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Chapter 4

Wild Beans (*Phaseolus* L.) of North America

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Abstract The wild relatives of the five domesticated species of bean (*Phaseolus* L.) are widely distributed across the tropics and subtropics of the New World, with taxa extending from the Canadian border to Argentina, and on the Caribbean Islands, Bermuda, and the Galapagos Islands. Mesoamerica holds the largest concentration of species, particularly in the highlands of central Mexico, northward along the Sierra Madre Occidental, and south to Chiapas. The progenitors and close relatives of all five domesticates are also concentrated in this region. Plant breeding involving the use of wild relatives has almost entirely been directed toward the improvement of common bean (*Phaseolus vulgaris* L.), the most widely cultivated species, and successful contributions have mostly come from its progenitor (*Phaseolus vulgaris* L.) and a few other taxa. Wild relatives are considered to possess novel useful genetic variation that has not yet been fully explored. A number of wild *Phaseolus* are rare endemics that are threatened in their natural habitats and are insufficiently protected *in situ*. Significant *ex situ* collections of wild *Phaseolus* are maintained at the International Center for Tropical Agriculture (CIAT), the USDA-ARS National Plant Germplasm System, within the Sistema Nacional de Recursos Fitogenéticos para la Alimentación y la Agricultura (SINAREFI) Conservation Centers Network in Mexico, and at the Botanic Garden Meise, Belgium. Unfortunately, over 26% of *Phaseolus* taxa are not represented at all in these *ex situ* conservation facilities, and another 29% are represented by less than ten accessions, making over half of the species highly underrepresented in genebanks. Further efforts to enhance the protection of vulnerable species in their natural habitats, and further collecting to fill critical gaps in germplasm collections, are warranted.

Keywords Genetic resources, *Ex situ* conservation, *In situ* conservation, Grain legumes

4.1 Introduction

Beans (*Phaseolus* L.) have been cultivated for over 7000 years in the neotropics and continue to be a critical source of plant protein, dietary fiber, iron, zinc, and other micronutrients for human nutrition (Broughton et al. 2003; Ramírez-Villegas et al. 2010). The plants are also important to sustainable agricultural production practices due to their ability to enrich soil nitrogen by way of their symbiotic association with nitrogen-fixing rhizobia bacteria (Rubiales and Mikic 2015).

The genus *Phaseolus* has five domesticated species; each of the product of independent domestication processes from different wild progenitor species: common bean (*Phaseolus vulgaris* L.), lima bean (*P. lunatus* L.), runner bean (*P. coccineus* L.), tepary bean (*P. acutifolius* A. Gray), and year bean (*P. dumosus* Macfady) (Bitocchi et al. 2017). Both common bean and lima bean were in fact domesticated more than once from different populations of their wild progenitor taxa, in Mesoamerica and in the Andes (Gepts 1998; Motta-Aldana et al. 2010; Bitocchi et al. 2013).

Common bean is the world's most important legume for direct human consumption, comprising more than 50% of the grain legumes eaten worldwide, holding primary importance in the staple diet of over 500 million people, and being cultivated on over 23 million hectares, on every inhabitable continent (Gepts 2001; McClean et al. 2004; CGIAR 2017). Major production

areas include Brazil, Mexico and Central America, the Iberian Peninsula, Central-Eastern and Southern Africa, China, and India (Bitocchi et al. 2017).

The other four domesticated species have more distinct and somewhat narrower ecological adaptations (Debouck and Smartt 1995; Bitocchi et al. 2017). Lima bean grows in the warm humid tropics, from sea level to over 2000 m asl (Baudoin 1988; Bitocchi et al. 2017; Serrano-Serrano et al. 2012). Runner bean is adapted to cool highland conditions and is now cultivated primarily in climatically appropriate regions of Spain, Italy, the UK, the Netherlands, and other northern European countries with cooler growing season temperatures (Rodino et al. 2007). Tepary bean, the most drought tolerant of cultivated *Phaseolus*, is adapted to arid and semi-arid conditions, with high temperatures, low and variable precipitation, and alkaline soils (Pratt and Nabhan 1988; Porch et al. 2013a). Tepary bean is still predominantly grown only in its region of origin in the warm deserts of Mexico and the USA, although it is the subject of increasing interest in similar agroecological regions of Africa and South Asia (Small 2014). Year bean is the domesticated form of a species that is the result of a naturally occurring hybridization event between the progenitors of common and runner bean (Mina-Vargas et al. 2016). Year bean is cultivated in Central America (particularly in the highlands of Guatemala), the Caribbean, and in the Northern Andes from Venezuela south to Peru, especially in climatic zones where common bean is highly susceptible to anthracnose, *Ascochyta* blight, and root rot (Mina-Vargas et al. 2016; USDA, ARS, National Plant Germplasm System 2017b; D. Debouck personal communication 2017).

Even with the incredible expansion and success of *Phaseolus* beans worldwide, a wide range of challenges to their cultivation exist. Common beans are vulnerable to drought and heat, which are likely to be exacerbated by climate change (Beebe et al. 2011; Jarvis et al. 2012). Major diseases for the crop include root rot, *Xanthomonas* blight, downy mildew, rust, angular leaf spot, anthracnose, web blight, white mold, halo blight, bean common mosaic virus (BCMV), and a variety of other viruses. Major insect pests include red spider, mealybug, white fly, leaf hoppers, weevils, various caterpillars, flea beetles, *Diabrotica*, and Mexican bean beetles (Beebe 2012).

Lima bean insect pests include thrips, aphids, leaf miners, *Heliothis*, and chrysomelid beetles. They are also susceptible to mycoplasmas (Freytag and Debouck 2002) and white mold (Boland and Hall 1994). Runner beans are primarily affected by rust, as well as angular leaf spot, anthracnose, and *Ascochyta* leaf spot, and by *Apion* pod weevil, chrysomelid beetles, thrips, flea beetle, and leaf-hoppers. Tepary beans are susceptible to powdery mildew, root rots, white mold, rust, and viruses including alfalfa mosaic, bean yellow mosaic, BCMV, bean golden mosaic, curly top, pod mottle, and four whitefly-transmitted viruses (Freytag and Debouck 2002). Insect pests of tepary bean include leafhopper, leaf-eating beetles, leaf miners, flea beetles, and leaf-eating caterpillars (Debouck 1999; Freytag and Debouck 2002).

This chapter provides an overview of the identities and relationships, distributions, genetic resource potential, and conservation status of the North American wild relatives of *Phaseolus* beans. We focus on the progenitors and close relatives of the domesticated species, as they are considered the most promising taxa with regard to successful present and future uses as genetic resources (Harlan and de Wet 1971). We also provide details on *Phaseolus polystachios*

(L.) Britton et al., a distant relative of lima bean which is the most northerly occurring wild species in the genus, known by the authors to be declining in portions of its natural habitat. We conclude with a discussion of the key steps needed to improve the conservation of North American *Phaseolus* crop wild relatives.

4.2 Crop Wild Relatives of *Phaseolus* Beans and the Relationships Between Wild Taxa and the Domesticated Species

Phaseolus is a monophyletic genus native to the New World, comprising some 70-85 species and ca. 30 infraspecific taxa, which are currently parsed into eight phylogenetic groups within two clades (Freytag and Debouck 2002; Delgado-Salinas et al. 2006; Ramírez-Villegas et al. 2010) (Fig. 4.1). The total number of species may reach 100 or more with thorough fieldwork in understudied areas of the neotropics in combination with phylogenetic analyses, in further search of narrow endemic taxa (D. Debouck personal communication 2017).

The *vulgaris* group includes all cultivated species except *P. lunatus*, along with four other noncultivated species, including the newly described *Phaseolus debouckii* A. Delgado, segregated from *P. vulgaris* based on genome-wide single nucleotide polymorphisms (Rendón-Anaya et al. 2017a, b). The *lunatus* group includes at least five wild species, while its sister clade, the *polystachios* group, includes nine or more taxa (Fig. 4.1).

