

Phaseolus Beans – Crop Vulnerability Statement (September 2020)

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1. Quad chart from the Phaseolus CGC (2018), updated September 2020

Crop Vulnerability Update for *Phaseolus* beans

(2018, updated Sept. 2020)

Vulnerabilities & Threats

- In centers of origin (mainly Mesoamerica, but also North, Central, and South America), threats include habitat loss near urban or/suburban areas, introduction of genetically uniform cultivars, urban migration, and changes in agriculture.
- In the US, vulnerability is limited by mosaic distribution across geographic regions, different uses (pod vs. seed), and different market classes
- Potential threat from localized genetic vulnerability within specific production regions due to limited diversity within and among commercial classes; however, recent breeding has introduced cultivars with broader genetic basis and diversified market classes
- Evolving diseases create critical need for new resistances, e.g., common bacterial blight (*fuscans*) and bacterial wilt; tolerance to abiotic stresses (water use efficiency, tolerance to drought and flooding, heat)

Genetic research & breeding capacities

- Whole-genome sequences of Andean and Mesoamerican common bean reference genotypes (G19833; BAT93, Pinto UI111, and OAC Rex, respectively. Sequencing of lima bean (*P. lunatus*) is completed; tepary bean (*P. acutifolius*) is under way.
- Genotyping of Andean and Mesoamerican diversity panels, wild common bean and lima bean, core collection of common bean
- Significant progress has been achieved through genomics of *P. vulgaris* of the structure of genetic diversity and control of agronomic and culinary traits (QTL & GWAS approaches)
- An assessment of potential additions to the core collection of common bean to increase its representativity has been completed
- Research efforts are threatened due to loss of positions because of retirements, affecting breeding, plant pathology

NPGS PGR Status & Impacts

- The *Phaseolus* collection of the USDA includes 17,653 accessions belonging to 57 taxa collected from 107 countries
- Other valuable, non-NPGS collections include those of Seed Savers Exchange and Native Seeds/SEARCH in the US and – among the largest – the CIAT (CGIAR), EMBRAPA (Brazil), and German (IPK) collections in the world.
- NPGS collection distributed 5826 packets of 3721 accessions in 312 orders (292 US and 20 foreign).
- Challenges include seed increase, especially of photoperiod-sensitive accessions, and clean-up of diseased accessions (mainly BCMV), and updating GRIN entries with available genotypic and phenotypic information

Priority Issues and Recommendations (see section 5.)

1. Need for adequate and permanent staffing, operating budget, and facilities (greenhouses)
2. Updating the *Phaseolus* collection: e.g., diversity panels, core collections, additional explorations
3. Genotyping of the collection and bioinformatic analysis to integrate phenotypic and genotypic data
4. Emphasize the phenotypic evaluation of the collection
5. Establish links to microbial germplasm collections
6. Further improvements to GRIN-Global

2. Background on the Genus *Phaseolus*

2.1. Economic, nutritional, and cultural roles: T. Parker, J.R. Myers, P. Gepts

The genus *Phaseolus* includes five domesticated species, two of which were domesticated twice, making the genus a hotspot of crop domestication. The domesticated species include – in order of decreasing economic importance: common bean (*P. vulgaris* L.), Lima bean (*P. lunatus* L.), runner bean (*P. coccineus* L.), tepary bean (*P. acutifolius* A. Gray), and year bean (*P. dumosus* Macfad.) (Freytag and Debouck 2002; Delgado-Salinas et al. 2006). Because of its economic importance, common bean is often used as representing all five *Phaseolus* domesticates. For example, production data that will be presented later in this section, reflect the production of common bean – whether dry or green beans – but, depending on the country or state, may also include production of the other species of *Phaseolus* or even other grain legumes (e.g., *Vigna* spp.) in aggregated fashion (although in most cases the production of common bean always predominates). Another example is the snap and string bean economic categories, which include

Phaseolus grown for pods, as well as yard-long bean (*Vigna unguiculata* var *sesquipedalis*).

Table 1. Worldwide production of grain legumes (FAO data) (accessed August 18, 2020)

Item	Total production (metric tons)
Soybeans	348,712,311
Groundnuts	45,950,901
Beans, dry	30,434,280
Chickpeas	17,192,188
Peas, dry	13,534,166
Cowpeas, dry	7,233,408
Lentils	6,333,352
Pigeon peas	5,960,575
Faba beans	4,923,090
Lupins	1,188,213
Bambara beans	195,151

Among grain legumes, *Phaseolus* beans play an important role as demonstrated by worldwide production and human utilization data of the Food and Agricultural Organization of the United Nations (FAO 2018:

<http://www.fao.org/faostat/en/#search/beans>.

