

Norihiko Tomooka, Takehisa Isemura, Ken Naito,
Akito Kaga, and Duncan Vaughan

Abstract

The scientific information about the genus *Vigna*, which contains nine important food legumes, has been accumulated in the past decade. In this chapter, progress of the genetics of domestication, important agronomic traits, ecological adaptations, and genomic information are summarized. Domestication genetics revealed by a detailed Quantitative trait locus (QTL) analysis for mung bean, black gram, azuki bean, rice bean, and yard-long bean have been described and compared. Amazing abilities of some wild *Vigna* species to adapt harsh environments were described. Some outstanding examples are adaptation to sandy and saline soils by *V. marina* and *V. trilobata*, alkaline limestone rock soils by *V. exilis*, exposed windy cliff top environments by *V. riukiensis*, waterlogged riverside by *V. luteola*, and shady forests by *V. minima*. *Vigna* genome project which is under way and aims to sequence 16 *Vigna* species will provide a foundation of clarifying genes which are responsible for the abilities to survive under extreme environments.

9.1 Introduction

Vigna species play a particularly important role in diets of people in Asia. In East Asia, azuki bean has a cultural significance as it is mixed with glutinous rice (red rice) on days of celebration (Lumpkin and McClary 1994). In the

hills of Southeast Asia, rice bean is a source of protein for poor people. Mung bean is used in a variety of forms including noodles, sprouts, flour, and whole seeds and is an ingredient of many Asian dishes. In South Asia, several different *Vigna* species form an essential component of a vegetarian's diet. Several of the wild *Vigna* species are harvested as an occasional food. In addition, cowpea introduced to Asia long ago from Africa is used for both its seeds and, in the form of yard-long bean, its pods as a vegetable.

The Asian *Vigna* generally refers to the *Vigna* species in the subgenus *Ceratotropis* (Tomooka

N. Tomooka (✉) • T. Isemura • K. Naito
A. Kaga • D. Vaughan
Genetic Resources Center, National Institute
of Agrobiological Sciences, Tsukuba, Japan
e-mail: tomooka@affrc.go.jp; isemura@affrc.go.jp;
knaito@affrc.go.jp; kaga@affrc.go.jp;
duncan@affrc.go.jp

et al. 2002a). However, there are *Vigna* species in other subgenera that occur in Asia; some of them are domesticated such as *V. unguiculata* and *V. vexillata*. In this chapter, we will discuss all the *Vigna* crops of Asia (Table 9.1). Despite the

obvious importance of *Vigna* in Asia, where most of the world's poor and undernourished live, it is only recently that there has been increased attention to their understudied genetic resources and application of biotechnology tools to them.

Table 9.1 *Vigna* species in Asia

Subgenus	Section	Species	Crop name
<i>Ceratotropis</i>	<i>Angulares</i>	<i>V. angularis</i> (Willd.) Ohwi & Ohashi var. <i>angularis</i>	Azuki bean
		<i>Vigna angularis</i> (Willd.) Ohwi & Ohashi var. <i>nipponensis</i>	
		<i>V. dalzelliana</i> (O. Kuntze) Verdcourt	
		<i>V. exilis</i> Tateishi & Maxted	
		<i>V. hirtella</i> Ridley	
		<i>V. minima</i> (Roxb.) Ohwi & Ohashi	
		<i>V. nakashimae</i> (Ohwi) Ohwi & Ohashi	
		<i>V. nepalensis</i> Tateishi & Maxted	
		<i>V. reflexo-pilosa</i> Hayata var. <i>glabra</i>	Creole bean
		<i>V. reflexo-pilosa</i> Hayata var. <i>reflexo-pilosa</i>	
		<i>V. riukiensis</i> (Ohwi) Ohwi & Ohashi	
		<i>V. tenuicaulis</i> N. Tomooka & Maxted	
		<i>V. trinervia</i> (Heyne ex Wall.) Tateishi & Maxted	
	<i>V. umbellata</i> (Thunb.) Ohwi & Ohashi	Rice bean	
	<i>Ceratotropis</i>	<i>V. grandiflora</i> (Prain) Tateishi & Maxted	
		<i>V. mungo</i> (L.) Hepper	Black gram
		<i>V. silvestris</i> (Lukoki, Maréchal et Otoul, Aitawada, Bhat et Yadav)	
		<i>V. sahyadriana</i> Aitawade, Bhat et Yadav	
		<i>V. radiata</i> (L.) Wilczek var. <i>radiata</i>	Mung bean
		<i>V. radiata</i> (L.) Wilczek var. <i>sublobata</i>	
<i>V. subramaniana</i> (Babu ex Raizada) M. Sharma			
<i>Aconitifolia</i>	<i>V. aconitifolia</i> (Jacq.) Maréchal	Moth bean	
	<i>V. aridicola</i> N. Tomooka & Maxted		
	<i>V. khandalensis</i> (Santapau) Raghavan & Wadhwa		
	<i>V. stipulacea</i> Kuntze		
	<i>V. trilobata</i> (L.) Verdc.		
	<i>V. indica</i> Dixit, Bhat & Yadav		
<i>Vigna</i>	<i>Catiang</i>	<i>V. unguiculata</i> (L.) Walpers cv.-gr. <i>Unguiculata</i>	Cowpea
		<i>V. unguiculata</i> (L.) Walpers cv.-gr. <i>Sesquipedalis</i>	Yard-long bean
	<i>Vigna</i>	<i>V. marina</i> (Burm.) Merrill	
	<i>Vigna</i>	<i>V. hosei</i> (Craib) Backer ex K. Heyne	
	<i>Vigna</i>	<i>V. luteola</i> (Jacq.) Benth.	
<i>Plectotropis</i>	<i>Plectotropis</i>	<i>V. vexillata</i> (L.) A. Rich.	Tuber cowpea

Surprisingly, a recent paper on “orphan grain legumes” does not mention the Asian *Vigna* (Varshney et al. 2009), so perhaps the Asian *Vigna* should be called the “forgotten grain legumes.” The international agricultural research community of the Consultative Group on International Agriculture Research (CGIAR) system has not conducted research on the *Vigna* crops of Asia, although an affiliate organization, the World Vegetable Center (AVRDC), does conduct research on mung bean. Despite this, there have been two recent genetic resource monographs, one on the Asian and the other on the African *Vigna* (Maxted et al. 2004; Tomooka et al. 2002a). Laboratories in different countries have conducted various genomic and genetic studies on the *Vigna* crops of Asia, but this research community has, unfortunately, not benefitted from a globally coordinated effort. A summary of the current status of *Vigna* genome maps (updated from Kaga et al. 2005) and molecular mapping of agronomically important traits is presented (Tables 9.2 and 9.3). In this chapter, we will discuss first the recent progress that has been made in understanding the *Vigna* crops of Asia and their wild progenitor species. Then the other wild *Vigna* species of Asia that may have a role to play in future crop improvement are discussed.

9.2 The *Vigna* Crops of Asia and Their Wild Progenitor Species

9.2.1 Mung Bean [*Vigna radiata* (L.) Wilczek]

Wild mung bean is very widely distributed from West Africa to Northern Australia. Within its range, germplasm from Australia and the island of New Guinea represents a distinct gene pool (Sangiri et al. 2007). Based on the diversity of domesticated mung bean and archaeobotanical records, mung bean seems to have been domesticated in India (Sangiri et al. 2007; Fuller and Harvey 2006). Recently, a comprehensive genome map of mung bean was published

(Isemura et al. 2012). In common with many crops, domestication traits in mung bean are controlled by a few major genes including some minor genes. However, compared to other crops, including domesticated *Vigna*, domestication-related traits in mung bean were more dispersed across the genome. Several genes, such as hilum and seed color, are found at a similar location in mung bean and other Asian *Vigna* species. Several QTLs for 100-seed weight in mung bean were located in a similar genomic position to other *Vigna* species, such as QTLs on linkage groups 1 and 2 that were at a similar location to those on the azuki bean and rice bean genome maps (Fig. 9.1). However, the QTL with the largest effect for 100-seed weight in mung bean was found on linkage group 8 and is specific to mung bean. Further studies of the differences among QTLs and their effect in relation to seed size in mung bean and other domesticated *Vigna* species will help to explain the marked differences for seed size among domesticated *Vigna*. Both the mitochondrial and chloroplast genomes of mung bean have been sequenced (Alverson et al. 2011; Tangphatsornruang et al. 2010). The mung bean mitochondrial genome sequence was the first for a legume and is of unexceptional size. The genome is unusually depauperate in repetitive DNA compared with the mitochondrial genomes of other species (Alverson et al. 2011). The chloroplast genome includes a pair of inverted repeats (IRs). In addition, compared to other plant chloroplast genome sequences, *V. radiata* has two distinct rearrangements of 50 and 78 kb (Tangphatsornruang et al. 2010).

Among domesticated pulses, mung bean has one of the smallest seed sizes, and seeds are usually green. It has a short growth duration and can readily be intercropped with cereals. Powdery mildew is a major disease of mung bean and breeding for resistance to this disease is a priority. However, breeding progress has been slow because there appear to be many races of the disease, and these races have not yet been described. Several sources of resistance or partial resistance to the disease have been identified. Results of different studies have identified sources of a major resistance QTL on both linkage groups 9 and 6