Phaseolus species have been organized into genetic relative categories, or “genepools,” based on crossing studies and phylogenetic analyses (Smartt 1981; Singh and Jauhar 2005; Rendón-Anaya et al. 2017a, b; The Harlan and de Wet Crop Wild Relative Inventory 2017; USDA, ARS, National Plant Germplasm System 2017b). The primary genepool of domesticated species includes both cultivated forms and wild populations, hybrids of which are generally fully fertile with no major reproductive barriers (Harlan and de Wet 1971) (Table 4.1).

The secondary genepool is comprised of related species that may be crossable with the cultivated forms, but with extra effort needed to overcome reproductive barriers and to eliminate linkage drag (Prohens et al. 2017; Miller and Khoury 2018). Common bean has been successfully crossed with species in its secondary genepool; lima and tepary bean may be less capable of gene exchange with their secondary relatives, although their potential has not been as comprehensively studied (Debouck 1999; D. Debouck personal communication 2017). Tertiary relatives and other distantly related taxa within the genus are not considered in detail here, as their potential for utilization as genetic resources is constrained by major biological barriers to interfertility, although advancing techniques may make utilization of distant relatives more feasible in the future (Zhang et al. 2014; Miller and Khoury 2018).

Table 4.1 Genepools of *Phaseolus* domesticated species

Common bean- <i>Phaseolus vulgaris</i> L., <i>Phaseolus vulgaris</i> L. var. <i>vulgaris</i>		
Primary relatives	Secondary relatives	Tertiary relatives
<i>Phaseolus vulgaris</i> L. (including <i>Phaseolus vulgaris</i> L. var. <i>aborigineus</i> (Burkart) Baudet and <i>Phaseolus vulgaris</i> L. var. <i>mexicanus</i> A. Delgado)	<i>Phaseolus albescens</i> McVaugh ex R. Ramírez & A. Delgado	<i>Phaseolus acutifolius</i> A. Gray
	<i>Phaseolus coccineus</i> L.	<i>Phaseolus acutifolius</i> A. Gray var. <i>acutifolius</i>
	<i>Phaseolus costaricensis</i> Freytag & Debouck	<i>Phaseolus acutifolius</i> A. Gray var. <i>tenuifolius</i> A. Gray
	<i>Phaseolus dumosus</i> Macfady	<i>Phaseolus angustissimus</i> A. Gray
	<i>Phaseolus debouckii</i> A. Delgado	<i>Phaseolus carteri</i> Freytag & Debouck
	<i>Phaseolus persistentus</i> Freytag & Debouck	<i>Phaseolus filiformis</i> Benth.
		<i>Phaseolus maculatus</i> Scheele subsp. <i>ritensis</i> (M. E. Jones) Freytag
		<i>Phaseolus parvifolius</i> Freytag
Runner bean- <i>Phaseolus coccineus</i> L.		
Primary	Secondary	Tertiary
<i>Phaseolus coccineus</i> L.	<i>Phaseolus albescens</i> McVaugh ex R. Ramírez & A. Delgado	<i>Phaseolus acutifolius</i> A. Gray
	<i>Phaseolus costaricensis</i> Freytag & Debouck	
	<i>Phaseolus dumosus</i> Macfady	
	<i>Phaseolus vulgaris</i> L.	
Year bean- <i>Phaseolus dumosus</i> Macfady		
Primary	Secondary	Tertiary
<i>Phaseolus dumosus</i> Macfady	<i>Phaseolus albescens</i> McVaugh ex R. Ramírez & A. Delgado	<i>Phaseolus parvifolius</i> Freytag
	<i>Phaseolus coccineus</i> L.	
	<i>Phaseolus costaricensis</i> Freytag & Debouck	
	<i>Phaseolus vulgaris</i> L.	
Tepary bean- <i>Phaseolus acutifolius</i> A. Gray		
Primary	Secondary	Tertiary
<i>Phaseolus acutifolius</i> A. Gray var. <i>acutifolius</i>	<i>Phaseolus parvifolius</i> Freytag	<i>Phaseolus albescens</i> McVaugh ex R. Ramírez & A. Delgado
<i>Phaseolus acutifolius</i> A. Gray var. <i>tenuifolius</i> A. Gray		<i>Phaseolus carteri</i> Freytag & Debouck
		<i>Phaseolus coccineus</i> L.
		<i>Phaseolus costaricensis</i> Freytag & Debouck
		<i>Phaseolus dumosus</i> Macfady
		<i>Phaseolus filiformis</i> Benth.
		<i>Phaseolus persistentus</i> Freytag & Debouck

		<i>Phaseolus vulgaris</i> L.
Lima bean- <i>Phaseolus lunatus</i> L.		
Primary	Secondary	Tertiary
<i>Phaseolus lunatus</i> L.	<i>Phaseolus augusti</i> Harms	<i>Phaseolus acinaciformis</i> Freytag & Debouck
	<i>Phaseolus longiplacentifer</i> Freytag	<i>Phaseolus albinervus</i> Freytag & Debouck
	<i>Phaseolus mollis</i> Hook. f.	<i>Phaseolus jaliscanus</i> Piper
	<i>Phaseolus pachyrrhizoides</i> Harms	<i>Phaseolus juquilensis</i> A. Delgado
	<i>Phaseolus viridis</i> Piper	<i>Phaseolus lignosus</i> Britton
		<i>Phaseolus maculatifolius</i> Freytag & Debouck
		<i>Phaseolus maculatus</i> Scheele
		<i>Phaseolus marechalii</i> A. Delgado
		<i>Phaseolus nodosus</i> Freytag & Debouck
		<i>Phaseolus novoleonensis</i> Debouck
		<i>Phaseolus polystachios</i> (L.) Britton et al.
		<i>Phaseolus reticulatus</i> Freytag & Debouck
		<i>Phaseolus rotundatus</i> Freytag & Debouck
		<i>Phaseolus salicifolius</i> Piper
		<i>Phaseolus scrobiculatifolius</i> Freytag
		<i>Phaseolus sonorensis</i> Standl.
		<i>Phaseolus venosus</i> Piper
		<i>Phaseolus xolocotzii</i> A. Delgado

Adapted from USDA, ARS, National Plant Germplasm System (2017b), The Harlan and de Wet Crop Wild Relative Inventory (2017), Rendón-Anaya et al. (2017a, b), and D. Debouck personal communication (2017)

4.3 Distribution of Wild *Phaseolus* in North America

The genus *Phaseolus* originated in the tropics and subtropics of the New World. Wild species belonging to the genus are naturally distributed from the USA south to Argentina (Ramírez - Villegas et al. 2010). Taxa are not known from Chile nor from Canada (Freytag and Debouck 2002), although Sousa and Delgado-Salinas (1993) report wild populations in southern Quebec and Ontario. Members also occur on the major Caribbean Islands (*Phaseolus dumosus* Macfady, *Phaseolus lunatus* L., and possibly *P. polystachios* [Liogier (1988)]), Bermuda (*Phaseolus lignosus* Britton), and the Galapagos Islands (*Phaseolus mollis* Hook. f.) (Ramírez - Villegas et al. 2010; Arani et al. 2017; Debouck 2017; USDA, ARS, National Plant Germplasm System 2017b).

