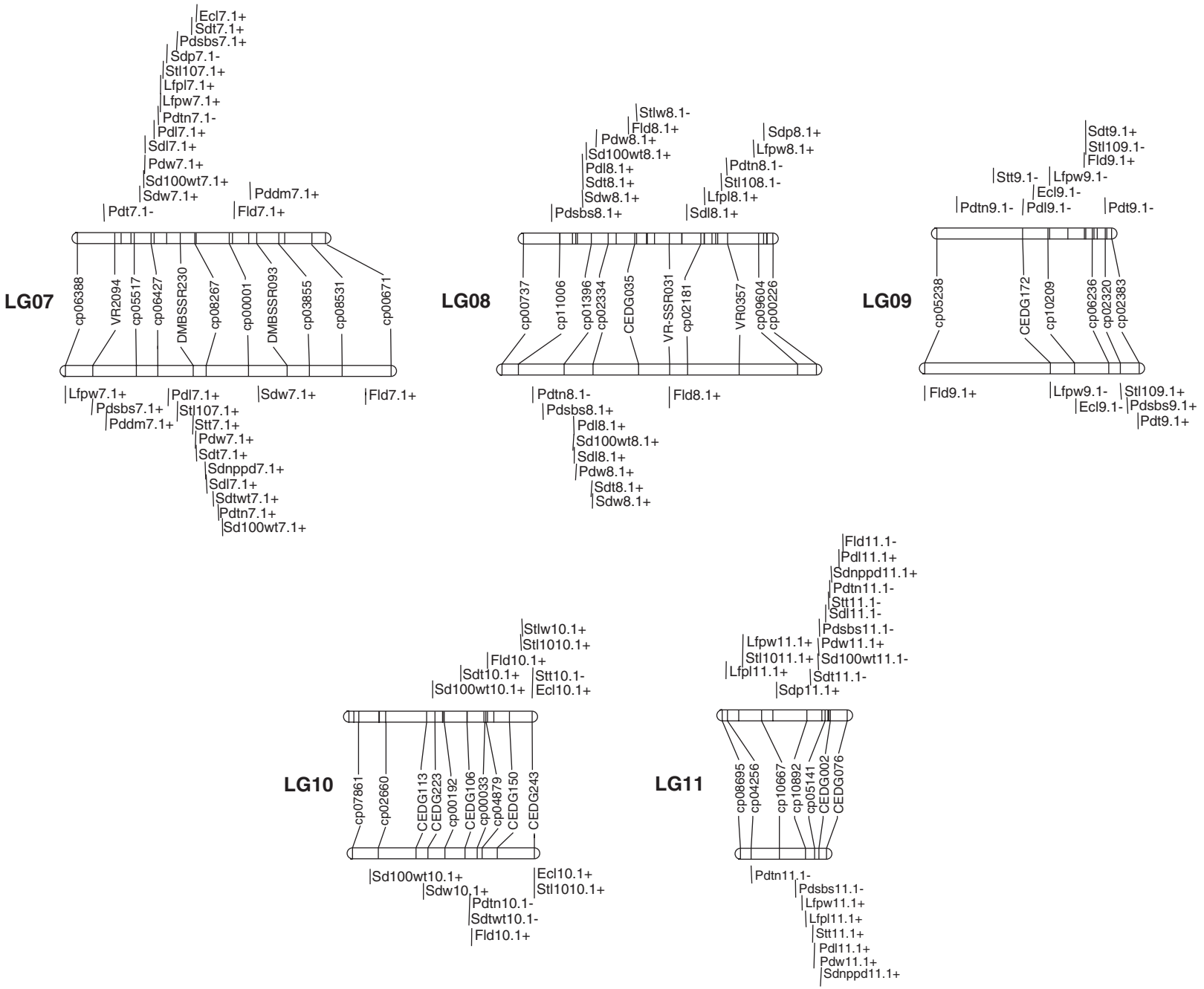

Fig. 2. *Continued*

TVnu457. Four QTLs were detected on LGs 1, 4, 7 and 9. Of these QTLs, the one on LG7 had the largest effect on phenotypic variance. Alleles of the cultivated parent reduced the number of twists on the pod at all QTLs.