Table 9.2 Genome linkage maps for *Vigna* species

Cross combination	Population (plants/lines) analyzed	Markers used	Linkage groups resolved	Map distance (cM)	Level of distortion (%)	Reference
<i>Asian Vigna</i>						
<i>V. nepalensis</i> (JP107881) × <i>V. angularis</i> (JP81481)	BC ₁ F ₁ (187)	205 SSRs, 187 AFLPs, and 94 RFLPs	11	832.1	3.9	Han et al. (2005)
<i>V. nepalensis</i> (JP107881) × <i>V. angularis</i> (JP81481)	F ₂ (141)	74 SSRs	11	649.7	28.4	Isemura et al. (2007)
<i>V. angularis</i> var. <i>angularis</i> (JP109685 cv. 'Kyoto Dainagon') × <i>V. angularis</i> var. <i>nipponensis</i> (JP110658)	F ₂ (188)	191 SSRs, 2 STSs, 1 CAPS, 2 SCARs, and 36 AFLPs	10	771.9	3.9	Kaga et al. (2008)
<i>V. mungo</i> (JP219132) × <i>V. mungo</i> var. <i>sibevstris</i> (JP107873)	BC ₁ F ₁ (180)	61 SSRs, 59 RFLPs, 27 AFLPs, and 1 morphological trait	11	783	0.0	Chaitieng et al. (2006)
<i>V. mungo</i> var. <i>mungo</i> (TU94-2) × <i>V. mungo</i> var. <i>sibevstris</i>	F ₉ RIL (104)	47 SSRs, 254 AFLPs, 86 RAPDs, and 41 ISSRs	11	865.1	44.6	Gupta et al. (2008)
<i>V. radiata</i> var. <i>radiata</i> (VC3890) × <i>V. radiata</i> var. <i>sublobata</i> (TC1966)	F ₂ (58)	151 genomic and 20 cDNA RFLPs and 1 pest locus	14	1,570	12.0	Menacio-Hautea et al. (1992, 1993)
<i>V. radiata</i> var. <i>radiata</i> (cv. 'Berken') × <i>V. radiata</i> var. <i>sublobata</i> (ACC41)	F ₂ (67)	52 RFLPs, 56 RAPDs, and 2 morphological traits	12	758.3	14.5	Lambrides et al. (2000)
<i>V. radiata</i> var. <i>sublobata</i> (TC1966) × <i>V. radiata</i> (cv. 'Pagasa 7')	F ₇ RIL (67)	113 RAPDs and 2 morphological traits	12	691.7	24.3	
<i>V. radiata</i> var. <i>sublobata</i> (TC1966) × <i>V. radiata</i> (cv. 'Pagasa 7')	F ₉ RIL (76)	103 AFLPs	9	655.5	58.0	Sholihin and Hautea (2002)
<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ACC41)	F ₈ RIL (80)	255 RFLPs	13	737.9	30.8	Humphry et al. (2002)
<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ATF 3640)	F ₇ RIL (147)	52 RFLPs	10	350	15.4	Humphry et al. (2003)

<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ACC41)	F ₇ RIL (227)	78 RFLPs and 1 morphological trait	13	684.7	34.2	Humphry et al. (2005)
<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ACC41)	F ₉ RIL (202)	97 SSRs, 76 RFLPs, 4 RAPDs, and 2 STSs	12	831.8	30.7	Zhao et al. (2010)
<i>V. radiata</i> var. <i>radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> var. <i>radiata</i> (V4718)	F ₂ (155)	56 SSRs	11	995.6	– ^a	Chankaew et al. (2011)
<i>V. radiata</i> (wild: JP211874) × <i>V. radiata</i> (cultivated: JP229096 cv. 'Sukhothai')	BC ₁ F ₁ (250)	237 SSRs and 193 EST-SSRs	11	727.6	14.4	Isemura et al. (2012)
<i>V. radiata</i> (susceptible cultivar: 'Kamphaeng Saen 2') × <i>V. radiata</i> (resistant line: NM10-12-1)	F ₈ RIL (122)	47 SSRs and 7 AFLPs	12	991.98	– ^a	Prathet et al. (2012)
<i>V. radiata</i> var. <i>radiata</i> (KUM129-1-3) × <i>V. radiata</i> var. <i>sublobata</i> (W021)	F ₂ (186)	150 SSRs	12	1,174.2	– ^a	Kajonphol et al. (2012)
<i>V. radiata</i> (cultivated line: NM92) × <i>V. radiata</i> ssp. <i>sublobata</i> (TC1966)	F ₁₂ RIL (200)	356 AFLPs, 113 RAPDs, 20 SSRs, 1 SCAR, and 1 CAPS	11	690.7	8.8	Chen et al. (2013)
Rice bean <i>V. umbellata</i> (cultivated: JP217439) × <i>V. umbellata</i> (wild: JP210639)	BC ₁ F ₁ (198)	223 SSRs and 103 AFLPs	11	796.1	18.7	Isemura et al. (2010)
Interspecific cross <i>V. angularis</i> (cv. 'Erimoshouzu') × <i>V. nakashimae</i>	F ₂ (80)	19 RFLPs, 108 RAPDs, and 5 morphological traits	14	1250	19.7	Kaga et al. (1996)
<i>V. angularis</i> (cv. 'Erimoshouzu') × <i>V. umbellata</i> (cv. 'Kagoshima')	F ₂ (86)	114 RFLPs, 74 RAPDs, and 1 morphological trait	14	1,701.9	29.8	Kaga et al. (2000)
<i>V. angularis</i> (cv. 'Tanba Dainagon') × <i>V. riukiensis</i>	BC ₁ F ₁ (77)	100 SSRs, 47 RFLPs, and 234 AFLPs	11	624	2.9	Kaga et al. (2003)
<i>V. umbellata</i> (cultivated: JP100304) × <i>V. nakashimae</i> (JP107879)	F ₂ (74)	101 SSRs and 74 RFLPs	11	652	24.0	Somta et al. (2006)

(continued)

Table 9.2 (continued)

Cross combination	Population (plants/lines) analyzed	Markers used	Linkage groups resolved	Map distance (cM)	Level of distortion (%)	Reference
<i>African Vigna</i>						
<i>Cowpea</i>						
<i>V. unguiculata</i> (IT2246-4) × <i>V. unguiculata</i> ssp. <i>dekindtiana</i> (TVNI 963)	F ₂ (58)	87 genomic and 5 cDNA RFLPs, 5 RAPDs, and 2 morphological traits	10	684	22.0	Menacio-Hautea et al. (1993)
<i>V. unguiculata</i> (IT84S-2049) × <i>V. unguiculata</i> (524B)	F ₈ RIL (94)	133 RAPDs, 19 RFLPs, 25 AFLPs, 3 morphological traits, and 1 biochemical marker	12	972	18.0	Fatokun et al. (1997) Menéndez et al. (1997)
<i>V. unguiculata</i> (IT84S-2246-4 improved line) × <i>V. unguiculata</i> ssp. <i>dekindtiana</i> var. <i>pubescens</i> (TVNu-110-3A)	F ₈ RIL (94)	77 RAPDs and 3 morphological traits	12	669.8	21.7	Ubi et al. (2000)
<i>V. unguiculata</i> (IT84S-2049) × <i>V. unguiculata</i> (524B)	F ₉ RIL (94)	133 RAPDs, 36 RFLPs, 267 AFLPs, 3 morphological traits, and 1 biochemical marker	11	2,670	19.7	Ouédraogo et al. (2002a)
<i>V. unguiculata</i> ('Sanzi') × <i>V. unguiculata</i> (VITA 7)	F ₁₀ RIL (145)	5 SSRs and 134 AFLPs	11	1,620.1	35.9	Omo-Ikerodah et al. (2008)
<i>V. unguiculata</i> (524B) × <i>V. unguiculata</i> (IT84S-2049)	RIL (79)	436 SNPs	11	665	41.6 (a total of 986 were polymorphic in at least one population. 410 markers exhibited segregation distortion in one or more populations)	Muchero et al. (2009a)
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (24-125B-1)	RIL (90)	299 SNPs	11	651		
<i>V. unguiculata</i> ('California Blackeye No.46') × <i>V. unguiculata</i> (IT93K-503-1)	RIL (103)	388 SNPs	11	601		
<i>V. unguiculata</i> ('Dan Ila') × <i>V. unguiculata</i> (TVu-7778)	RIL (109)	288 SNPs	11	665		
<i>V. unguiculata</i> (TVu-14676) × <i>V. unguiculata</i> (IT84S-2246-4)	RIL (137)	349 SNPs	11	600		
<i>V. unguiculata</i> ('Yacine') × <i>V. unguiculata</i> (58-77)	RIL (114)	415 SNPs	11	657		
Consensus map	RIL (632)	928 SNPs	11	680		

<i>V. unguiculata</i> (IT93K503-1) × <i>V. unguiculata</i> ('California Blackeye No.46')	F ₈ RIL (127)	306 AFLPs	11	643	0.0	Muchero et al. (2009b)
<i>V. unguiculata</i> (cultivated: 524B) × <i>V. unguiculata</i> (wild: 219-01)	F ₇ RIL (159)	202 SSRs	11	677	10.7	Andargie et al. (2011)
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (IT97K-566-6)	RIL (92) ^b	438 SNPs	23	505.56	— ^a	Lucas et al. (2011)
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (IT82E-18)	RIL (160) ^b	430 SNPs	23	701.15	— ^a	
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (UCR 779)	RIL (56) ^b	560 SNPs	22	489.40	— ^a	
<i>V. unguiculata</i> ('California Blackeye No.46') × <i>V. unguiculata</i> (IT93K-503-1)	RIL (114) ^b	374 SNPs	17	639.59	— ^a	
<i>V. unguiculata</i> (524B) × <i>V. unguiculata</i> (IT84S-2049)	RIL (89) ^b	438 SNPs	22	710.09	— ^a	
<i>V. unguiculata</i> ('Dan Ila') × <i>V. unguiculata</i> (Tvu-7778)	RIL (79) ^b	288 SNPs	22	549.56	— ^a	
<i>V. unguiculata</i> ('Yacine') × <i>V. unguiculata</i> (58-77)	RIL (97) ^b	435 SNPs	22	650.98	— ^a	
<i>V. unguiculata</i> ('Sanzi') × <i>V. unguiculata</i> ('Vita 7')	RIL (182) ^b	413 SNPs	19	753.22	— ^a	
<i>V. unguiculata</i> (IT84S-2246) × <i>V. unguiculata</i> (IT93K-503)	F _{3,4} (88)	155 SNPs	14	302.46	— ^a	
<i>V. unguiculata</i> (IT84S-2246) × <i>V. unguiculata</i> ('Mouride')	F _{3,4} (87)	347 SNPs	15	595.33	— ^a	
<i>V. unguiculata</i> (TVu14676) × <i>V. unguiculata</i> (IT84S-2246-4)	RIL (136) ^b	345 SNPs	14	666.89	— ^a	
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (24-125B-1)	RIL (87) ^b	329 SNPs	23	526.75	— ^a	

(continued)

Table 9.2 (continued)