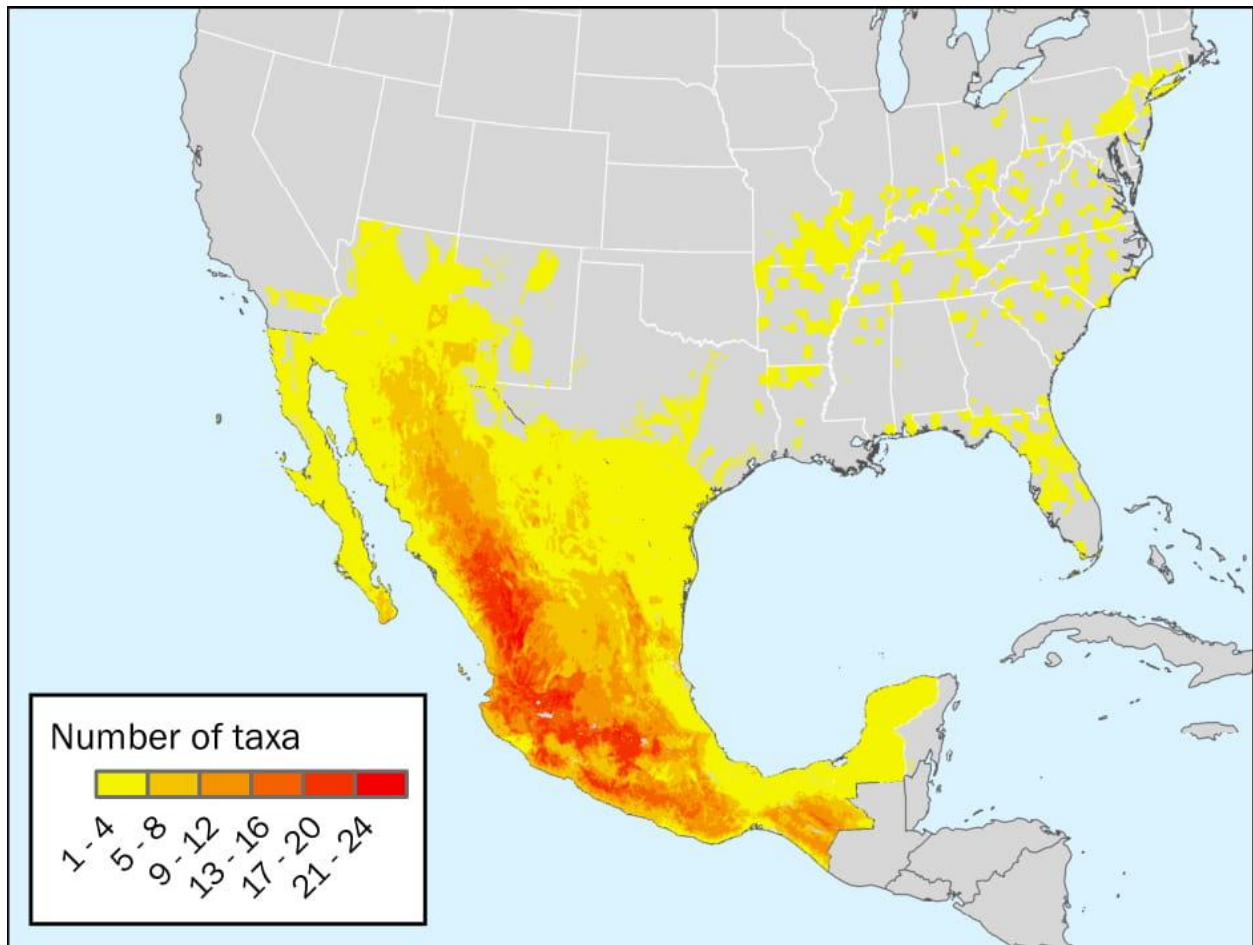


Fig. 4.2 Species richness map of modeled potential distributions of 57 North American *Phaseolus* taxa. The map displays overlapping potential distribution models for assessed taxa. Potential distribution models are based on climatic and edaphic similarities with herbarium and genebank reference localities and reflect potential for occurrence rather than confirmed presence. Warmer colors indicate areas where greater numbers of taxa potentially occur in the same geographic localities. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

The main areas of richness of species are Mesoamerica (from southern USA, Mexico, and Central America down to Panama), the northern Andean region (Colombia to northern Peru), and the central Andes (northern Peru, Bolivia, and northwest Argentina). Of these, the Mesoamerican center is the richest in number of taxa, reaching the highest concentrations in the highlands of central Mexico, northward along the Sierra Madre Occidental, and south to Chiapas (Nabhan 1990; Debouck 2000; Freytag and Debouck 2002; Ramírez-Villegas et al. 2010) (Fig 4.2). Numerous rare endemic species are distributed in North America, especially in the Sierra Madre Occidental and Sierra Madre Oriental of Mexico.

The distributions of the primary and secondary relatives of the cultivated species are detailed below.

4.3.1 Distributions of Close Relatives of Common Bean

Wild common bean (*P. vulgaris* L.) occurs from southern Chihuahua, Mexico, south through Central America and the Andes to Argentina (Nabhan 1985; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.3). Populations are found from very arid conditions to over 100 cm annual precipitation (Gentry 1969; Freytag and Debouck 2002). The plant is often found growing over or in shrubs on the edges and within open pine-oak forests and woodlands, usually from 800 to 2000 m asl (Freytag and Debouck 2002). Wild common bean is usually found in shallow, often friable but sometimes heavy soils, derived from limestone, schist, granite, lava or tufa (Freytag and Debouck 2002). The plant is a short-lived perennial, generally producing seeds during its first year of growth on indeterminate climbing vines reaching over 3 meters long (Gentry 1969). The species produces vegetative growth during the rainy season, developing pods during the dry season, which varies by region, indicating a strong population-level adaptation to local climates (Gentry 1969). Wild common bean has been separated into multiple varieties, including *P. vulgaris* L. var. *aborigineus* [Burkart] Baudet and *Phaseolus vulgaris* L. var. *mexicanus* A. Delgado based on geographic and morphological differences. Here we follow Freytag and Debouck (2002) in treating the plants as one continuum within the species.

Secondary relative *Phaseolus albescens* McVaugh ex R. Ramírez & A. Delgado is known from 16 populations distributed in montane forests in central Mexico, in the states of Colima, Guerrero, Jalisco, and Michoacan (Ramírez-Delgadillo and Delgado-Salinas 1999; Debouck 2017; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.3). *Phaseolus costaricensis* Freytag & Debouck occurs in Costa Rica and Panama (USDA, ARS, National Plant Germplasm System 2017b), the newly described *Phaseolus debouckii* A. Delgado is distributed in Ecuador and northern Peru (Rendón-Anaya et al. 2017a), and *Phaseolus persistentus* Freytag & Debouck occurs in Guatemala (USDA, ARS, National Plant Germplasm System 2017b). Wild *Phaseolus coccineus* L. and *P. dumosus* are covered in the sections below. North American occurrences of these species are mapped in Fig. 4.3.

4.3.2 Distributions of Close Relatives of Runner Bean

Wild runner bean (*P. coccineus*) occurs from southern Chihuahua, Mexico south to Matagalpa, Nicaragua; reports outside that range are likely to be escapes from cultivation or misidentifications (Nabhan 1985; Freytag and Debouck 2002; USDA, ARS, National Plant Germplasm System 2017b; D. Debouck personal communication 2017) (Fig. 4.3). Wild runner bean is a climbing perennial with large red flowers that can vine up to 5 m. The species has been assigned several subspecies, some of which have purple flowers; white flowers are generally restricted to cultivated types (Freytag and Debouck 2002). Wild runner bean is normally found from 1500 to 2500 m asl in mixed forests of pine, oak, juniper, liquidambar, and hawthorn, growing over shrubs and herbs (Freytag and Debouck 2002). The various subspecies and varieties of wild *coccineus* appear to be adapted to specific climates and habitats, from cloud forest to desert, and from rich to poor soils (Freytag and Debouck 2002). Some types are quite rare, such as *Phaseolus coccineus* L. subsp. *coccineus* var. *griseus* (Piper) Freytag, occurring in dry conditions of southern Oaxaca in scrub oak and mesquite (Freytag and Debouck 2002).



Fig. 4.3 Occurrence localities of North American *Phaseolus* primary and secondary wild relatives within the common bean (*P. vulgaris* L.), runner bean (*P. coccineus* L.), and year bean (*P. dumosus* Macfad.) gene pools. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

4.3.3 Distributions of Close Relatives of Year Bean

Wild year bean (*P. dumosus*) is distributed in Chiapas in southern Mexico and in Guatemala, and is naturalized in other regions of Central America as well as in the Caribbean (USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.3). Only four populations are known in Mexico (Freytag and Debouck 2002; Debouck 2017), in humid pine-oak forests, growing on very steep slopes and along streams, mostly in open places, often over weeds and small trees, in deep, moist, well-drained, often sandy or rocky, humic soil derived from volcanic ash (Freytag and Debouck 2002).