Organ size (seed size, pod size, spacing between seeds and stem thickness). Domestication of yardlong bean resulted in an approx. eight-fold increase in seed weight (Table 3). Eight to ten QTLs for traits related to seed size (SD100WT, SDL, SDW and SDT) were located on all LGs. At all QTLs, alleles from the cultivated parent increases the size of each trait, except alleles of the QTLs on LG11, which decreased SD100WT, SDL and SDT. The QTLs with the largest phenotypic contribution for SD100WT (24·6 %), SDL (26·5 %) and SDW (20·9 %) were located on LG7, and that for SDT (26·4 %) was located on LG3 (Table 5).

The most remarkable domesticated trait of yardlong bean is its pod length. Domestication of yardlong bean has resulted in an approx. eight-fold increase in pod length. Seven to nine QTLs were identified for pod-related traits on LGs 1, 2, 3, 4, 5, 7, 8, 9 and 11 (Table 5). The alleles from yardlong bean increased pod size at almost all QTLs. Alleles from wild cowpea reduced the value of pod size only on LG9 for PDL and on LG11 for PDSBS. The QTLs located on LG7 had the greatest effect for PDL and PDW. For PDSBS, the QTLs showing the largest effect were located on LGs 3, 7 and 11. Generally, QTLs for pod size were clustered with or located close to QTLs for seed size-related traits, especially the QTLs on LGs 3, 4, 7, 8 and 11 (Fig. 2). The QTLs on LG7 for PDL, PDW and PDSBS were also located near to the QTL for pod dehiscence.

Four QTLs for leaf length were found on LGs 3, 6, 7 and 11 in the BC_1F_1 population. However, only that on LG11 was confirmed in the F_2 population. For leaf width, nine QTLs were detected on LGs 1, 2, 3, 6, 7, 8, 9 and 11. In both traits, the QTLs on LG7 had the greatest effect and were at the same position (Table 5, Fig. 2).

Nine QTLs for stem thickness were detected on LGs 1, 2, 3, 4, 6, 7, 9, 10 and 11. The QTL on LG7 had the greatest effect. Except for the QTLs on LGs 1, 9, 10 and 11, the cultivated alleles at these QTLs increased STT.

Growth habit (ECL, STL10 and STLW). Epicotyl length, stem length within the first ten internodes and whole stem length (ECL, STL10 and STLW) in the cultivated parents were higher than those in the wild parent. Six QTLs for ECL were found on LGs 2, 4, 6, 7, 9 and 10. The cultivated alleles at QTLs *Ecl2·1*-, *Ecl6·1*- and *Ecl9*.1- decreased epicotyl length. Eleven QTLs for STL10 were detected on all LGs. The cultivated alleles at QTLs *Stl102·1–*, *Stl105·1–*, *Stl106·1–*, *Stl108·1–* and *Stl109·1–* lowered internode length. Seven QTLs for STLW were identified on LGs 1, 2, 3, 5, 6, 8 and 10. At QTLs *Stlw2·1–*, *Stl3·1–*, *Stlw5·1–*, *Stlw6·1–* and *Stlw8·1*, the alleles from the cultivated parent decreased upper internode length. For all growth habit traits, the QTLs on LG10 had the greatest effect, with alleles increasing trait values. The QTLs for epicotyl and internode lengths were located on the same or similar position on LGs 5, 7 and 10. QTLs for lower and upper internode lengths were also mapped to the same or similar location on LGs 2, 6 and 10.

Flowering time (FLD). Days to first flowering of the cultivated and wild parents were almost the same (58 vs. 57 d) in Japan, but relatively different (55 vs. 44 d) in Thailand. However, large variation existed in the two populations. Ten QTLs were detected on all LGs except LG3 for FLD. QTLs on LGs 2, 10 and 11 had a large effect on phenotypic variance. Unexpectedly, alleles from the cultivated parent at all QTLs except LG5 and LG11 delayed flowering.