	Cross combination	Population (plants/lines) analyzed	Markers used	Linkage groups resolved	Map distance (cM)	Level of distortion (%)	Reference
	<i>V. unguiculata</i> (LB30#1) × <i>V. unguiculata</i> (LB1162#7)	RIL (90) ^b	180 SNPs	20	409.94	— ^a	
	Consensus map	RIL (1293)	1,107 SNPs	11	680		
Yard-long bean	<i>V. unguiculata</i> ssp. <i>sesquipedalis</i> (ZN016) × <i>V. unguiculata</i> ssp. <i>sesquipedalis</i> (Zhijiang 282)	F _{7,8} RIL (114)	191 SNPs and 184 SSRs	11	745	13.8	Xu et al. (2011a)
(asparagus bean)	<i>V. unguiculata</i> ssp. <i>unguiculata</i> cv.-gr. <i>sesquipedalis</i> (JP81610) × <i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i> (JP89083 = TVnu457)	BC ₁ F ₁ (190)	226 SSRs	11	852.4	9.7	Kongjaimun et al. (2012a)
	<i>V. unguiculata</i> ssp. <i>unguiculata</i> cv.-gr. <i>sesquipedalis</i> (JP81610) × <i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i> (JP89083 = TVnu457)	F ₂ (188)	113 SSRs	11	977.1	48.7	Kongjaimun et al. (2012b)
Bambara groundnut	<i>V. subterranea</i> var. <i>subterranea</i> ('DipC') × <i>V. subterranea</i> var. <i>subterranea</i> ('Tiga necaru')	F ₃ (73)	29 SSRs and 209 DARTs	21	608.6	31.8	Ahmad (2012)
	<i>V. subterranea</i> var. <i>subterranea</i> ('DipC') × <i>V. subterranea</i> var. <i>subterranea</i> ('Tiga necaru')	F ₂ (98)	12 SSRs, 106 DARTs, and 76 AFLPs	20	901.2	27.6	
Others	<i>V. vexillata</i> var. <i>angustifolia</i> (TVnu1443) × <i>V. vexillata</i> var. <i>vexillata</i> (TVnu73)	F ₂ (94)	70 RAPDs, 47 AFLPs, 1 SSR, and 2 morphological traits	14	1,564.1	33.5	Ogundiwin et al. (2005)

^aThere is no description^bF₈ to F₁₀ generations

Table 9.3 Molecular mapping of agronomically important traits in *Vigna*

Cross combination	Population (plants/lines) analyzed	Molecular markers used	Trait of interest	Gene/QTL (linkage group, LG)	References
<i>Asian Vigna</i>					
Azuki bean (<i>V. angularis</i>)	BC ₁ F ₁ (187)	SSR, RFLP, AFLP	Domestication-related traits (qualitative trait: seed coat color)	Gene (LG1)	Isemura et al. (2007)
<i>V. nepalensis</i> (JP107881) × <i>V. angularis</i> (JP81481)			Domestication-related traits (qualitative trait: black mottle on seed coat)	Gene (LG4)	
			Domestication-related traits (three qualitative and 29 quantitative traits)	QTLs (for each trait, 1–6 QTLs are detected mainly on LG1, LG2, LG4, LG7, and LG9)	
	F ₂ (141)	SSR	Domestication-related traits (qualitative trait: seed coat color)	Gene (LG1)	
			Domestication-related traits (qualitative trait: black mottle on seed coat)	Gene (LG4)	
			Domestication-related traits (qualitative trait: epicotyl color)	Gene (LG4)	
			Domestication-related traits (three qualitative and 30 quantitative traits)	QTLs (for each trait, 1–6 QTLs are detected mainly on LG1, LG2, LG4, LG7, and LG9)	
Azuki bean (<i>V. angularis</i>)	BC ₁ F ₁ (187)	SSR, RFLP, AFLP	Bruchid (<i>Callosobruchus chinensis</i>) resistance	QTLs (LG1, LG2, LG4, and LG10)	Kaga et al. 2008; Somta P et al. (2008)
<i>V. nepalensis</i> (JP107881) × <i>V. angularis</i> (JP81481)			Bruchid (<i>Callosobruchus maculatus</i>) resistance	QTL (LG3)	
			Seed weight	QTLs (LG1, LG2, LG8, and LG9)	
	F ₂ (141)	SSR	Bruchid (<i>Callosobruchus chinensis</i>) resistance	QTLs (LG1, LG2, LG4, and LG10)	
			Bruchid (<i>Callosobruchus maculatus</i>) resistance	QTL (LG3)	
			Seed weight	QTLs (LG1, LG2, LG8, and LG9)	

(continued)

Table 9.3 (continued)

	Population (plants/ lines) analyzed	Molecular markers used	Trait of interest	Gene/QTL (linkage group, LG)	References
Black gram (<i>V. mungo</i>)	<i>V. mungo</i> (JP219132) × <i>V. mungo</i> var. <i>silvestris</i> (JP107873)	SSR, RFLP, and AFLP	Twisted and curly leaf	Gene (LG8)	Chaitieng et al. (2006)
Black gram (<i>V. mungo</i>)	<i>V. mungo</i> var. <i>mungo</i> (TU94-2) × <i>V. mungo</i> var. <i>silvestris</i>	SSR, AFLP, RAPD, and ISSR	Bruchid resistance	QTLs (LG1, LG2, LG3, LG4, and LG10)	Souframaniyan et al. (2010)
Black gram (<i>V. mungo</i>)	<i>V. mungo</i> var. <i>mungo</i> (DPU 88-31) × <i>V. mungo</i> var. <i>mungo</i> (AKU 9904)	SSR	Resistance to mung bean yellow mosaic India virus	Gene (closely linked to SSR marker CEDG180)	Gupta et al. (2013)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (VC3890) × <i>V. radiata</i> var. <i>sublobata</i> (TC1966)	RFLP	Seed weight	QTLs (LG: I, II, III, and VI)	Fatokun et al. (1992)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (VC3890) × <i>V. radiata</i> var. <i>sublobata</i> (TC1966)	RFLP	Bruchid resistance	Gene (LG: VIII)	Young et al. (1992)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (VC3890) × <i>V. radiata</i> var. <i>sublobata</i> (TC1966)	RFLP	Powdery mildew resistance	QTLs (LG3, LG7, and LG8)	Young et al. (1993)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (Osaka-ryokuto) × <i>V. radiata</i> var. <i>sublobata</i> (TC1966)	RFLP and RAPD	Bruchid resistance	Gene (LG9)	Kaga and Ishimoto (1998)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (cv. 'Berken') × <i>V. radiata</i> var. <i>sublobata</i> (ACC41)	RFLP and RAPD	Seed testa color Pigmentation of the texture layer Seed testa color Pigmentation of the texture layer	Gene (LG2b) Gene (LG2a) Gene (LG2) Gene (LG2)	Lambrides et al. (2000)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>sublobata</i> (TC1966) × <i>V. radiata</i> (cv. 'Pagasa 7')	AFLP	Drought resistance	QTLs (LG: A, B, D, E, and I)	Sholihin and Hautea (2002)

Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (VC1210A) × <i>V. radiata</i> var. <i>sublobata</i> (TC1966)	F ₂ (96)	RFLP and AFLP	Powdery mildew resistance	QTLs (two QTLs are detected. One is tightly linked to RFLP markers Mac71a, Mac71d, and Mac114. Another is linked to RFLP marker Bng065)	Chaitieng et al. (2002)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ATF 3640)	F ₇ RIL (147)	RFLP	Powdery mildew resistance	QTL (LG: K)	Humphry et al. (2003)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ACC41)	F ₇ RIL (227)	RFLP	Leaf lobbing Seed weight	Gene (LG: B) QTLs (LG: A, B, D, E, F, G, I, J, and K)	Humphry et al. (2005)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ACC41)	F ₈ RIL (80)	RFLP	Hard seededness Bruchid resistance Seed mass	QTLs (LG: A, B, C, and K) QTL (LG: I) QTLs (LG: A, B, D, F, G, I, and K)	Mei et al. (2009)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (cv. 'Berken') × <i>V. radiata</i> ssp. <i>sublobata</i> (ACC41)	F ₉ RIL (217)	RFLP	Bruchid resistance Seed mass	QTL (LG: I) QTLs (LG: A, B, D, E, G, I, J, and K)	
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> var. <i>radiata</i> (VC6468-11-1A)	F ₉ RIL (210)	RFLP	Bruchid resistance	QTL (LG: I)	
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> var. <i>radiata</i> (VC6468-11-1A)	F ₁₀ RIL (191)	RFLP	Bruchid resistance Seed mass	QTLs (LG: A, B, D, E, F, I, J, and K) QTL (LG: I)	
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> var. <i>radiata</i> (VC6468-11-1A)	F ₇ RIL (190)	SSR	Powdery mildew resistance	QTLs (LG: E, J, and K) QTLs (LG: I and II)	Kasettranran et al. (2010)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (Opaque leaf mutant) × <i>V. radiata</i> var. <i>radiata</i> ('Berken')	F ₂ (85)	AFLP	Opaque leaf mutant	Gene (closely linked to AFLP marker AGG/ATA)	Rungnoi et al. (2010)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (Kamphaeng Saen 1) × <i>V. radiata</i> (NM10-12)	F ₂ (160)	AFLP	Resistance to iron deficiency chlorosis	Gene (closely linked to AFLP markers E-ACT/M-CTA and E-ACC/M-CTG)	Srinives et al. (2010)

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Table 9.3 (continued)