4.3.4 Distributions of Close Relatives of Tepary Bean

Wild tepary bean (*Phaseolus acutifolius* A. Gray) mostly occurs at elevations of 335-2000 m asl from Arizona and New Mexico, USA, south to Jalisco in central Mexico (Freytag and Debouck 2002; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.4). Populations may extend into Texas and Baja California (Freytag and Debouck 2002). Wild tepary beans are annuals, with fibrous roots and small slender climbing vines. Plants are generally found along

dry washes, streambeds, canyon bottoms and floodplains in pine-oak forest and along trails, abandoned fields, and fence rows in drier areas (Freytag and Debouck 2002). *Phaseolus acutifolius* A. Gray var. *acutifolius* is somewhat sympatric with *Phaseolus acutifolius* A. Gray var. *tenuifolius* A. Gray, although variety *acutifolius* is thought to occur in drier conditions and generally more westerly in the Sierra Madre and lowlands, whereas variety *tenuifolius* occurs in the higher parts of the mountains and eastward (Freytag and Debouck 2002; D. Debouck personal communication 2017). A wild *Phaseolus acutifolius* A. Gray var. *latifolius* Freeman has been described as occurring from northwest Mexico and the southwestern USA (Freytag and Debouck 2002). Here we follow USDA ARS National Plant Germplasm System (2017b) in considering it a synonym of var. *acutifolius*. Secondary relative *Phaseolus parvifolius* Freytag is distributed from Sonora and Baja California Sur, Mexico south to Guatemala (Fig. 4.4).

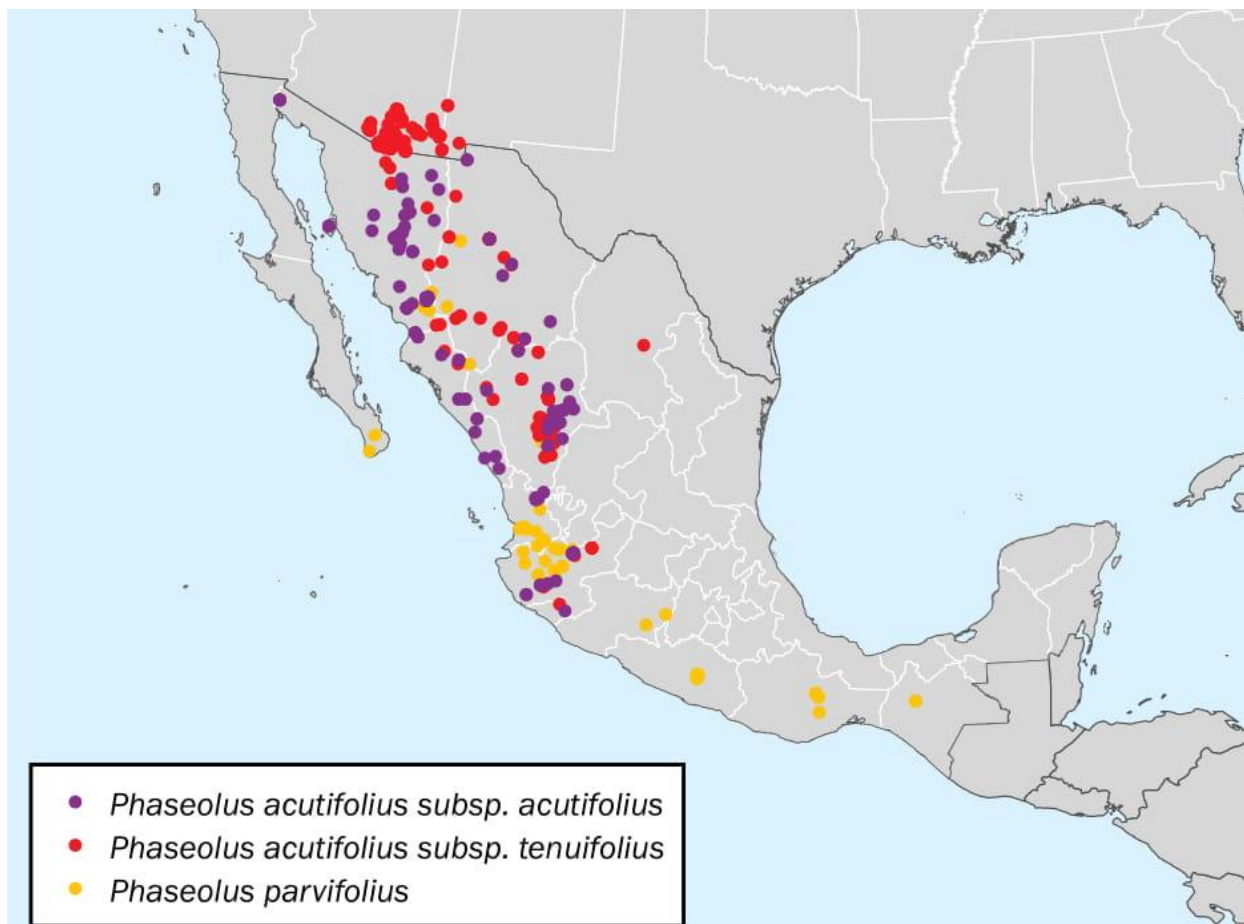


Fig. 4.4 Occurrence localities of North American *Phaseolus* primary and secondary wild relatives within the tepary bean (*P. acutifolius* A. Gray) gene pool. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

4.3.5 Distributions of Close Relatives of Lima Bean

Wild lima bean (*P. lunatus* L.) is distributed from Sinaloa, Mexico, south through Central America to Brazil and Argentina (Freytag and Debouck 2002; USDA, ARS, National Plant Germplasm System 2017b) (Fig. 4.5). One population is known from Baja California Sur,

Mexico. Wild lima bean is a climber, with vines up to 8 m long and with perennial, fibrous and sometimes fleshy roots. The plant is mostly found along stream banks or other moist areas of pine-oak forests between 0 and 1600 m asl (Freitag and Debouck 2002). Wild lima bean often grows over shrubs and small trees in areas cleared for coffee, sugarcane and other crops, and is more abundant in areas inaccessible to grazing. The plant is adapted to a wide range of soil types derived from volcanic rock and ash, metamorphic schists, limestones, and basalt, from black clay to brown friable rock, and even in sand dunes (Freitag and Debouck 2002).

Phaseolus longiplacentifer Freitag is a narrow endemic species described by the senior author in Freitag and Debouck (2002), known only from its type collection north of Orizaba, Veracruz, Mexico. Delgado-Salinas et al. (2006) assigned *longiplacentifer* as a synonym of *Phaseolus viridis* Piper (1926), which is found in scattered places in Veracruz, Oaxaca, and Chiapas, Mexico, and in Alta Verapaz, Guatemala (Debouck 2017), while the senior author in Freitag and Debouck (2002) considered *P. viridis* a synonym of (wild) *P. lunatus*. *Phaseolus augusti* Harms is distributed in Ecuador, Peru, Bolivia, and Argentina; *Phaseolus pachyrrhizoides* Harms occurs in Peru; and *P. mollis* is distributed only in the Galapagos Islands (USDA, ARS, National Plant Germplasm System 2017b).