Maturity time (PDDM). The cultivated parent had a much larger seed and pod than the wild parent. Yardlong bean would be expected to take longer to reach pod maturity than the wild parent due to greater translocation of dry matter to seeds and pods. Six QTLs associated with days to maturity were found on LGs 1, 2, 3, 4, 6 and 7. The alleles from the cultivated parent that delayed maturity were on LGs 2, 3, 4, 6 and 7, whereas a QTL on LG1 hastened maturity. The QTL on LG3 had the greatest effect and was located near the QTLs for seed- and pod-related traits.

Yield-related traits (PDTN, SDNPPD and SDTWT). The cultivated parent produced a markedly lower number of pods than the wild parent. Ten QTLs were detected on all LGs, except LG5. Of these QTLs, only at LG6 did the allele from yardlong bean increase PDTN. This QTL had the largest effect, accounting for 57·1 % of the phenotypic variation.

Although yardlong bean has much longer pods than wild cowpea, the average seed number per pod was only slightly different (three seeds). Two QTLs were found on LGs 7 and 11 for SDNPPD. The QTL on LG11 had largest effect, explaining 70 % of the phenotypic variation in the BC_1F_1 population. This QTL was co-located with QTLs for flowering time, stem thickness, leaf size, and seed- and pod-related traits. As expected, the alleles from the yardlong bean parent increased the number of seeds per pod at both QTLs (Table 5, Fig. 2).

The wild parent has smaller seed size but higher total seed weight than the cultivated parent. SDTWT was investigated only in the F_2 population. Six QTLs were found on LGs 2, 4, 5, 6, 7 and 10. The QTL with the largest effect was located on LG7. This QTL was clustered with stem-, seed- and pod-related traits. The alleles from the cultivated parent at all QTLs increased total seed weight.

Seed coat colour (SDC). Seed coat colour was characterized as a qualitative trait. The cultivated parent had a black seed coat whereas the wild parent had a brown seed coat. F_2 progeny segregated for seed coat colour at a ratio of 33 (brown) to 155 (black). Although the segregation ratio fitted to 3 : 13 ($\chi^2 = 0{\cdot}18$, $P = 0{\cdot}67$), it also fitted to 1 : 3 at $P = 0{\cdot}01$ ($\chi^2 = 5{\cdot}56$, $P = 0{\cdot}018$). The BC_1F_1 progenies showed no segregation and all had a black seed coat. These suggested that seed coat colour may be governed by dominant and recessive epistasis or by a single gene and that black is dominant over brown. However, when this trait was mapped as a morphological marker, seed coat colour was located near to marker cp03855, which showed high segregation distortion.

TABLE 6. *Observed and expected numbers of QTLs and their chi-square values on each linkage groups*

	BC_1F_1				F_2			
LG	Length (cM)	Detected QTLs	Expected QTLs	χ^2	Length (cM)	Detected QTLs	Expected QTLs	χ^2
LG1	147·3	14	20·9	2·3	140·4	11	15·2	1·2
LG2	76·4	8	10·8	0·7	93·4	12	10·1	0·3
LG3	78·8	10	11·2	0·1	105·7	11	11·5	0·0
LG4	67·4	14	9·6	2·0	87·2	11	9·5	0·3
LG5	64·9	7	9·2	0·5	73·7	6	8·0	0·5
LG6	79·5	10	11·3	0·1	107·7	7	11·7	1·9
LG7	85·6	15	12·1	0·7	107·1	16	11·6	1·7
LG8	86·0	14	12·2	0·3	103·4	10	11·2	0·1
LG9	60·3	8	8·6	0·0	70·5	6	7·6	0·4
LG10	63·2	7	9·0	0·4	59·8	7	6·5	0·0
LG11	43·1	14	6·1	10·2**	28·3	9	3·1	11·5***
Total	852·4	121	121	17·5***	977·1	106	106	17·8***

Asterisks indicate significant differences between the observed and expected numbers of QTLs in each linkage group at $^{**}P < 0{\cdot}01$ and $^{***}P < 0{\cdot}001$.