	Cross combination	Population (plants/lines) analyzed	Molecular markers used	Trait of interest	Gene/QTL (linkage group, LG)	References
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> var. <i>radiata</i> (V4718)	F ₂ (155) BC ₁ F ₁ (760)	SSR	Cercospora leaf spot resistance Cercospora leaf spot resistance	QTL (LG3) QTL (LG3)	Chankaew et al. (2011)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (wild: JP211874) × <i>V. radiata</i> (cultivated: JP229096 cv. 'Sukhothai')	BC ₁ F ₁ (250)	SSR and EST-SSR	Domestication-related traits (qualitative traits: seed coat color) Domestication-related traits (qualitative traits: black mottle on seed coat) Domestication-related traits (qualitative traits: hilum color) Domestication-related traits (qualitative traits: stem determinacy) Domestication-related traits (34 quantitative traits) Nine quantitative traits	Gene (LG5) Gene (LG4) Gene (LG5) Gene (LG9) QTLs (for each trait, 1–7 QTLs are detected mainly on LG1, LG2, LG4, LG7, LG8, LG9, and LG10) QTLs (for each trait, 2–6 QTLs are detected mainly on LG 2 and LG4)	Isemura et al. (2012) Kajonphol et al. (2012)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> var. <i>radiata</i> (KUML29-1-3) × <i>V. radiata</i> var. <i>sublobata</i> (W021)	F ₂ (186)	SSR	Nine quantitative traits	QTLs (for each trait, 1–7 QTLs are detected mainly on LG1, LG2, LG4, LG7, LG8, LG9, and LG10)	Kajonphol et al. (2012)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> ('Kamphaeng Saen 2') × <i>V. radiata</i> (NM10-12-1)	F ₈ RIL (122)	SSR and AFLP	Resistance to iron deficiency chlorosis	QTLs (LG2 and LG3)	Prathet et al. (2012)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> (V4718)	F _{2:3} (134)	SSR	Powdery mildew resistance	QTLs (LG4 and LG9)	Chankaew et al. (2013)
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> ('Kamphaeng Saen 1') × <i>V. radiata</i> (V4718)	F _{2:4} (134)	SSR	Powdery mildew resistance	QTLs (LG4 and LG9)	
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> ('Chainat 60') × <i>V. radiata</i> ('RUM5')	F _{2:3} (190)	SSR	Powdery mildew resistance	QTLs (LG4, LG6, and LG9)	
Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> ('Chainat 60') × <i>V. radiata</i> ('RUM5')	BC ₁ F _{1:2} (74)	SSR	Powdery mildew resistance	QTLs (LG6 and LG9)	

Mung bean (<i>V. radiata</i>)	<i>V. radiata</i> (cultivated line NM92) × <i>V. radiata</i> ssp. <i>sublobata</i> (TC1966)	F ₁₂ RIL (200)	AFLP, RAPD, SSR, SCAR, and CAPS	Mung bean yellow mosaic India virus resistance Bruchid resistance Seed germination rate 100-seed weight	QTLs (LG7, LG8, and LG9) QTLs (LG7 and LG9) QTLs (LG7 and LG9) QTLs (LG1, LG3, and LG9)	Chen et al. (2013)
Rice bean (<i>V. umbellata</i>)	<i>V. umbellata</i> (cultivated: JP217439) × <i>V. umbellata</i> (wild: JP210639)	BC ₂ F ₁ (198)	SSR and AFLP	Domestication-related traits (qualitative traits: hilum color) Domestication-related traits (30 quantitative traits)	Gene (LG5) QTLs (for each trait, 1–7 QTLs are detected mainly on LG1, LG2, LG4, and LG7)	Isemura et al. (2010)
<i>Interspecific cross</i>						
<i>V. angularis</i> × <i>V. nakashimae</i>	<i>V. angularis</i> (cv. Erimoshouzu) × <i>V. nakashimae</i>	F ₂ (80)	RFLP and RAPD	Epicotyl color Intensity of epicotyl color Black mottle on seed testa Pod color Pod shattering Hilum cushion	Gene (LG4) Gene (LG2) Gene (LG4) Gene (LG2) Gene (Unlinked) Gene (LG7)	Kaga et al. (1996)
<i>V. angularis</i> × <i>V. umbellata</i>	<i>V. angularis</i> (cv. 'Erimoshouzu') × <i>V. umbellata</i> (cv. 'Kagoshima')	F ₂ (86)	RFLP and RAPD	Epicotyl color Intensity of epicotyl color	Gene (LG1) Gene (LG5; mapped with a low LOD score)	Kaga et al. (2000)
<i>V. umbellata</i> × <i>V. nakashimae</i>	<i>V. umbellata</i> (cultivated: JP100304) × <i>V. nakashimae</i> (JP107879)	F ₂ (74)	SSR and RFLP	Bruchid (<i>Callosobruchus chinensis</i>) resistance Bruchid (<i>Callosobruchus maculatus</i>) resistance Seed weight	QTLs (LG1 and LG7) QTLs (LG1 and LG4) QTL (LG10)	Somta et al. (2006)
<i>African Vigna</i>						
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT2246-4) × <i>V. unguiculata</i> ssp. <i>dekindiana</i> (TVNI 963)	F ₂ (58)	RFLP	Seed weight	QTLs (LG: II and VI)	Fatokun et al. (1992)
Cowpea (<i>V. unguiculata</i>)	<i>Vigna unguiculata</i> (IT84S-2246-4) × <i>Vigna unguiculata</i> ssp. <i>dekindiana</i> (NI 963)	F ₂ (58)	RFLP	Aphid resistance	Genes (LG1 and LG8)	Myers et al. (1996)

(continued)

Table 9.3 (continued)

	Cross combination	Population (plants/ lines) analyzed	Molecular markers used	Trait of interest	Gene/QTL (linkage group, LG)	References
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT84S-2049) × <i>V. unguiculata</i> (524B)	F ₈ RIL (94)	RFLP, RAPD, and AFLP	Flower color Pod color Petiole pigmentation Pod position Internode length Dehydrin protein Chitinase Nodal position of 1st flower Seed weight Mature pod color Inverted V mark on leaf Pod dehiscence 11 quantitative traits	Gene (LG1) Gene (LG1) - ^a Gene (unlinked) - ^a Gene (LG7) Gene (unlinked) QTL (LG2) QTL (LG5) Gene (LG: V) Gene (LG: I) Gene (LG: XII) QTLs (for each trait, 2–15 QTLs are detected mainly on LG I, II, IV, and V)	Menéndez et al. (1997) Ubi et al. (2000)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT84S-2246-4 improved line) × <i>V. unguiculata</i> ssp. <i>dekintiana</i> var. <i>pubescens</i> (TVNu-110-3A)	F ₈ RIL (94)	RAPD	Resistance to <i>Striga</i> <i>gesnerioides</i> race 1	Gene (LG1 of map by Menéndez et al. (1997))	Ouédraogo et al. (2001)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT84S-2246-4) × <i>V. unguiculata</i> (Tvu 14676)	F ₂ (150)	AFLP	Resistance to <i>Striga</i> <i>gesnerioides</i> race 3	Gene (LG1 of map by Menéndez et al. (1997))	
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT84S-2049) × <i>V. unguiculata</i> (524B)	F ₉ RIL (94)	RAPD, RFLP, and AFLP	Resistance to <i>Striga</i> <i>gesnerioides</i> race 1 Resistance to <i>Striga</i> <i>gesnerioides</i> race 3 Cowpea mosaic virus Cowpea severe mosaic virus Blackeye cowpea mosaic virus	Genes (LG1 and LG6) Gene (LG1) Gene (LG3) Gene (LG3) Gene (LG8)	Ouédraogo et al. (2002a)

		Southern bean mosaic virus	Gene (LG6)	
		Fusarium wilt	Gene (LG3)	
		Root-knot nematode	Gene (LG1)	
		Dehydrin protein	Gene (LG2)	
Cowpea (<i>V. unguiculata</i>)	F ₂ (150)	Resistance to <i>Striga gesnerioides</i> race 1	Gene (LG6 of map by Ouédraogo et al. (2002a))	Ouédraogo et al. (2002b)
		Resistance to <i>Striga gesnerioides</i> race 1	Gene (LG6 of map by Ouédraogo et al. (2002a))	
Cowpea (<i>V. unguiculata</i>)	F ₁₀ RIL (145)	Flower bud thrips	QTLs (LG1, LG2, LG3, LG6, and LG7)	Omo-Ikerodah et al. (2008)
Cowpea (<i>V. unguiculata</i>)	F ₈ RIL (127)	Drought stress-induced senescence	QTLs (LG1, LG2, LG3, LG5, LG6, LG7, LG9, and LG10)	Muchero et al. (2009b)
		Maturity	QTLs (LG7 and LG8)	
Cowpea (<i>V. unguiculata</i>)	RIL (113)	Bacterial blight resistance	QTLs (LG3, LG5, and LG9)	Agbicodo et al. (2010)
Cowpea (<i>V. unguiculata</i>)	F _{2:8} RIL (127)	Foliar damage resistance	QTLs (LG5 and LG7)	Muchero et al. (2010a)
Cowpea (<i>V. unguiculata</i>)	F _{2:8} RIL (113)	Seedling drought tolerance	QTLs (LG1, LG2, LG3, and LG5)	Muchero et al. (2010b)
Cowpea (<i>V. unguiculata</i>)	F ₇ RIL (159)	Seed weight	QTLs (LG1, LG2, LG3, and LG10)	Andargie et al. (2011)
		Pod fiber layer thickness	QTLs (LG1, LG6, and LG10)	

(continued)

Table 9.3 (continued)

	Population (plants/ lines) analyzed	Molecular markers used	Trait of interest	Gene/QTL (linkage group, LG)	References
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT93K503-1) × <i>V. unguiculata</i> (‘California Blackeye No.46’)	SNP and AFLP	Macrophomina phaseolina resistance Maturity	QTLs (LG2, LG3, LG5, LG6, and LG11) QTL (LG5)	Muchero et al. (2011)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (‘California Blackeye No.27’) × <i>V. unguiculata</i> (IT82E-18)	SNP	Foliar thrips	QTLs (LG2 and LG10)	Lucas et al. (2012)
	<i>V. unguiculata</i> (‘California Blackeye No.46’) × <i>V. unguiculata</i> (IT93K-503-1)	SNP	Foliar thrips	QTLs (LG2 and LG4)	
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (‘Sanzi’) × <i>V. unguiculata</i> (‘Vita 7’)	SNP	Leaf shape morphology	QTL (LG15)	Pottorff et al. (2012)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (‘California Blackeye No.27’) × <i>V. unguiculata</i> (24-125B-1)	SNP	<i>Fusarium oxysporum</i> f. sp. <i>tracheiphilum</i> race 3	QTL (LG1)	Pottorff et al. (2013)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (IT97K-499-35) × <i>V. unguiculata</i> (‘Canapu T16’)	AFLP	Cowpea golden mosaic virus	Gene (tightly linked to AFLP markers E.AAC/M.CCC ₅₁₅ and E.AGG/M.CTT ₃₈₀)	Rodrigues et al. (2012)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> var. <i>unguiculata</i> (524B) × <i>V. unguiculata</i> var. <i>spontanea</i> (219-01)	SSR	Time of flower opening Days to flower	QTLs (LG1, LG2, and LG10) QTLs (LG1, LG2, and LG7)	Andargie et al. (2013)
Cowpea (<i>V. unguiculata</i>)	<i>V. unguiculata</i> (‘California Blackeye No.27’) × <i>V. unguiculata</i> (IT82E-18)	SNP	Heat tolerance	QTLs (LG2, LG3, LG6, LG7, and LG10)	Lucas et al. (2013a)