Fig. 4.5 Occurrence localities of North American *Phaseolus* primary and secondary wild relatives within the lima bean (*P. lunatus* L.) genepool. Full methods for generation of maps and occurrence data providers are listed in Appendix 1

4.4 Utilization of Wild *Phaseolus*

4.4.1 Utilization of Wild *Phaseolus* as Genetic Resources

Considerable genetic variation in cultivated common bean has existed historically as the result of multiple domestication events as well as further naturally occurring gene flow between wild progenitors and early domesticates, resulting in six to seven “races” within two main “genepools” with clear genetic structure (Acosta-Gallegos et al. 2007). The diversity in major commercial common bean varieties has been considered to be relatively narrow, though, and numerous authors have recommended a widening of this genetic base (e.g. Adams 1977; Singh 1992; Sonnante et al. 1994; Beebe et al. 1995; Singh 1999; Métais et al. 2002; Rosales-Serna et al. 2004).

Interspecific crosses are possible between domesticated *P. vulgaris*, *P. coccineus*, *P. dumosus*, and *P. acutifolius* (Fig. 4.6). *Phaseolus coccineus* and *P. dumosus* readily cross with *P. vulgaris* without embryo rescue, although the progeny have reduced viability when using *P. vulgaris* as the male parent (Al-Yasiri and Coyne 1966; Debouck 1999). *Phaseolus acutifolius* has been utilized in interspecific crosses with common bean, mostly through congruity crosses (alternate backcrossing), using embryo rescue with *P. vulgaris* as the cytoplasm source (Waines et al. 1988; Mejía-Jiménez et al. 1994; Anderson et al. 1996).

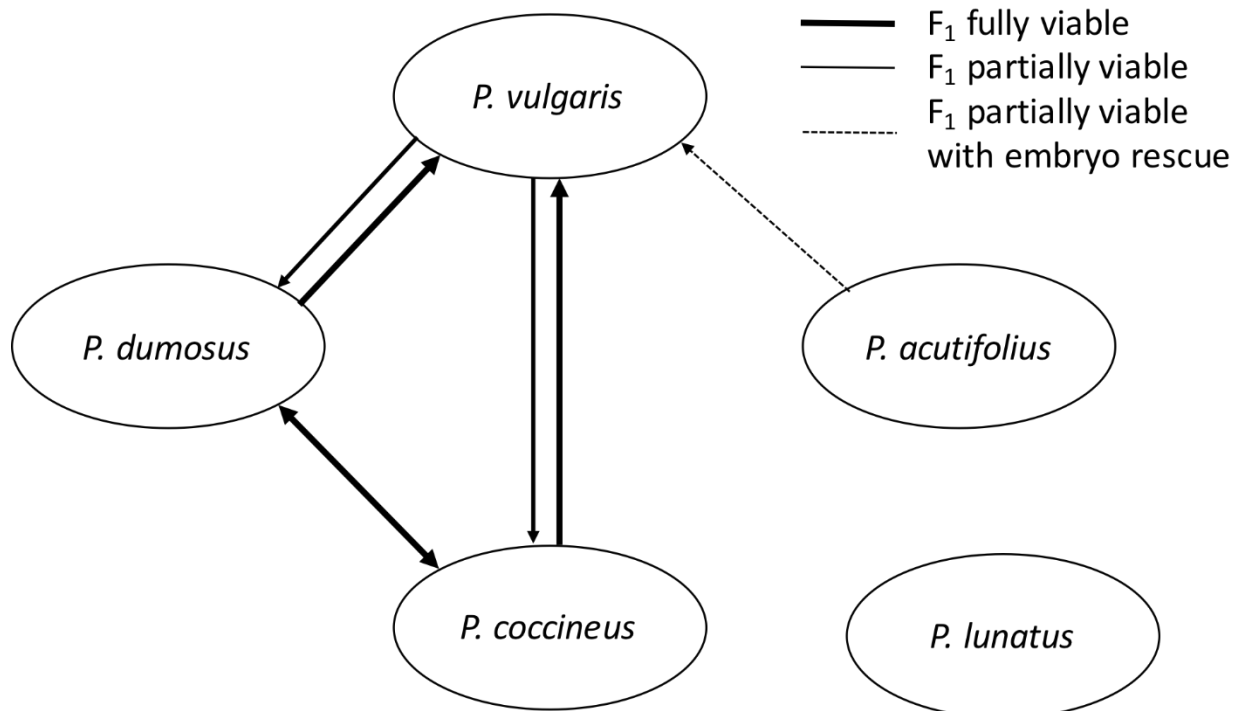


Fig. 4.6 Viability of interspecific crosses of the five domesticated species of *Phaseolus* based on Al-Yasiri and Coyne (1966), Smartt (1970), and Debouck (1999). The arrow points toward the female in the cross

Runner bean accessions have been employed in common bean breeding as new sources of resistance to bean golden yellow mosaic virus (Osorno et al. 2007), white mold (Schwartz et

al. 2006; Singh et al. 2009; Vasconcellos et al. 2017), and common bacterial blight (Freytag et al. 1982; Miklas et al. 1999). Year bean accessions have been researched for resistance to anthracnose (Mahuku et al. 2002), Ascochyta leaf blight (Schmit and Baudoin 1992), and white mold (Hunter et al. 1982) as well as to enhance nutritional quality (Blair 2013). Tepary bean accessions have contributed new sources of resistance to common bacterial blight, leafhopper, and bruchid (Singh et al. 1998), and the species has been explored for drought and heat tolerance (Rao et al. 2013). Although attempts to cross *P. vulgaris* and *P. lunatus* have mostly been unsuccessful (Al-Yasiri and Coyne 1966; Smartt 1970), viable but infertile plants have been reported (Mok et al. 1978), although not replicated (Debouck 1999).

Practical limitations constrain the use of wild germplasm for common bean cultivar improvement, as breeding is mainly restricted to the variation within market classes (Kelly et al. 1998; Singh 2001). The complexity of inheritance and genetic linkage of traits of commercial importance, such as seed color, seed size, and growth habit, has hindered the introgression of novel variation (Koinange et al. 1996; Kelly et al. 1999; Singh 2001; McClean et al. 2002; Blair et al. 2006; Moghaddam et al. 2016). The lack of useful characterization and evaluation data on wild accessions has also been considered a constraint. Wild accessions are avoided because of the limited power of evaluation of the germplasm for agronomically useful traits, due to attributes such as vigorous growth habits, long growing cycles, photoperiod sensitivity, and dehiscence (Singh 2001; Acosta-Gallegos et al. 2007). Finally, a simple lack of readily available wild germplasm may have constrained its use in bean breeding, particularly prior to the 1970s (Freytag and Debouck 2002).

That said, *Phaseolus* wild relatives are considered to possess valuable traits that may be difficult to find in domesticated materials (Porch et al. 2013b; Rao et al. 2013). Target traits in common bean research with focus on wild *vulgaris* germplasm have included resistance to storage insects, leafhoppers, Ascochyta blight, common bacterial blight, white mold, BCMV, Fusarium root rot, and rust, and tolerance to abiotic stresses and low soil fertility, as well as early maturity, adaptation to higher latitudes, upright plant type, pod quality, seed size, seed yield, protein digestibility, and nodulation traits (Kornegay and Cardona 1991; Shellie-Dessert and Bliss 1991; Kipe-Nolt et al. 1992; Kornegay et al. 1993; Delgado-Salinas et al. 1999; Singh 2001; Acevedo et al. 2006; Blair et al. 2006; Acosta-Gallegos et al. 2007; Cortés et al. 2013; De Ron et al. 2015; Blair et al. 2016; Rodriguez et al. 2016).

Wild *P. vulgaris* has been successfully used in common bean breeding as a source of resistance to bruchids (Osborn et al. 1988, 2003; Kornegay et al. 1993), common bacterial and web blight (Beaver et al. 2012), white mold (Mkwaila et al. 2011), and for yield (Acosta-Gallegos et al. 2007; Wright and Kelly 2011; Porch et al. 2013b). In addition, wild *P. acutifolius* has been utilized in common bean breeding as a source of resistance to bruchids (Singh et al. 1998; Kusolwa et al. 2016), low temperatures, and drought tolerance (Souter et al. 2017). *Phaseolus costaricensis* has contributed white mold resistance (Singh et al. 2009; Schwartz and Singh 2013). Wild *Phaseolus* accessions published as sources of traits utilized in common bean plant breeding programs are listed in Table 4.2.