Distribution of domestication trait-related QTLs

Although it is not known whether all the 153 QTLs detected for domestication-related traits had independent actions on each trait, the observed number of QTLs was compared with the expected number based on each LG length (Table 6). The observed and expected numbers agreed well throughout all LGs, except for LG11 for which the number of QTLs was statistically higher than expected. The departure in LG11 caused significant differences in total χ^2 values for both F_2 and BC_1F_1 at 17·5 and 17·8, respectively.

DISCUSSION

Linkage maps of yardlong bean

The yardlong bean QTL genetic maps presented here are the first for comprehensive domestication-related traits derived from an inter-subspecific cross of this crop. The number of linkage groups corresponded to the haploid chromosome number ($n = 11$) of yardlong bean (cowpea). In this study, 113 SSR markers derived from cowpea, azuki bean and mungbean were chosen from our previous map constructed from a BC_1F_1 population (Kongjaimun *et al.*, 2012), and were integrated into the F_2 genetic map. The LG and marker orders on each LG have been confirmed. Therefore, these yardlong bean maps are useful for understanding genome synteny among *Vigna* species, as well as for identifying QTLs for useful traits.

Some genetic barriers exist in inter-subspecific crosses between cowpea and its wild progenitor. Ng (1995) reported partial incompatibility between cultivated cowpea *V. unguiculata* ssp. *unguiculata* and wild cowpea *V. unguiculata* ssp. *dekindtiana*. In our study, in which yardlong bean and wild cowpea were crossed, 27 plants in the F_2 population did not set pod, and 15 had a very low pod set (≤ 15) or had shrivelled seeds. In the BC_1F_1 population, one plant failed to produce any pods and nine plants produced a small number of pods (ten or fewer). Those plants were excluded from the mapping population.

Markers showing segregation distortion were observed on some LGs on both the F_2 and the BC_1F_1 maps. The F_2 map had more distorted markers than the BC_1F_1 map ($P < 0{\cdot}05$, 48·7 vs. 9·7 %). In particular, the markers located on LG11, where 7/9 and 13/14 of the F_2 and BC_1F_1 maps, respectively, showed distorted segregation. The direction of skewed markers on LG11 in both maps was toward the homozygous yardlong bean genotype. The same results have been found in an F_2 interspecific linkage map of *V. umbellata* × *V. nakashimae* (Somta *et al.*, 2006), and in a BC_1F_1 linkage map of *V. umbellata* (Isemura *et al.*, 2010). They reported that none out of ten markers and all markers on LG11 of the respective linkage maps were highly distorted. The cluster of distorted markers may result from the presence of a gene(s) controlling sterility and/or compatibility (Zamir and Tadmor, 1986). Therefore, a gene(s) on LG11 may play an important role in genetic differentiation, both within yardlong bean (cowpea) and among *Vigna* species.

Highly distorted segregation may affect inheritance of nearby traits, even with simply inherited traits. In mungbean, Lambrides *et al.* (2004) found that the segregation ratio suggested dominant and recessive epistasis controlling seed coat colour. However, this was rejected and a single-gene model was accepted based on molecular marker data. They eventually mapped seed coat colour locus to a distorted genomic region with an understanding that the aberrant segregation ratio was due to the effect of segregation distortion. In our study on seed coat colour, segregation ratios suggest either dominant and recessive epistasis or single gene control, although gene mapping supported the latter.

The genetics of domestication-related traits

In yardlong bean the majority of domestication-related traits are controlled by one major QTL and several minor QTLs, and a few are controlled by single major genes. Results from this study revealed that yardlong bean differs from other *Vigna* crops in the genetic control of some simply inherited traits. For example, pod dehiscence, which is controlled by a single gene in azuki bean (Isemura *et al.*, 2007; Kaga *et al.*, 2008) and rice bean (Isemura *et al.* 2010), is controlled by several genes/QTLs in yardlong bean. Nonetheless, in a related crop,

common bean (*Phaseolus vulgaris*) pod dehiscence is also governed by several genes (Koinange *et al.*, 1996).