Cowpea (<i>V. unguiculata</i>)	RIL (160) ^b	SNP	Seed weight	QTLs (LG5, LG6, and LG7)	Lucas et al. (2013b)
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (IT82E-18)	RIL (56) ^b	SNP	Seed weight	QTL (LG5)	
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (UCR 779)	RIL (87) ^b	SNP	Seed weight	QTLs (LG5 and LG6)	
<i>V. unguiculata</i> ('California Blackeye No.27') × <i>V. unguiculata</i> (24-125B-1)	RIL (114) ^b	SNP	Seed weight	QTLs (LG2, LG7, and LG8)	
<i>V. unguiculata</i> ('Dan IIa') × <i>V. unguiculata</i> (Tvu-7778)	RIL (79) ^b	SNP	Seed weight	QTL (LG10)	
<i>V. unguiculata</i> (524B) × <i>V. unguiculata</i> (IT84S-2049)	RIL (89) ^b	SNP	Seed weight	QTL (LG2)	
<i>V. unguiculata</i> (TVu14676) × <i>V. unguiculata</i> (IT84S-2246)	RIL (136) ^b	SNP	Seed weight	QTLs (LG2, LG5, and LG7)	
<i>V. unguiculata</i> (IT84S-2246) × <i>V. unguiculata</i> ('Mouride')	F ₄ (87)	SNP	Seed weight	QTLs (LG2, LG6, and LG10)	

(continued)

Table 9.3 (continued)

	Cross combination	Population (plants/ lines) analyzed	Molecular markers used	Trait of interest	Gene/QTL (linkage group, LG)	References
Yard-long bean (asparagus bean) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i>) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i>)	<i>V. unguiculata</i> ssp. <i>sesquipedalis</i> (ZN016) × <i>V. unguiculata</i> ssp. <i>sesquipedalis</i>	F ₇₋₈ RIL (209)	SSR and SNP	Flower color Seed coat color	Gene (LG8) Gene (LG8)	Xu et al. (2011b)
Yard-long bean (asparagus bean) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i>)	<i>V. unguiculata</i> ssp. <i>unguiculata</i> cv.-gr. <i>sesquipedalis</i> (JP81610) × <i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i> (JP89083)	BC ₁ F ₁ (190) F ₂ (188)	SSR	Pod length Pod length	QTLs (LG1, LG3, LG4, LG5, LG7, LG8, and LG11) QTLs (LG1, LG3, LG4, LG5, LG7, LG8, and LG11)	Kongjaimun et al. (2012a)
Yard-long bean (asparagus bean) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i>)	<i>V. unguiculata</i> ssp. <i>unguiculata</i> cv.-gr. <i>sesquipedalis</i> (JP81610) × <i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i> (JP89083)	BC ₁ F ₁ (190) F ₂ (188)	SSR	Domestication-related traits (qualitative traits: seed coat color) Domestication-related traits (qualitative traits: seed coat color)	QTLs (for each trait, 1–11 QTLs are detected mainly on LG3, LG7, LG8, and LG11) Gene (LG7)	Kongjaimun et al. (2012b)
Yard-long bean (asparagus bean) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i>)	<i>V. unguiculata</i> ssp. <i>unguiculata</i> cv.-gr. <i>sesquipedalis</i> (JP81610) × <i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i> (JP89083)	BC ₁ F ₁ (190) F ₂ (188)	SSR	Domestication-related traits (qualitative traits: pod dehiscence) Domestication-related traits (18 quantitative traits)	Gene (not mapped; dehiscence: indehiscence = 9:7) QTLs (for each trait, 1–9 QTLs are detected mainly on LG3, LG7, LG8, and LG11)	Kongjaimun et al. (2013)
Yard-long bean (asparagus bean) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i>)	<i>V. unguiculata</i> ssp. <i>unguiculata</i> cv.-gr. <i>sesquipedalis</i> (JP81610) × <i>V. unguiculata</i> ssp. <i>unguiculata</i> var. <i>spontanea</i> (JP89083)	BC ₁ F ₁ (190) F ₂ (188)	SSR	Pod tenderness Pod total soluble solid Pod tenderness Pod total soluble solid	QTLs (LG7, LG8, and LG11) QTL (not detected) QTLs (LG7 and LG8) QTLs (LG1 and LG3)	Kongjaimun et al. (2013)

Yard-long bean (asparagus bean) (<i>V. unguiculata</i> ssp. <i>sesquipedalis</i> (ZN016) × <i>V. unguiculata</i> ssp. <i>sesquipedalis</i> (ZJ282))	F _{8:9} RIL (209)	SSR and SNP	Days to first flowering Nodes to first flower Leaf senescence Pod number per plant	QTLs (LG10 and LG11) QTLs (LG4 and LG11) QTL (LG11) QTLs (LG2 and LG3)	Xu et al. (2013)
Bambara groundnut (<i>V. subterranea</i> var. <i>subterranea</i> ('DipC') × <i>V. subterranea</i> var. <i>subterranea</i> ('Tiga necan')	F ₃ (73)	SSR, DArT, and AFLP	26 quantitative traits	QTLs (for each trait, 1–3 QTLs are detected on LG1, LG7, LG9, LG10, LG13, LG14, and LG15)	Ahmad (2012)
<i>V. subterranea</i> var. <i>subterranea</i> ('DipC') × <i>V. subterranea</i> var. <i>spontanea</i> ('VSSP1')	F ₂ (98)	SSR, DArT, and AFLP	6 quantitative traits	QTLs (for each trait, 1–3 QTLs are detected on LG1, LG3, LG4, LG5, LG7, LG8, LG10, LG11, LG12, and LG18)	
Others					
<i>V. vexillata</i> var. <i>angustifolia</i> (TVnu1443) × <i>V. vexillata</i> var. <i>vexillata</i> (TVnu73)	F ₂ (94)	RAPD, AFLP, and SSR	Cowpea mottle carmovirus resistance Leaf shape Nine quantitative traits	Gene (LG4) Gene (LG1) QTLs (for each trait, 3–8 QTLs are detected mainly on LG1, LG2, and LG7)	Ogundiwin et al. (2005)

^aThere is no description

^bThese populations are at least F₈ generations

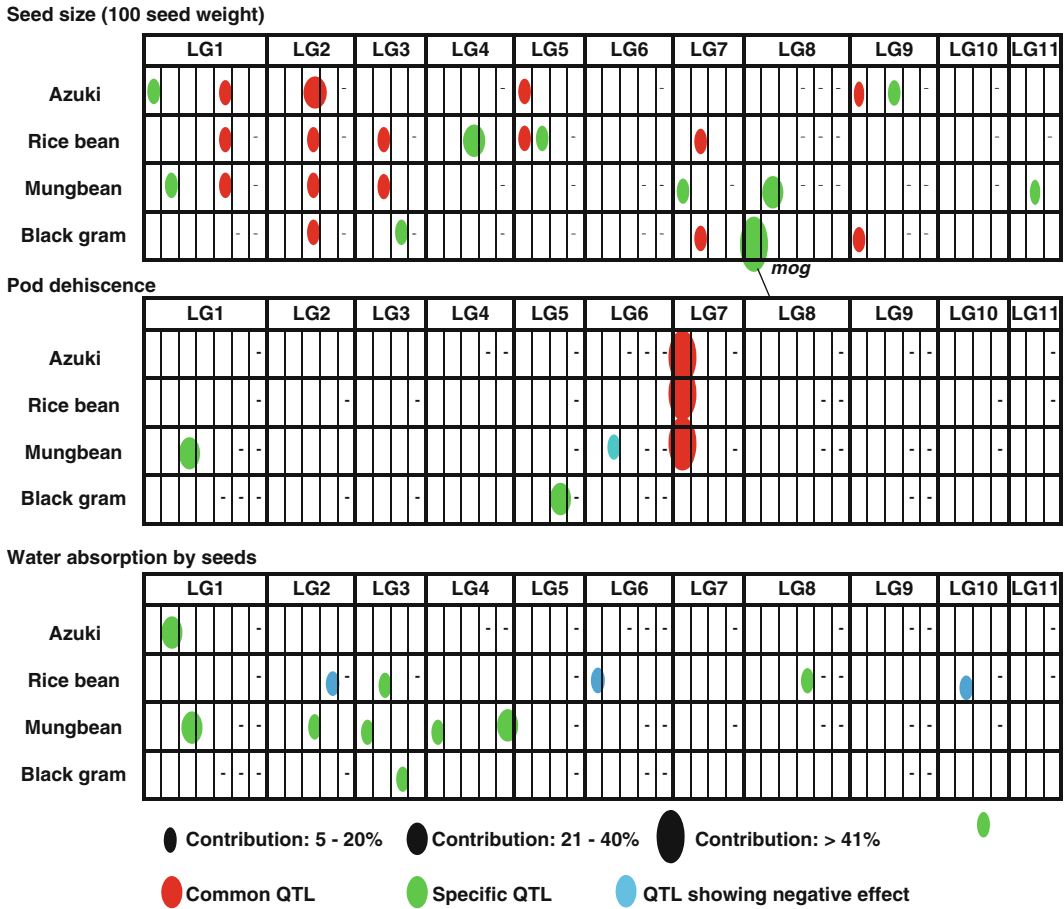


Fig. 9.1 Comparison of QTLs for three domestication-related traits among four *Vigna* crop species

(Chankaew et al. 2013; Kasettranan et al. 2010). Other resistance genes have been found on linkage group 4 (Chaitieng et al. 2002; Chankaew et al. 2013). Chaitieng et al. (2002) analyzed a mapping population using mung bean accession VC1210A as the resistant parent and found a QTL for field resistance to Thai races of powdery mildew that explained 65 % of the variation to powdery mildew resistance. Mung bean yellow mosaic viruses belong to the geminivirus group (Sunitha et al. 2013) and are highly destructive diseases of mung bean. Breeders have focused on finding resistance to MYMV (mung bean yellow mosaic virus) that is mainly found in south and west South Asia and MYMIV (mung bean yellow mosaic Indian virus) that is prevalent in central and northern South

Asia. They are also a threat to a wide range of other legumes such as black gram and soybean.