Table 4.2 Accessions of wild *Phaseolus* published as utilized in common bean breeding. For accession codes, G refers to International Center for Tropical Agriculture (CIAT) collections and PI to USDA-ARS National Plant Germplasm System accessions

Trait	Source species	Accession	References
Bruchids	<i>P. vulgaris</i> L.	G12882 G12866 G12952 G02771	Osborn et al. 1988, 2003; Kornegay et al. 1993
Bruchids	<i>P. acutifolius</i> A. Gray	G40199	Singh et al. 1998; Kusolwa et al. 2016
Cold and drought	<i>P. acutifolius</i> A. Gray	PI 638833	Souter et al. 2017
Common bacterial blight	<i>P. vulgaris</i> L.	PI 417662	Beaver et al. 2012
Web blight	<i>P. vulgaris</i> L.	PI 417662	Beaver et al. 2012
White mold	<i>P. vulgaris</i> L.	PI 318695	Mkwaila et al. 2011
White mold	<i>P. costaricensis</i> Freytag & Debouck	G40604	Singh et al. 2009; Schwartz and Singh 2013
Yield	<i>P. vulgaris</i> L.	G24423	Acosta-Gallegos et al. 2007

Secondary relative *P. costaricensis* has also been noted as belonging to a germplasm group potentially having resistance to angular leaf spot, anthracnose, Ascochyta blight, bean golden mosaic virus, bean yellow mosaic virus, common bacterial blight, and Fusarium root rot, as well as cold tolerance (Singh 2001). Some distant relatives of common bean have been recorded as possessing interesting characteristics of potential value to breeding, although successful introgression would be difficult. Examples include *Phaseolus leptostachyus* Benth. for its determinate growth habit (Freytag and Debouck 2002), *Phaseolus angustissimus* A. Gray for cold tolerance (Balasubramanian et al. 2004), and the Mexican restricted endemic *Phaseolus leptophyllus* G. Don, whose unique leaf morphology may provide protection from water loss during drought stress (Freytag and Debouck 2002).

Widening of genetic diversity in the other *Phaseolus* crop species may also prove important, as species such as tepary bean are thought to possess relatively low levels of genetic variation in cultivated forms (Schinkel and Gepts 1988; Garvin and Weeden 1994; Munoz et al. 2006). With regard to lima bean, tertiary relatives *Phaseolus jaliscanus* Piper, *Phaseolus maculatus* Scheele, *Phaseolus maculatus* Scheele subsp. *ritensis* (M. E. Jones) Freytag, *P. polystachios*, and *Phaseolus salicifolius* Piper have been noted for their disease resistance (van der Maesen and Somaatmadja 1992).

4.4.2 Direct Uses of Wild *Phaseolus* Species

The seeds of wild common and lima beans are used as food by indigenous peoples in times of scarcity but are not regularly consumed (Gentry 1969; Freytag and Debouck 2002; Zizumbo-Villareal et al. 2012). Kaplan (1965) noted that the roots of wild runner bean are poisonous, but that tubers which form on the roots are occasionally boiled for consumption. Wild *vulgaris*, *coccineus*, and *acutifolius* var. *tenuifolius* are known to be grazed by cattle and goats (Freytag and Debouck 2002). A number of additional wild *Phaseolus* species were probably occasionally consumed and possibly even cultivated, including *P. polystachios* (possibly cultivated) (Kaplan 1965), *P. leptostachyus*, and *Phaseolus glabellus* Piper (Freytag and Debouck 2002).

4.5 Conservation of Wild *Phaseolus* in North America

4.5.1 In Situ Conservation of Wild *Phaseolus* in North America

NatureServe has published conservation assessments for 17 currently accepted *Phaseolus* taxa (NatureServe 2017). Of these only *Phaseolus texensis* A. Delgado & W. R. Carr is listed as a threatened species (i.e. G1 or G2), assigned a G2 (imperiled) status. The species is narrowly endemic to rocky canyons in the eastern and southern parts of the Edwards Plateau of Texas and is known from only a few localities (Delgado-Salinas and Carr 2007). *Phaseolus supinus* Wiggins & Rollins is also listed imperiled, and is also present (although not listed) in the US Fish and Wildlife Service Environmental Conservation Online System (USFWS 2017), but this species is no longer an accepted *Phaseolus* taxon, having been reassigned as *Macroptilium supinum* (Wiggins & Rollins) A. Delgado et al. (USDA, ARS, National Plant Germplasm System 2017b).

The IUCN Red List of Threatened Species lists *P. lignosus*, the Bermuda endemic, as Critically Endangered (Copeland et al. 2014). The species is restricted to six populations due to habitat loss and invasive species, and surveys completed in 2004 counted a total of only 29 mature individuals, which may be all that are left of naturally occurring plants. Surveys conducted in 2014 were successful in finding populations only within Walsingham Natural Reserve, although it may also occur in three other protected areas in Bermuda. *Phaseolus lignosus* is listed as Critical Risk B1, C, at Level 3 in Bermuda, under the Protected Species Order 2012, and benefits from a recovery plan led by Bermuda Department of Environment Protection, including habitat protection and restoration as well as *ex situ* conservation. Seeds are in long-term storage at the International Center for Tropical Agriculture and at Kew's Millennium Seed Bank, and propagation efforts have translocated the species to five sites, where populations appear to be viable (Copeland et al. 2014; Debouck 2015).

The Red List also covers *P. polystachios* and *Phaseolus xanthotrichus* Piper, both as species of Least Concern, assessed as widespread species with generally stable populations (Contu 2012; Groom 2012). Recent efforts by authors Kisha and Egan to document the extant range of *P. polystachios* relative to historical collections have revealed a striking decline in range and commonality therein, particularly along northern and western range boundaries (T. Kisha &

A.N. Egan personal observations 2017). Furthermore, while *P. polystachios* has a wide range within North America, it is now declared extirpated from Michigan (MI DNR 2017), Connecticut (CT DEEP 2015), and Pennsylvania (PA Natural Heritage Program Species Lists 2014) and imperiled in several others (NatureServe 2017).

The IUCN Red List and NatureServe programs currently offer no information on a large number of endemic and otherwise rare North American *Phaseolus* taxa, including *Phaseolus polystachios* (L.) Britton et al. subsp. *smilacifolius* (Pollard) Freytag occurring in Florida; *Phaseolus carteri* Freytag & Debouck in Baja California Sur, *Phaseolus amabilis* Standl. in Chihuahua; *Phaseolus reticulatus* Freytag & Debouck in Durango; *Phaseolus albiflorus* Freytag & Debouck, *Phaseolus albiviolaecus* Freytag & Debouck, *Phaseolus altimontanus* Freytag & Debouck, *Phaseolus maculatifolius* Freytag & Debouck, *Phaseolus novoleonensis* Debouck, *Phaseolus neglectus* F. J. Herm., and *Phaseolus trifidus* Freytag in Nuevo Leon, Tamaulipas, and/or Coahuila; *Phaseolus purpusii* Brandegees in San Luis Potosi; *P. jaliscanus*, *Phaseolus esperanzae* Seaton, *Phaseolus magnilobatus* Freytag & Debouck, *Phaseolus marechalii* A. Delgado, and *Phaseolus rotundatus* Freytag & Debouck in central Mexico; *Phaseolus leptophyllus* G. Don in Guerrero; and *Phaseolus chiapasanus* Piper in southern Mexico. Conservation status and threat assessment information are needed for such species to be able to prioritize conservation action.

Aside potentially from the populations of wild *Phaseolus* monitored in the Sierra de Manantlan Biosphere Reserve in Jalisco and Colima, Mexico (Vázquez-García 1995), no active management of wild *Phaseolus* in protected areas is known by the authors to be ongoing in North America. And even in the Biosphere Reserve, the mention by Vázquez-García et al. (1995) of two unidentified species clearly indicates that the first limiting factor for *in situ* conservation is that protected areas lack a complete inventory of plants (D. Debouck personal communication 2017).