In most of the domestication-related traits measured, 2–11 QTLs on two or more linkage groups were detected. QTLs for many related traits such as pod size, seed size, leaf size and stem-related traits were co-located on the same position on the same linkage groups. The same findings were reported for azuki bean (Isemura *et al.*, 2007; Kaga *et al.*, 2008) and rice bean (Isemura *et al.*, 2010). Co-location of QTLs for these traits may be due to the effect of developmental allometry (Smartt, 1976).

Genomic regions and distribution of QTLs for domestication-related traits

The QTLs controlling domestication traits are generally not randomly distributed across the crop genome (Gepts, 2004). The non-randomness of the domestication QTLs may be related to 'cultivation magnetism' and should be considered under the 'protracted transition paradigm' of crop domestication (Allaby, 2010). Domestication-related traits have been studied in several legume crops such as common bean (Koinange *et al.*, 1996), azuki bean (Isemura *et al.*, 2007; Kaga *et al.*, 2008), rice bean (Isemura *et al.*, 2010) and soybean (Liu *et al.*, 2007); the results revealed that domestication traits are controlled by several QTLs/genes with each trait controlled by a few large QTLs or by a major QTL and several minor QTLs. The results from our study demonstrated that for most traits the latter case exists in yardlong bean. For example, one QTL with large effect and 3–9 minor QTLs control SDP, SDT, SD100WT, PDL, PDW, STL10 and STLW.

The distribution of domestication-related QTLs across the yardlong bean genome is shown by co-location of the QTLs on several narrow genomic regions on almost all linkage groups, especially LG3, LG7, LG8 and LG11 (Fig. 2). LG3 is associated with QTLs for increased organ size, such as seed, pod and leaf, which were detected in a limited region of 16 cM. LG7 is associated with pod dehiscence, organ size (seed, pod, stem and leaf), stem length and yield potential. Major QTLs for organ size were principally located on this LG. In addition, the QTLs for days to first flower and days to maturity of first pod are closely linked in a region of 6 cM on LG7. LG8 is associated with increased seed and pod size. LG11 is associated with organ size (seed, pod, stem and leaf), earliness and yield potential traits.

QTL clusters for domestication are reported in several crops. Clustering of QTLs is due to either close linkage or pleiotropy or both. Single mutations can have pleiotropic effects on various organs. In common bean, the determinacy gene (*fin*) has pleiotropic effects on the number of nodes on the main stem, the number of pods, and the number of days to flowering and maturity (Koinange *et al.*, 1996). In maize, QTLs related to change in inflorescence sex, and number and length of internodes in lateral branches and inflorescences are distributed within a narrow genomic region (Doebley *et al.*, 1995). Change in these traits is explained by the pleiotropic effect of a single *tb1* gene. In tomato, the seed testa colour mutant gene *bks* decreases seed weight and increases fruit pH (Downie *et al.*, 2003). In sunflower, the unbranched allele (*B*) decreased seed oil content and increased capitula diameter and seed weight (Bachlava *et al.*, 2010).

Comparison of domestication QTLs between yardlong bean and related Vigna *and other crops*

QTLs with larger effect [≥20 % phenotypic variation explained (PVE)] are considered here.

Comparison with azuki bean. Distribution of the main QTLs between the two species showed a marked difference. In yardlong bean, large-effect QTLs were detected on seven linkage groups – LGs 1, 3, 6, 7, 8, 10 and 11. In azuki bean, large-effect QTLs were found on only five linkage groups – LGs 1, 2, 7, 8 and 9 (Isemura *et al.*, 2007; Kaga *et al.*, 2008). Marked differences between yardlong bean and azuki bean were found on LG6 and LG7. Several large-effect QTLs were detected on LG6 of azuki bean, whereas only one QTL was detected on this LG in yardlong bean. Major QTLs for domestication-related traits were abundant on LG7 in yardlong bean, but only a few QTLs were detected in azuki bean (Supplementary Data, Table S4).