There are a number of reports analyzing resistance to MYMV in different germplasm and both recessive and dominant genes. The resistant variety SML-668 has two recessive genes for resistance. Sudha et al. (2013) reported that the resistance of mung bean variety ‘KMG189’ is controlled by a single recessive gene. Two studies using different sources of MYMIV resistance, one using the wild mung bean (*V. radiata* var. *sublobata*) and the other a breeding line from Pakistan, have found a common major resistance QTL (variously named MYMIV’9_25, qMYMIV1, qMYMIV4) (Chen et al. 2013; Kitsanachandee et al. 2013). This locus was

detected in different locations, years, sources of resistance, and scoring systems. The locus has been associated with specific markers; hence, these can be used in marker-assisted selection. Other QTLs have also been detected for MYMIV resistance, but these have not been consistently found in different tests.

Overcoming yellow mosaic virus may require various approaches, both genetic and agronomic, because this virus undergoes genetic recombination in its host whitefly (*Bemisia tabaci*) which is an efficient vector. Two iron deficiency chlorosis QTL (qIDC) for resistance to iron deficiency have been identified in a cross between susceptible ‘Kamphaeng Saen 2’ and a resistant line from Pakistan (NM10-12) (Prathet et al. 2012). The major QTL on linkage group 3 was the same as the dominant gene (IR) reported by Srinives et al. (2010)

in a cross between ‘Kamphaeng Saen 1’ and the same resistant Pakistan line. Resistance to bruchid has been reported in mung bean cultivars (Somta P et al. 2006, 2008; Somta C et al. 2008); however, mung bean breeders are interested in new sources of resistance to this important pest from other Asian *Vigna* species such as *V. umbellata* and *V. nepalensis* (Pandiyan et al. 2010; Somta P et al. 2008; Somta C et al. 2008).

9.2.2 Azuki Bean [*Vigna angularis* (Willd.) Ohwi and Ohashi]

Wild azuki bean (*Vigna angularis* var. *nipponensis*) is widely distributed in the ecological and cultural zone associated with broad-leaved evergreen forests (Isemura et al. 2011) (Fig. 9.2).

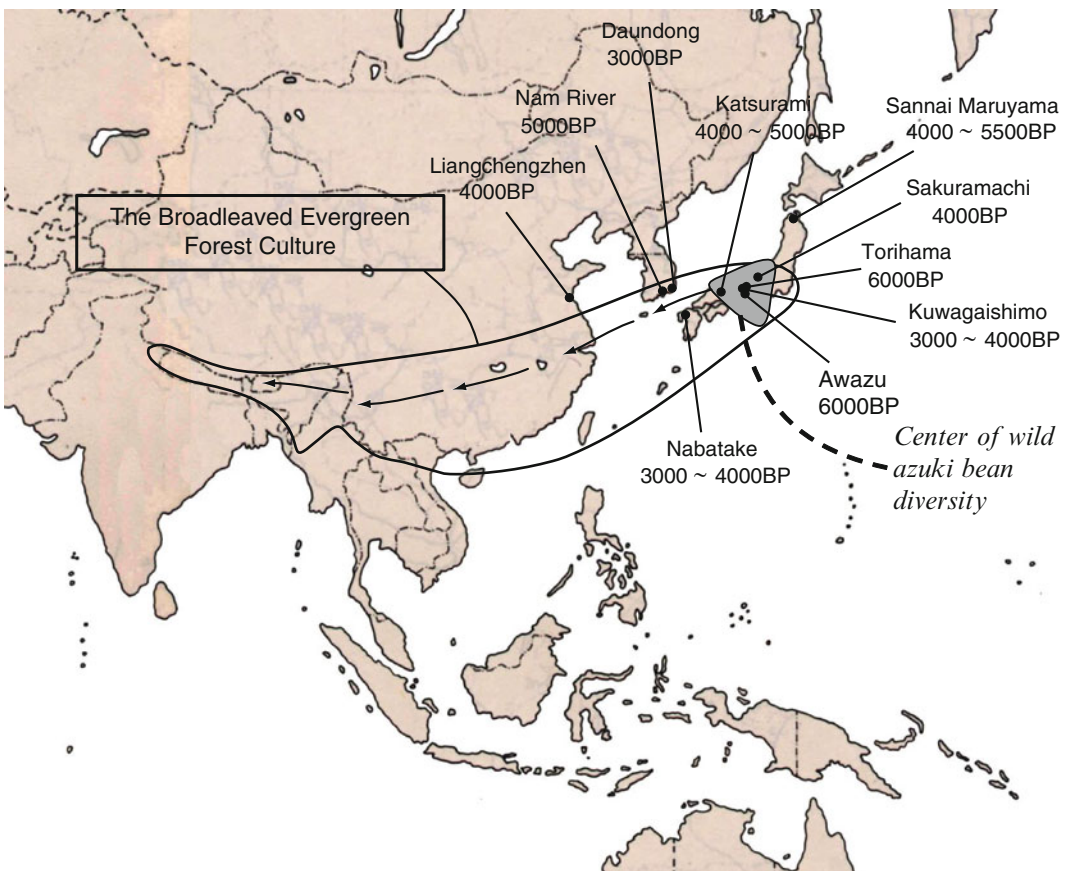


Fig.9.2 Distribution of the “Broad-leaved Evergreen Forest Culture (Laurel Forest Culture),” center of wild azuki bean diversity and sites of the archaeological remains where putative azuki bean seeds were found (after Isemura et al. (2011))

Analysis of the present-day diversity of azuki beans and abundance of wild azuki beans suggests that Japan is the center of diversity of azuki beans (Yamaguchi 1992; Xu et al. 2000a, b, 2008). The earliest archaeobotanical remains of domesticated azuki bean have been found in the central regions of Japan, Shiga, and Fukui prefectures, dated at 5–6000 BP (Tomooka 2007). These dates are earlier than for archaeobotanical remains in China and Korea (Crawford 2005), suggesting azuki bean was domesticated in Japan. Two paper analyses domestication-related traits by the same method and with similar markers, but involving different parents (Isemura et al. 2007; Kaga et al. 2008). One paper results from a cross between *V. angularis* and its closely related species, *V. nepalensis* (female). The other mapping population was derived from wild and cultivated (female) azuki bean parents from Japan. While some results were similar, such as single QTL for pod dehiscence, about 60 % of the QTLs were considered to be different. This highlights the extent of genetic diversity that is available for *Vigna* breeders among the close relatives of *Vigna* crops. The useful diversity in species closely related to azuki bean was also shown when resistance to azuki brown stem rot was analyzed (Kondo and Tomooka 2012). Eight disease responses were observed, of which four were newly detected and 28 accessions (of 4 species) among 252 accessions from 26 Asian *Vigna* species were considered as potential sources of multiple resistance to azuki brown stem rot.

The chloroplast and mitochondrial genomes of azuki bean have been sequenced (Naito et al. 2013). The results were very similar to those for the chloroplast and mitochondrial genomes of mung bean (Alverson et al. 2011; Tangphatsornruang et al. 2010). The results have confirmed the relative stability of the chloroplast genome compared to the mitochondrial genome as has been shown in other species including mung bean. Since *Vigna* species in Asia are relatively recently evolved, the mitochondrial genome may be more suitable for understanding their evolutionary dynamics than the chloroplast genome (Naito et al. 2013).

9.2.3 Rice Bean [*Vigna umbellata* (Thunb.) Ohwi and Ohashi]

Wild rice bean (*V. umbellata*) is not taxonomically distinguished from its domesticated form. This reflects the lack of prominent differentiation between the two forms and possibly the recent domestication of rice bean (Tomooka et al. 2002a). The wild form is distributed in tropical monsoon climate areas from Nepal to East Timor but with most diversity centered on Southeast Asia (Isemura et al. 2011; Tian et al. 2013; Tomooka 2009). Rice bean is cultivated on small scale across a wide area of South, Southeast, and East Asia. It is most common in highlands, sometimes cultivated in the slash-and-burn agriculture of northeast India (Arora et al. 1980), Myanmar, Laos, Thailand, Vietnam, and southern China. It is occasionally grown in Japan, Korea, Indonesia, and East Timor. Rice bean is of particular interest, because it has the highest level of bruchid resistance among the species of *Vigna* subgenus *Ceratotropis* (Kashiwaba et al. 2002; Tomooka et al. 2000). Three chemicals, based on the structure of the flavonoid naringenin, were found to be associated with bruchid resistance in rice bean (Tomooka et al. 2006). There have been many efforts to introduce bruchid resistance from rice bean to other domesticated *Vigna* species. Somta et al. (2006) used a wild species *V. nakashimae* to develop rice bean linkage map and identify a source of resistance to bruchids. In India, direct crossing between mung bean and rice bean resulted in viable hybrids, and this may enable introduction of bruchid resistance to mung bean varieties (Pandiyan et al. 2010). In addition, resistance to mung bean yellow mosaic virus in rice bean has been analyzed in a cross with mung bean, and it was found to be conferred by a single recessive gene (Sudha et al. 2012, 2013). In Thailand, scientists have attempted to transfer useful traits from rice bean to mung bean by developing tetraploid interspecific hybrids from sterile F₁ hybrids (Chaisan et al. 2013). The fertile tetraploid produced artificially may have a potential for improving *V. reflexo-pilosa* var. *glabra* (*V. glabrescens*); the only domesticated Asian *Vigna* that is tetraploid. Rice bean is a highly

prolific seed producer which may reflect its similarity to the wild form. In legumes, domestication has not always resulted in higher seed yield on plant basis (Kaga et al. 2008). A genome map developed for *V. umbellata* revealed many differences in the location of QTLs for domestication-related traits compared with *V. angularis*. Major QTLs for domestication-related traits in rice bean were reported to be on linkage group 4, whereas for azuki bean, they were mainly on linkage group 9 (Isemura et al. 2010). Among the QTLs detected in rice bean (69) and azuki bean (76) for domestication-related traits, only 15 were considered to be common. Of these, 15 QTLs were for seed size-related traits such as 100-seed weight, seed length, width, and thickness (Isemura et al. 2011). The numerous species-specific QTLs between these closely related species suggest that they can provide novel genes for breeding.