In situ conservation is certainly occurring in federal, state, provincial, Native American, Indigenous Peoples, nongovernmental, and privately managed protected areas without inventories, active management plans, or regularly scheduled monitoring. But information on these populations is not available. Outside of these areas, wild *Phaseolus* populations are considered to be vulnerable to habitat destruction (Freytag and Debouck 2002) and potentially (for progenitor species) to genetic contamination due to gene flow with cultivated forms (Papa and Gepts 2003).

4.5.1.1 Remarks on *Phaseolus polystachios*

Phaseolus polystachios, the North American wild kidney bean or thicket bean, is the only *Phaseolus* species native to temperate North America, with a distribution from Texas to Connecticut, USA. As such, it has evolutionarily adapted to different climatic, ecological, and pest conditions compared to most of its congeners, and may thus harbor unique genetic traits that could prove useful for *Phaseolus* breeding efforts. The thicket bean is an herbaceous, perennial vine with tuberous roots that overwinter. Thicket bean is known to have hypogeal germination wherein the seed and cotyledons can stay below ground through germination, a trait that may have enabled *P. polystachios* to flourish in colder latitudes (Dhaliwal and Pollard 1962).

Phaseolus polystachios has a documented distribution reaching from New England to Florida, west to the eastern edges of Texas, and north to Michigan. The plant favors the edges of forests, roads, and streams where it has garnered its name by twining into thickets in rather open areas, particularly on slopes with southwestern, southern, and southeastern aspects. The thicket bean can establish colonies on open forest slopes, but it much prefers well-drained soils and full-sun conditions (Allard 1947). The thicket bean prefers an intermediate day length, with too-short or too-long days hampering its growth. Depending on latitude, *P. polystachios* will flower between June and September and fruit between August and November.

Thicket bean's wide range may have been historically augmented by indigenous gathering, caching, or even cultivation. Seeds or phytoliths of *P. polystachios* have been identified at the Parkin site in Arkansas, dating from the fifteenth to sixteenth centuries (Scarry and Reitz 2005) and much earlier from the Hunter's Home site in New York, with potential dates as early as 2500 B.C. (Hart et al. 2008). That said, even with its wide distribution, the thicket bean is not commonly found within its range and seems to be on the decline. The plant is considered extirpated in Michigan, where it was historically documented from the Detroit River International Wildlife Refuge, Pennsylvania, where author A.N. Egan failed to find any extant populations at 21 historical localities, and in Connecticut, listed as special concern by state agencies as of November 2017 (see above). Thicket bean's decline may be due to competitive exclusion from nonnative, introduced vines, habitat destruction from urban development (e.g., there are old herbarium records of populations located within what are now highly urbanized New York City and Washington DC [D. Debouck personal communication 2017]), quarrying, mowing, herbicide use, and fire suppression around human-built structures (A.N. Egan, personal observation 2017). Authors A.N. Egan and T. Kisha have completed extensive locality studies across its range, visiting over 200 locations in efforts to collect plants, but averaged about a 25% success rate of finding extant populations from historical collection locality information or firsthand knowledge of state and federal botanists.

The closest cultivated relative of *P. polystachios* is lima bean, which is susceptible to white mold (*Sclerotinia sclerotiorum* (Lib.) de Bary), leading to flower drop, emergence issues, and pod set failure. Through coevolution in its natural habitat, *P. polystachios* may have acquired true resistance to the ubiquitous pathogen. Further, transfer of the hypogeal germination trait to lima bean may be useful. Several decades ago, successful crosses between the two species were made, but hybrids showed high pollen sterility, likely due to meiotic irregularities due to chromosomal and genetic differences (Dhaliwal and Pollard 1962). With advances in plant breeding and genetics techniques, renewed efforts to tap into the *P. polystachios* genome may be fruitful for lima bean improvement. One *P. lunatus* x *P. polystachios* hybrid accession (G40503) is represented in the CIAT collection, originating from the work of Albert P. Lorz of the University of Florida (D. Debouck personal communication 2017).

The USDA-ARS National Plant Germplasm System (NPGS) safeguarded until recently only 13 accessions of *P. polystachios*, six of which were collected in 2013 in Florida. Recent explorations supported by the NPGS have augmented the holdings. A trip throughout Ohio in 2015 by authors Egan and Kisha increased holdings by 11 accessions, and a 2016 trip to Virginia, North Carolina, and South Carolina by Egan increased holdings by 19 accessions. In

2017, trips by Egan to Alabama, Arkansas, Mississippi, and Louisiana yielded 25 more accessions, while a trip by Kisha to Kentucky and Tennessee yielded an additional 10. Enrichment of germplasm collections from across the range of *P. polystachios* will enable a much more comprehensive assessment of genetic diversity within the species, providing valuable knowledge to *in situ* conservation efforts, and may in addition help to reveal further traits of value for crop improvement. Genetic diversity studies are currently underway by Kisha and Egan.

4.5.2 Ex Situ Conservation of Wild Phaseolus in North America

Significant *ex situ* collections of wild *Phaseolus* are maintained at the International Center for Tropical Agriculture (CIAT), Colombia (ca. 2000 accessions), the USDA-ARS National Plant Germplasm System (ca. 900 accessions), within the Sistema Nacional de Recursos Fitogenéticos para la Alimentación y la Agricultura (SINAREFI) Conservation Centers Network in Mexico (ca. 400 accessions), and the Botanic Garden Meise, Belgium (ca. 400 accessions).

Counts of accessions of *Phaseolus* taxa are provided in Table 4.3. Of 94 taxa, 25 (26.6%) are not represented at all in these *ex situ* conservation facilities, and another 27 (28.7%) are represented by less than ten accessions, making over half of *Phaseolus* taxa highly under-represented in these genebanks. Given that some duplication exists between the major collections as a result of collaborative collecting missions and recent repatriation (e.g., repatriation of 915 wild Mexican *Phaseolus* accessions maintained at CIAT to the Centro Nacional de Recursos Genéticos [CNRG] of the Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias [INIFAP]) (F. de la Torre personal communication 2017), the number of unique accessions held in these facilities is likely even less than the total counts for most taxa. Moreover, many of these accessions are unavailable to researchers due to a lack of adequate seed for distribution.

Table 4.3 Counts of accessions in major wild *Phaseolus* collections databases

Taxon	CIAT	USDA-ARS NPGS	Mexico SINAREFI	Botanic Garden Meise	BGCI	GENESYS
<i>Phaseolus acinaciformis</i>	1					
<i>Phaseolus acutifolius</i>		53 (33)	101*		10*	1130*
<i>Phaseolus acutifolius</i> var. <i>acutifolius</i>	81	36 (16)		34	2	92
<i>Phaseolus acutifolius</i> var. <i>tenuifolius</i>	84	55 (50)	2	10	2	75
<i>Phaseolus albescens</i>	1		1			
<i>Phaseolus albicarminus</i>	1					
<i>Phaseolus albiflorus</i>	7	1 (1)	1	1	1	9
<i>Phaseolus albinervus</i>						
<i>Phaseolus albiviolaceus</i>	2		6			
<i>Phaseolus altimontanus</i>	1	1 (0)	2	1	1	3
<i>Phaseolus amabilis</i>						
<i>Phaseolus amblyosepalus</i>						
<i>Phaseolus angustissimus</i>	5	4 (2)		3	2	13
<i>Phaseolus anisophyllus</i>						
<i>Phaseolus augusti</i>	29	16 (1)		2	1	59
<i>Phaseolus campanulatus</i>						
<i>Phaseolus carteri</i>	1	2	1	1		4
<i>Phaseolus chiapanus</i>	4	1		2	1	5
<i>Phaseolus coccineus</i>	168	74 (18)	716*	46	44*	2871*
<i>Phaseolus coccineus</i> subsp. <i>coccineus</i>		5 (0)				154
<i>Phaseolus coccineus</i> var. <i>coccineus</i>		17 (1)				243
<i>Phaseolus coccineus</i> var. <i>griseus</i>		2 (0)			1	2
<i>Phaseolus coccineus</i> var. <i>tridentatus</i>		1 (0)			1	1
<i>Phaseolus costaricensis</i>	27	6			1	18
<i>Phaseolus dasycarpus</i>						
<i>Phaseolus dumosus</i>	9	6 (3)	24*	2	2*	604*
<i>Phaseolus esperanzae</i>	7			1		8
<i>Phaseolus esquinensis</i>						
<i>Phaseolus filiformis</i>	36	19 (15)	4	10	4	97
<i>Phaseolus glabellus</i>	8	5 (1)	3	5	1	22
<i>Phaseolus gladiolatus</i>						
<i>Phaseolus grayanus</i>	2	18 (0)		5	2	25
<i>Phaseolus hintonii</i>	5	5 (2)	3	8	2	21
<i>Phaseolus hygrophilus</i>	1					
<i>Phaseolus jaliscanus</i>		2 (0)	1	1	1	3
<i>Phaseolus juquilensis</i>						
<i>Phaseolus laxiflorus</i>						
<i>Phaseolus leptophyllus</i>						
<i>Phaseolus leptostachyus</i>	105	31 (23)	45		2	144
<i>Phaseolus leptostachyus</i> var. <i>leptostachyus</i>		1 (0)		43	1	43