Seed size. Seed weight of the mapping parents used in this study showed an eight-fold variance. The 100-seed weight of cultivated yardlong bean was 19·4 g while that of the wild parent was 2·5 g. Ten QTLs were detected for 100-seed weight and that with the largest effect (PVE = 21·1 %) was found on LG7 for yardlong bean, whereas eight QTLs for this trait were detected in azuki bean that with the largest effect (PVE = 31·3 %) was located on LG2. QTLs for 100-seed weight in yardlong bean and azuki bean on LG1, LG10 and LG11 may be common. QTLs for seed size in both crops on LG1 were linked to markers CEDG090 and CEDG051, on LG10 were between markers CEDG113 and CEDG106, and on LG11 were linked to marker CEDG076.

Pod dehiscence. Reducing seed dispersal is one of the first steps in crop domestication (Ladizinsky, 1979). Pod dehiscence results from the presence of fibres surrounding the vascular bundles in the pod walls and a fibrous parchment layer lining the pod cavity (Roth, 1977). Pod twisting is caused by the oblique orientation of the fibres in the parchment layer. Four QTLs were detected for pod dehiscence in yardlong bean. The QTL with the highest contribution (48 %) was found on LG7 whereas a single QTL for this trait with a higher contribution (90·5 %) was detected on the same LG7 in azuki bean (Isemura *et al.*, 2007). The pod size QTL with the largest effect in azuki bean and yardlong bean were both found on LG7.

Pod length. Among the pod-related traits, length of pod is the main distinguishing trait of yardlong bean. The distinct pod character of yardlong bean may be because it has been domesticated solely for edible young pods. The domesticated yardlong bean parent used here had a pod length of 78·1 cm, while domesticated azuki bean had a pod length of 9·2 cm (Isemura *et al.*, 2007). The yardlong bean and wild cowpea parents in this study showed an eight-fold difference in pod length, whereas azuki bean and its wild relative have similar pod length (Isemura *et al.*, 2007). Nine QTLs were involved in pod length in yardlong bean. Five were associated with the same trait in azuki bean. Largest-effect QTLs for the two

species were detected on LG7. These QTL and that on LG1 were considered to be common in both *Vigna* crops.

Seed dormancy. Physical seed dormancy is generally caused by the presence of water-impermeable layers of palisade cells in the seed coat (Finch-Savage and Leubner-Metzger, 2006). Water absorption occurs through the structure of the strophiole (parenchymatous tissue) adjacent to the hilum in *Vigna* species (Gopinathan and Babu, 1985). Six QTLs were identified for seed dormancy-related traits in yardlong bean whereas two to five were identified in azuki bean. The largest-effect QTLs for dormancy-related traits in yardlong bean and azuki bean were both found on LG1 and were likely to be common as they are linked to the same markers, CEDG256 and CEDG214.

Comparison with rice bean. In rice bean, large-effect QTLs were found on three linkage groups (Isemura *et al.*, 2010): LG2 and LG4 for seed and pod size, LG4 for water absorption by seeds (seed dormancy), and LG7 for pod dehiscence and growth habit (stem length). Differences between yardlong bean and rice bean were found on LG4 and LG7. Several QTLs with large effect were detected on LG7 of yardlong bean, whereas a few QTLs were detected on this LG7 of rice bean. In contrast, major QTLs for domestication-related traits were found on LG4 of rice bean while no major QTL was detected on LG4 of yardlong bean (Supplementary Data, Table S4).

Seed size. A QTL for 100-seed weight on LG1 of rice bean and azuki bean was common (Isemura *et al.*, 2010), and thus this QTL of rice bean may be the same as that for seed weight in yardlong bean (see discussion above regarding yardlong bean and azuki bean).

Pod dehiscence. A major difference seen between yardlong bean and rice bean is pod dehiscence. Only a single major QTL (42·4 % PVE) controlling pod dehiscence was found on LG7 in rice bean, but one major and six minor QTLs were detected for this trait in yardlong bean. The major QTLs in both rice bean and yardlong bean were located on LG7, and are possibly the same. Marker CEDG111 is linked to both QTLs on LG7 of rice bean and yardlong bean (18·5 and 17·2 cM, respectively).

Pod length. As in azuki bean, pod length of rice bean and its wild relative was only slightly different (Isemura *et al.*, 2010). Nine and three QTLs were detected for pod length in yardlong bean and rice bean, respectively. QTLs on LG2 and LG4 were considered common in both species. The two QTLs were linked to markers cp08299 and CEDG062, respectively. However, the largest-effect QTL in yardlong bean was on LG7 while that of rice bean was on LG4.