9.2.4 Black Gram (*Vigna mungo* (L.) Hepper)

Black gram is thought to have been domesticated in Gujarat and northern Peninsular India (Fuller 2007). Recently, the close relatives of black gram that still grow in northern Peninsular India have been studied and a new nomenclature has been published; *Vigna silvestris* is the presumed progenitor of black gram, and *V. sahyadriana* is a species closely related to black gram and other species in India of the section *Ceratotropis*, *V. hainiana*, *V. radiata*, and *V. subramaniana* (Aitawade et al. 2012). The largest production area for black gram is India. Black gram shows complete resistance to azuki bean weevil (*Callosobruchus chinensis*) but is susceptible to cowpea weevil (*C. maculatus*). In contrast, the wild progenitor of black gram shows complete resistance to both azuki bean weevil and cowpea weevil (Tomooka et al. 2000; Souframanien et al. 2010). Genome maps for black gram have been developed and compared to *V. angularis* (Chaitieng et al. 2006; Gupta et al. 2008). There have been a number of studies of a gigantism mutant of black gram that produces seeds, pods,

and vegetative parts much larger than the parent from which it was derived, e.g., parent has 100-seed weight of 4.8 g compared to the mutant's 7.9 g (Tomooka et al. 2010). The mutant gene is located on linkage group 8 at a site different from seed size (100-seed weight) QTLs in other *Vigna* species. The potential of transferring this gene to other species is being explored to produce super-domesticated legumes (Vaughan et al. 2007).

Resistance to mung bean yellow mosaic India virus (MYMIV) has been found in an accession of black gram, and this resistance gene has been mapped using SSR markers (Gupta et al. 2013). An SSR marker closely linked to the resistant locus was found that can be used for marker-assisted selection.

9.2.5 Moth Bean (*Vigna aconitifolia* (Jacq.) Maréchal)

Moth bean is thought to have been domesticated in South Asia where its wild conspecific progenitor is reported to be widely distributed (Arora and Nayar 1984). The outstanding characteristic of this species is its drought and heat tolerance. Consequently, it is grown in arid and semiarid zones of northwest South Asia (Jain and Mehra 1980). Among 15 *Vigna* species, moth bean showed the highest heat tolerance, surviving conditions of 36 °C for 12 days followed by 40 °C for 11 days; all other *Vigna* species tested died at 40 °C (Tomooka et al. 2001).

9.2.6 Creole Bean (*Vigna reflexo-pilosa* Hayata var. *glabra* (*Vigna glabrescens*))

Vigna reflexo-pilosa var. *glabra* is a rare domesticated species, and very few accessions are to be found in the world's germplasm collections (Tomooka et al. 2002a). It seems, based on herbarium specimens and direct collection, to be mainly grown in Vietnam although there are reports of it being cultivated in Angola, Mauritius, West Bengal, and the Philippines.

Little is known about the agronomic aspects of this crop. On the other hand, the wild progenitor, var. *reflexo-pilosa*, is widely distributed across Southeast Asia into the Pacific (Tomooka et al. 2002a). There have been a number of studies to determine the origins of the two genomes that constitute this allotetraploid (Egawa and Tomooka 1994). The most recent and comprehensive survey confirms some earlier reports that the likely donor species are *V. trinervia* and *V. hirtella* (Chankaew et al. 2014b).

9.2.7 Cowpea Complex

Evidence suggests that cowpea (*V. unguiculata*) was domesticated in West Africa (Ng and Maréchal 1985). Early archaeological remains of domesticated cowpea in Ghana, West Africa, have been dated at between 3360 and 3840 BP (D'Andrea et al. 2007). It is presumed that sometime not long after domestication, the crop came to Asia by trading networks that developed from about 4,000 years ago (Fuller 2003; Fuller et al. 2011). In Africa, cowpea was selected for its seeds (*V. unguiculata* subsp. *unguiculata* cv.-gr. *Unguiculata*), but sometime after it arrived in Asia, divergent selection resulted in a new form of cowpea with long tender pods that could be eaten raw or cooked—yard-long bean (*V. unguiculata* subsp. *unguiculata* cv.-gr. *Sesquipedalis*). In some parts of Asia, such as Sri Lanka, cowpea is being planted instead of other *Vigna* species because of its higher yield and suitability to double cropping due to its short life cycle. Yard-long bean has the longest pod of any domesticated legume, and the pod can reach up to 90 cm long (35.4 in.) which is quite close to being a yard (36 in.) (http://www.gene.affrc.go.jp/databases-plant_images_detail_en.php?plno=5420610049). However, this is well short of the pod length of some wild legumes with *Cassia fistula* reported as having pods up to 238 cm (Jayasuriya 2012).

Three recent studies have analyzed the important agronomic traits related to the domestication of yard-long bean (Kongjaimun et al. 2012a, b, 2013). QTLs for domestication-related traits show co-localization on many linkage groups, but linkage groups 3, 7, 8, and 11 appear to be

most important. Genomic dissection of pod length revealed 6 and 7 QTLs for this trait on different linkage groups in two populations, F₂ and BC₁F₁, respectively. The QTL with the main effect was on linkage group 7, explaining 30.5 % of the variation. A QTL with a large effect for pod length was also found on linkage group 7 in azuki bean. Linkage group 7 in yard-long bean appears to be important for a range of other domestication-related traits such as size of seed, stem, and leaf. This suggests that further study of genes for trait gigantism in yard-long bean should focus on linkage group 7.

9.3 Wild *Vigna* in Asia

9.3.1 *Vigna aridicola* N. Tomooka and Maxted

This species is recently found in the dry zone of Sri Lanka (Tomooka et al. 2002c). It is closely related to the wild form of *V. aconitifolia*. *V. aridicola* has been little studied, and there is an urgent need to understand the adaptive mechanism of this species and *V. aconitifolia* to harsh dry habitats.

9.3.2 *Vigna dalzelliana* (Kuntze) Verdc.

This species is poorly understood and previously was confused with *V. minima* (Tomooka et al. 2006). Recent germplasm collecting has found this species in Sri Lanka and India. There have also been collections of *Vigna* from southern Myanmar that appear to be *V. dalzelliana* (Tomooka et al. 2006).

9.3.3 *Vigna exilis* Tateishi & Maxted

Vigna exilis is only found growing in limestone outcrops (Tomooka et al. 2011b). It has been little studied but its distinctive habitat suggests that it may have useful genes for adaptation to specific high pH and dry soil conditions.

9.3.4 *Vigna grandiflora* (Prain) Tateishi & Maxted

This species should join *V. khandalensis* on the IUCN Red List of Threatened Species, since it is known currently from only a few rather vulnerable populations in Thailand.

9.3.5 *Vigna hirtella* Ridley and *V. tenuicaulis* N. Tomooka and Maxted

Based on AFLP analysis, *V. hirtella* appears to be a variable species with two eco-types, one of low altitude and another of high altitude (Seehalak et al. 2006; Tomooka et al. 2002b). *V. hirtella* grows sympatrically with a number of other species in section *Angulares* of the subgenus *Ceratotropis* in highland Southeast Asia. A natural hybrid between *V. hirtella* and *V. minima* has been found at one site (author's unpublished data). It is probable that this variable species may naturally hybridize with other species where it grows. *Vigna tenuicaulis* is relatively recently described using an accession collected in northern Thailand and is closely related to *V. hirtella* to which it is sometimes confused (Tomooka et al. 2002c). It has a low level of trypsin inhibitor activity that might be a useful characteristic to transfer to *Vigna* crops (Konarev et al. 2002).

9.3.6 *Vigna khandalensis* (Santapau) Raghavan & Wadhwa

V. khandalensis is poorly known; not even its chromosome number has been reported. It is considered "near threatened" in the IUCN Red List of Threatened Species (<http://www.iucnredlist.org/details/19892969/0>). Among the wild Asian *Vigna*, this species is an erect herb rather than a climbing vine. It is only found in India, mainly in the Western Ghats. It is reported that the seeds are sometimes used as a famine food (Babu et al. 1985).

9.3.7 *Vigna minima* (Roxb.) Ohwi & Ohashi, *V. nakashimae* (Ohwi) Ohwi and Ohashi, *V. riukiensis* (Ohwi) Ohwi & Ohashi

Vigna minima is widely distributed in variable habitats across East Asia (China), Southeast Asia, and as far east as Papua New Guinea (Tomooka et al. 2002a). The closely related species *V. nakashimae* and *V. riukiensis* have more restricted distributions. These three species are genetically closely related and are called *Vigna minima* complex (Yoon et al. 2000). *V. nakashimae* is widely distributed on the Korean peninsula and the Goto islands, Nagasaki, Japan (Yoon et al. 2007; Tomooka et al. 2013). Some populations of *V. nakashimae* from the Goto islands, living on a hill exposed to strong sea winds, are revealed to have a high level of salt tolerance. *V. riukiensis* is found in the southern Okinawa Islands in Japan. It grows on a cliff near the sea and shows a high level of salt tolerance. *V. minima* is found in both shaded forest floor and open habitats such as around paddy field, suggesting a high level of diversity. Since it has been little studied, it may well consist of several varieties or subspecies. Recently, studies have shown that some accessions of *V. minima* and *V. nakashimae* have a high level of resistance to all races of soybean cyst nematode found in Japan (Kushida et al. 2013). These resistant sources are being used in azuki breeding since soybean cyst nematode is becoming an increasingly problematic pest on legumes in Hokkaido, Japan. *V. nakashimae* has been used to develop an inter-specific linkage map with *V. umbellata* (Somta et al. 2006).

9.3.8 *Vigna nepalensis* Tateishi & Maxted

V. nepalensis is closely related to *V. angularis* with which it makes fertile hybrids. *V. nepalensis* was used as the female parent in a mapping population to analyze domestication-related traits in azuki bean (Isemura et al. 2007). It has a restricted distribution in Nepal and its adjacent localities in

India and Bhutan, and it was found growing between the altitude of 350 and 1,650 m (Tomooka et al. 2002a). QTLs for bruchid resistance have been reported from *V. nepalensis*, and some of these appear to be new sources of resistance including one QTL that is unrelated to seed size (Somta P et al. 2008).

9.3.9 *Vigna stipulacea* Kuntze

This species is characterized by extremely long peduncles 22–30 cm long that result in the flower and pod rising conspicuously above canopy. This characteristic is probably why this species has been harvested, and some harvested forms have been semidomesticated having increased vegetative organs and weak seed dormancy (Tomooka et al. 2011a). In Tamil Nadu, India, semidomesticated *V. stipulacea* is grown before or after rice in paddy fields and is considered good forage for cattle and green manure. Despite the labor required to harvest it because of shattering pods, this species is also sometimes used as a human food. Based on comments by farmers, *V. stipulacea* is resistant to many insects and diseases such as stinkbug and powdery mildew, grows faster (early flowering and maturing) than mung bean and black gram, and has high palatability (Tomooka et al. 2006, 2011b). Seeds are sold in a local seed shop in Tamil Nadu (Tomooka et al. 2011b). Given these positive attributes, the species warrants particular study of its agronomic potential and potential for furnishing new and useful genes to legume breeding.