<i>Phaseolus lignosus</i>	2				1	1
<i>Phaseolus longiplacentifer</i>						
<i>Phaseolus lunatus</i>	220	74 (46)	280*	62	25*	6223*
<i>Phaseolus macrolepis</i>	2	2 (0)			1	3
<i>Phaseolus maculatifolius</i>			3			
<i>Phaseolus maculatus</i>	1	18 (0)		10	5	33
<i>Phaseolus maculatus</i> subsp. <i>maculatus</i>		1 (0)				2
<i>Phaseolus maculatus</i> subsp. <i>ritensis</i>		23 (4)		8		32
<i>Phaseolus macvaughii</i>	2	1	4	2	1	5
<i>Phaseolus magnilobatus</i>	4	1		1	1	3
<i>Phaseolus marechalii</i>	5	2 (0)		3	2	12
<i>Phaseolus micranthus</i>	1	1 (0)	2	2	1	4
<i>Phaseolus microcarpus</i>	29	17 (6)	19	15	3	76
<i>Phaseolus mollis</i>						
<i>Phaseolus neglectus</i>		1 (0)	2	2	1	5
<i>Phaseolus nelsonii</i>						
<i>Phaseolus nodosus</i>	1					
<i>Phaseolus novoleonensis</i>	1		2	1		1
<i>Phaseolus oaxacanus</i>	1					
<i>Phaseolus oligospermus</i>	13	2 (1)		6	1	21
<i>Phaseolus opacus</i>						
<i>Phaseolus pachyrrhizoides</i>	21	8		3	1	31
<i>Phaseolus parvifolius</i>	20	2 (0)	9	1	1	46
<i>Phaseolus parvulus</i>		12 (1)		3	2	15
<i>Phaseolus pauciflorus</i>				2		2
<i>Phaseolus pedicellatus</i>	7	3 (0)	12	3	2	12
<i>Phaseolus perplexus</i>		1 (0)			1	1
<i>Phaseolus persistentus</i>						
<i>Phaseolus plagiocylis</i>						
<i>Phaseolus pluriflorus</i>	1	3 (0)	1	3	1	7
<i>Phaseolus polymorphus</i>	1					1
<i>Phaseolus polystachios</i>	3	57 (1)			2	8
<i>Phaseolus polystachios</i> subsp. <i>polystachios</i>		7 (0)		3	1	10
<i>Phaseolus polystachios</i> subsp. <i>sinuatus</i>		3			1	2
<i>Phaseolus purpusii</i>						
<i>Phaseolus reticulatus</i>		1 (0)			1	1
<i>Phaseolus rotundatus</i>	2	2	6		1	4
<i>Phaseolus salicifolius</i>	1	1 (0)		1	1	2
<i>Phaseolus scabrellus</i>						
<i>Phaseolus scrobiculatifolius</i>						
<i>Phaseolus smilacifolius</i>						
<i>Phaseolus sonorensis</i>						
<i>Phaseolus talamancensis</i>	2	1 (0)			1	4
<i>Phaseolus tenellus</i>		2 (0)			1	2

<i>Phaseolus teulensis</i>						
<i>Phaseolus texensis</i>	1	1 (0)				1
<i>Phaseolus trifidus</i>						
<i>Phaseolus tuerckheimii</i>	13	2		1	1	6
<i>Phaseolus venosus</i>						
<i>Phaseolus vulgaris</i>	1032	176 (156)	3995*	99	33*	83092*
<i>Phaseolus vulgaris</i> var. <i>aborigineus</i>		112 (81)		7	2	225
<i>Phaseolus xanthotrichus</i>	41	8 (3)		11	1	55
<i>Phaseolus xolocotzii</i>				1		1
<i>Phaseolus zimapanensis</i>	8	8 (4)	12	7	2	24

Data from CIAT (2017); USDA ARS National Plant Germplasm System (2017a), R. González Santos personal communication (2017), Botanic Garden Meise (2017), BGCI (2017), Data Providers and the Crop Trust (2017) CIAT, USDA-ARS NPGS, and Botanic Garden Meise databases were queried only for accessions noted as wild; Mexico SINAREFI, BGCI, and GENESYS database counts for *P. acutifolius*, *P. coccineus*, *P. dumosus*, *P. lunatus*, and *P. vulgaris* are likely to include cultivated forms and are marked with an “*.” The GENESYS database includes information from over 400 institutes, mainly in the CGIAR, USDA-ARS NPGS, and European genebank systems (Data Providers and the Crop Trust 2017) and thus replicates the information from CIAT and USDA-ARS NPGS. For USDA-ARS NPGS, counts of currently available accessions are given in parentheses

Ramírez-Villegas et al. (2010) assessed the comprehensiveness of major *ex situ* collections with regard to taxonomic, geographic, and environmental or ecological niche gaps (i.e., the degree of representation of the range of climates that wild *Phaseolus* species occupy). Of 85 assessed taxa, they assigned 48 (56.5%) a high priority for further collecting due to being completely absent or highly underrepresented in major genebanks. Seventeen taxa were assigned medium priority for further collecting, 15 low priority, and only 5 assessed as adequately represented *ex situ*. Geographic hotspots for further collecting were concentrated in central Mexico, although various narrow endemic species occurring in other parts of the country were also prioritized (Ramírez-Villegas et al. 2010). Gap analyses for close relatives of common and lima bean performed more recently corroborated these results (Castañeda-Álvarez et al. 2016).

4.6 Final Remarks

The wild relatives of the five domesticated species of *Phaseolus* beans are clearly a very diverse group of plants extending widely across the New World. The majority of these species appear to be fairly well resolved and understood with regard to their taxonomy and distributions. Further research is still needed to clarify the identities and relationships among an additional dozen or more taxa, particularly with regard to narrow endemic species.

Aside from the progenitor of common bean and a few studies involving other relatives, the wild members of the bean crop gene pools are still largely unexplored, despite indications that novel useful diversity may be found within them. Given the relative sensitivity of common bean to heat, drought, and other effects of climate change, numerous promising wild species, as well as domesticates such as *P. acutifolius*, may play an increasing role as contributors of valuable genetic resources to the crop. Contributions from wild relatives to improving agronomic and market-related traits in the other domesticated species would also be valuable to increasing their importance worldwide.

But these contributions can only be made if these resources are well conserved and available to plant breeders and other researchers. A number of wild *Phaseolus* are rare endemics that are threatened in their natural habitats and are insufficiently protected *in situ*. Aside perhaps from the progenitors and a few other species, the wild taxa are also largely underrepresented in major genebanks. Further efforts to enhance protection of vulnerable species in their natural habitats, and further collecting to fill critical gaps in germplasm collections, are highly warranted.

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