Seed dormancy. Six seed dormancy-related QTLs were detected in yardlong bean. Of these, five were detected in rice bean. Two QTLs for yardlong bean each on LG4 and LG8 appear to be common to rice bean. The QTL mapped on LG4 of yardlong bean and rice bean were both linked to marker CEDG062 (22 and 19·7 cM, respectively). The QTL on LG8 of the two species was linked to marker cp10549 at 1·2 and 6·1 cM, respectively.

Comparison with cowpea and mungbean: seed size. Seed weight is an important trait related to yield in domesticated *Vigna*. QTLs for seed weight of cowpea and mungbean have been reported by Fatokun *et al.* (1992), two QTLs for cowpea and four for mungbean. LGs ii and vi in the cowpea map correspond to LG1 and LG4, respectively, in the azuki bean map (Isemura *et al.*, 2007), which also correspond to the same linkage groups in the yardlong bean map. LGs i, ii, iii and vi in the mungbean map correspond to LGs 9, 1, 8 and 10, respectively, in the azuki bean map (Isemura *et al.*, 2007) and yardlong bean map in our study.

In this study, a QTL for seed weight was detected on LG1 at the location corresponding to that of a QTL for this trait on LG ii in cowpea and mungbean. Other QTLs for seed weight were also detected at similar locations on LG4 of yardlong bean and LG vi of cowpea, as well as LG8 and LG10 of yardlong bean and LG iii and vi of mungbean. Although the QTL with the largest effect for seed weight was detected on LG7 in yardlong bean, no QTL was detected on the corresponding linkage groups in cowpea and mungbean.

Conclusions

This is the first report of QTLs for domestication-related traits in yardlong bean/cowpea. Twenty-three domestication-related traits (three qualitative and 21 quantitative traits) were investigated in the F_2 and BC_1F_1 populations. The 21 quantitative traits were dissected into 153 QTLs. The differences between wild cowpea and cultivated yardlong bean were found to be controlled by several major QTLs. Major QTLs for unrelated organs were distributed in clusters on LGs 3, 7 and 11. This study revealed that domestication-related traits are controlled by a few major and many minor QTLs. Comparing these results with other domesticated *Vigna* species showed similarity to azuki bean but differences from rice bean. High genome synteny in the genus *Vigna* enabled QTL comparison between yardlong bean and azuki bean, rice bean, mungbean and cowpea. Major QTLs in yardlong bean were found on LG7, whereas those of azuki bean were on LG9 and for rice bean were on LG4. Some genomic regions for seed dormancy, pod dehiscence and seed and pod size are conserved between yardlong bean and azuki bean and/or rice bean. Some genomic regions for seed size are conserved between yardlong bean, cowpea and/or mungbean. The results provide a foundation for marker-assisted selection of domestication-related QTLs in yardlong bean and enhance our understanding of domestication in the *Vigna.*

SUPPLEMENTARY DATA

Supplementary data are available online at www.aob.oxfordjournals.org and consist of the following. Figure S1: domestication-related traits examined in the F_2 population (JP81610 × TVnu457). Figure S2: domestication-related traits examined in the BC_1F_1 population [(JP81610 × TVnu457) × JP81610]. Table S1: SSR markers showing segregation distortion in the F_2 population of the cross between yardlong bean JP81610 and wild cowpea TVnu457. Table S2: correlation coefficients among traits in the BC_1F_1 (or $BC_1F_{1:2}$) population of the cross between yardlong bean JP81610 and wild cowpea TVnu457. Table S3: correlation coefficient among traits in the F_2 (or $F_{2:3}$) population of the cross between yardlong bean JP81610 and wild cowpea TVnu457.

Table S4: comparison of domestication-related QTLs between yardlong bean and related *Vigna* crops. All supplementary tables are presented in a single Excel file.

ACKNOWLEDGEMENTS

This study was financially supported by the Royal Golden Jubilee PhD programme (RGJ) of the Thailand Research Fund (TRF).

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