9.3.10 *Vigna subramaniana* (Babu ex Raizada) M. Sharma and *Vigna hainiana* Babu, Gopinathan, and Sharma

V. subramaniana has the lowest level of trypsin inhibitor activity among the subgenus *Ceratotropis* species studied and absence of chymotrypsin inhibitor activity (Konarev et al. 2002). Taxonomic confusion surrounding this species and *V. hainiana* has been discussed by

Tomooka et al. (2006). There remains a need to more thoroughly understand relationships in the mung bean complex to which these two species belong. There is now sufficient germplasm in various gene banks to permit these studies to be conducted.

9.3.11 *Vigna trinervia* (Heyne ex Wall.) Tateishi & Maxted

V. trinervia consists of two varieties. *Vigna trinervia* var. *trinervia* is widely distributed in South and Southeast Asia and also in the Indian Ocean Islands and Tanzania. *Vigna trinervia* var. *bourneae* (*Vigna bourneae*) is found only in southern India and is distinguished by being covered with white villose hairs. This species is an important cover crop in between plantations of coconut and rubber.

9.3.12 *Vigna trilobata* (L.) Verdc. and *V. indica* T.M. Dixit, K.V. Bhat & S.R. Yadav

Vigna trilobata characteristically is found in sandy soils; hence, it is found along the beaches in Sri Lanka. However, it is more commonly found inland where sandy soils predominate such as Tamil Nadu, India, and Sagaing, Myanmar. This species is characterized by its very long taproot and so is found along the coastline of the dry zone, whereas *V. marina* with shallower roots is found predominately along the coast of the wet zone in Sri Lanka (Liyanage 2013, personal communication to the authors). Previously, variation in the *V. trilobata* gene pool resulted in the species being divided into two subspecies, subsp. *trilobata* and subsp. *pusilla*. However, recently, subsp. *pusilla* has been raised to the rank of a species called *V. indica*, differing from *V. trilobata* in various characteristics of which cylindrical seeds with truncated ends are most obvious. The two subspecies in India are found in the western, central, and northern regions for *V. indica* and southern and eastern India for *V. trilobata*

(Dixit et al. 2011). *V. trilobata* is occasionally harvested as seeds or young pods in India (Tomooka et al. 2011a). It has been successfully hybridized with mung bean (female parent) (Pandiyan et al. 2012).

9.3.13 *Vigna vexillata* (L.) A. Rich. (Tuber Cowpea)

V. vexillata has a pantropical distribution and, like many legumes, produces tubers. In Bali and Timor, Indonesia, this species is cultivated. Since Bali's cultivated accession seeds increased their size remarkably and lost strong dormancy and pods are indehiscent, it may be considered as fully domesticated. In Bali and Timor, *V. vexillata* is used for its tubers and seeds as well as forage with estimated yields of 18–30 t ha⁻¹ and 0.8–1.2 t ha⁻¹ for tubers and seeds, respectively. Root protein content is ca. 15 % which is about 2.5 times higher than that of yam (6 %), 3 times higher than that of potato (5 %) and sweet potato (5 %), and 5 times higher than that of cassava (3 %) (Karuniawan et al. 2006). It is also reported to be cultivated in parts of India and harvested by aboriginals in Australia. Based on the genetic study of agronomic traits by hybridization, it was concluded that the wild African and Australian accessions could be used along with var. *macrosperma* (putative cultivated form) for breeding improved varieties of *V. vexillata* for forage, cover crop, and vegetable uses (Damayanti et al. 2010a). They also reported a high level of cross incompatibility between the wild and cultivated form in Bali (Damayanti et al. 2010b).

9.3.14 *Vigna hosei* (Craib) Backer (*V. parkeri* Backer)

V. hosei is widely distributed in Asia, Africa, and both North and South America. It is a useful legume in intensively grazed pastures and forms a good ground cover in lightly shaded areas. (http://www.tropicalforages.info/key/Forages/Media/Html/Vigna_parkeri.htm).

9.3.15 *Vigna luteola* (Jacq.) Benth.

V. luteola is native to Africa, Asia, and Australasia but has been used as a short-season and highly palatable pasture or green manure in Europe and the New World. It is particularly useful in wet or waterlogged conditions. It has a wide range of adaptation to soil types, light conditions, and temperatures. An Australian accession, CPI 60428, has been reported to have some jassid insect resistance in humid, subtropical Australia (http://www.tropicalforages.info/key/Forages/Media/Html/Vigna_luteola.htm). It has been used to develop a linkage map to analyze salt tolerance in *V. marina* (Chankaew et al. 2014a).

9.3.16 *Vigna marina* (Burm.) Merr.

This species consists of two subspecies that have different geographic distributions: subspecies *marina* is found in Asia, Australia, the coast of Indian Ocean, and countries of Africa, whereas subspecies *oblonga* is found on the coastal areas of the tropical Atlantic countries of Africa. The species is reportedly used by some African farmers as a cover crop and green manure and has a potential as a sand-binding agent (Padulosi and Ng 1993). It also produces edible tubers that are eaten by aboriginals in Australia, while in the Maldives seeds are harvested and eaten (Padulosi and Ng 1993). The seeds are used as a coffee substitute in Gabon (Burkill 1995). Diversity analysis has shown that *V. marina* subsp. *oblonga* is more closely related to *V. luteola* than subsp. *marina* (Sonnante et al. 1997). As a consequence, recent studies to identify genes for salt tolerance in *Vigna marina* have concentrated on an interspecific mapping population between subsp. *oblonga* and *V. luteola* (Chankaew et al. 2014a). The F_{2,3} population was evaluated for salt tolerance under hydroponic conditions at the seedling and developmental stages. Segregation analysis indicated that salt tolerance in *V. marina* is controlled by a few genes. Multiple-interval mapping (MIM) consistently identified one major QTL for each trait—*Saltol1.1*, *Saltol1.2*, and *Saltol1.3* for the percentage of surviving plants in salt water at

the seedling stage and leaf wilt and recovery score during vegetative stage, respectively. All of the QTLs detected were located on LG1. These QTLs explained 50.7 %, 41.4 %, and 20.0 % of variation in the evaluated trait, respectively. All of the detected salt-tolerant QTLs, alleles from *V. marina* subsp. *oblonga*, increased salt tolerance. The flanking markers of each QTL can facilitate transferring of the salt-tolerant allele from *V. marina* subsp. *oblonga* into related *Vigna* crops. Unlike other *Vigna* species, *Sinorhizobium* spp. not *Bradyrhizobium* spp. forms nodules on *V. marina* roots (Akatsu, personal communication). The isolated *Sinorhizobium* strains showed an extremely high level of salt tolerance. The isolates could grow even in a nutrient solution with 5 % NaCl (Tomooka et al. 2011b).

9.3.17 *Vigna adenantha* (G.F. Meyer) Maréchal, Mascherpa & Stainier

V. adenantha has a pantropical distribution and is occasionally cultivated (Brink and Belay 2006). The green pods and ripe seeds are used as an emergency food. In India, its tuberous roots are eaten in times of food scarcity. It grows in humid swampy locations, along seashores and rivers. The seed has a large cavity between the cotyledons that enables it to float, and distribution patterns suggest it can be dispersed by sea (Brink and Belay 2006).

9.3.18 Interspecific Hybridization

Cross compatibility studies have been reviewed by Tomooka et al. (2002a). Generally, there is no barrier to gene flow between domesticated forms and their closest relatives. Species in the same section of the subgenus *Ceratotropis* can usually cross with little difficulty. Natural interspecific hybrids have been found between *V. hirtella* and *V. minima* in northern Thailand (author's unpublished observations). Recently, Pandiyan et al. (2010) reported a number of cross-sectional and cross subgenus hybrids. Among these hybrids,

the cross between *V. radiata* and *V. umbellata* is particularly significant as *V. umbellata* possesses a high level of resistance to bruchid beetles, one of the most serious pests of *Vigna*.

9.4 Domestication

The *Vigna* of Asia offer an unusually broad spectrum of species in various stages of domestication. Plant parts used by humans vary from seeds, green pods, to swollen roots. Several are useful forage species, such as *V. stipulacea*, *V. luteola*, and *V. marina*. Among them, *V. marina* may be de-domesticated since it has large seeds with non-dehiscent pods. Also in many parts of southern Japan and Southeast Asia, nonnative populations of escaped (de-domesticated or feral) cowpea are common with dehiscent pods (Bervillé et al. 2005).

The *Vigna* of Asia exhibit extremes in certain agronomic characteristics; among domesticated legumes, the longest pod is found in yard-long bean (*V. unguiculata* subsp. *unguiculata* cv.-gr. *Sesquipedalis*), and among the smallest seeds for a domesticated pulse used for its seeds are mung bean (*V. radiata*), black gram (*V. mungo*), and moth bean (*V. aconitifolia*).

9.5 Ecological Adaptation

The *Vigna* of Asia are adapted to a range of ecological conditions, among them harsh environments such as arid conditions (*V. aconitifolia*), sandy and saline soils (*V. marina* and *V. trilobata*), alkaline limestone rock soils (*V. exilis*), exposed windy cliff top environments (*V. riukiensis*), waterlogged riverside (*V. luteola*), and shady forests (*V. minima*).

9.6 Genomic Studies

Currently, a large sequencing project is under way that aims to sequence 16 *Vigna* species of Asia (Naito et al. 2013). This information coupled with complete sequence information for the

chloroplast and mitochondria of azuki bean and mung bean will provide a foundation of genome information resources for *Vigna* improvement in the future. Although the *Vigna* of Asia have been “forgotten” by much of the international agricultural research community, considerable progress has been made by national programs. However, the effort devoted to research on Asian *Vigna* does not do justice to their importance and potential contribution to agriculture in the future. The very wide ecological adaptation of *Vigna* in Asia, highlighted in this chapter, suggests that *Vigna* have much to offer other crops. Gigantism exhibited by the pods of yard-long bean and very high levels of salt tolerance in *Vigna marina* are two outstanding examples.

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