Table 1). While soybean (*Glycine max*) and, to a lesser extent, groundnut (*Arachis hypogea*), are grown mainly for extraction of oils, *Phaseolus* beans are grown for direct human consumption after cooking, generally for its grains, harvested at physiological maturity (i.e., maximum fresh weight: shell

beans; stage R8, Fernández et al. 1982) or, most frequently, as dry maturity [dry beans; stage R9). Alternatively, they are grown as a vegetable (snap beans), harvested at the end of the pod growth phase (stage R7). The geographic distribution of *Phaseolus* bean production and the per capita consumption, whether for dry beans (Table 2), green (shell-out) beans (Table 3), or snap beans (Table 4), illustrates very well how this crop has achieved a global status, having been disseminated from its multiple domestication centers in the Americas (Figure 1). Dry bean production from 2008-2018 averaged approximately 4kg per person per year, and this production has been concentrated in

Table 2. Twenty largest dry-bean-producing countries (FAO data) (accessed August 18, 2020)

Country	Total production (metric tons) ¹
India	6,220,000
Myanmar	4,779,927
Brazil	2,915,030
United States of America	1,700,510
China, mainland	1,324,407
United Republic of Tanzania	1,210,359
Mexico	1,196,156
Uganda	1,039,109
Kenya	765,977
Ethiopia	607,929
Argentina	473,389
Rwanda	454,174
Kazakhstan	409,800
Cameroon	402,054
Burundi	393,233
Canada	341,100
Democratic People's Republic of Korea	323,204
Angola	314,932
Guatemala	253,037
Total across all countries	30,447,423

¹Production amounts from FAO data combine common bean with other grain legumes, leading to inflated figures for SE Asia and China (Myers & Kmiecik, 2017). It is estimated that *Vigna* spp. account for 93% of dry bean production in India and 56% in China (Akibode and Maredia, 2011). Proportions for other SE Asian countries are unknown.

Table 3. Twenty largest green (shell-out)-bean-producing countries (FAO data) (accessed August 18, 2020)¹

Country	Total production (metric tons)
China, mainland	19,897,100
Indonesia	939,598
India	715,141
Turkey	580,949
Thailand	315,293
Egypt	284,299
Italy	163,824
Morocco	148,392
Spain	138,925
Bangladesh	134,860
Belgium	98,248
Algeria	93,184
Mexico	91,853
Sri Lanka	83,966
Iran (Islamic Republic of)	65,591
Greece	57,860
Romania	53,591
Canada	53,456
Australia	45,903
Chile	41,493
Total across all countries	24,752,673

¹See footnote for Table 2. Production figures for SE Asia and China are inflated because other species are recorded as “green beans” in these countries.

South Asia, East Africa, and the Americas (Figure 1A). On a per capita basis, production is highest in Myanmar, with most of the production exported to India (FAOSTAT 2020, Figure 1). Per capita production for local consumption is high in Latin America and East Africa. Consumption of dry bean is highest in East Africa, where it is primarily grown by subsistence farmers. In Rwanda, for example, average consumption is approximately 36-

38 kg per person each year (FAOSTAT 2008-2018, Kalyebara and Buruchara 2008). FAO data are believed to underestimate production and consumption in these areas, as direct on-farm consumption is more likely to go unreported than trade and sales (Debouck 2016). Beans provide 65% of the protein consumed in Rwanda, compared to 4% provided by animal sources (Larochelle and Alwang 2014). This highlights the extreme importance of *Phaseolus* beans to food security, particularly in developing countries.

Production of string or snap bean (Table 4) is dominated by the US. While *Phaseolus* and *Vigna* species may be combined in FAO statistical data, particularly for Asia, the vast majority of Chinese production is common bean rather than yard-long bean (Wu et al. 2020). On a per capita basis, production is more evenly distributed globally, with production centers in the Mediterranean and the Americas. Production of snap bean tends to be shifted towards more temperate and higher-income countries relative to dry bean.

As a grain legume, *Phaseolus* beans fulfill several important roles from agronomic, human nutritional, socio-economic, and cultural standpoints. Agronomically, they fix atmospheric nitrogen in a form accessible to plants through a symbiotic relationship with soil bacteria like *Bradyrhizobium*, *Rhizobium*, and related genera (Hohenberg et al. 1982; Hernandez-Lucas et al. 1995; Crews et al. 2004; Ribeiro et al. 2013; Ormeño-Orrillo et al. 2006, 2015; Servín-Garcidueñas et al. 2014; de Araujo et al. 2017; Ramírez-Puebla et al. 2019; Shamseldin & Velázquez 2020). Beans also complement other crops, either dicots (e.g., Solanaceae, Brassicaceae, or Cucurbitaceae) or monocots (e.g., Poaceae), in associated cropping agroecosystems, like the *milpa* system originating in Mesoamerica and now distributed in Latin America and Africa. In the *milpa* system, the main crops – bean, maize, and squash (Heindorf et al. 2019) – have complementary functions, including root systems, leading to up to higher yields compared to the yields of component

Table 4. Twenty largest string (snap) bean-producing countries FAO data) (accessed September 23, 2020)¹

Country	Total production (metric tons)
United States of America	798,110
France	339,400
Morocco	156,017
Mexico	128,030
Philippines	114,380
Turkey	88,024
Poland	51,776
Argentina	49,105
Japan	37,538
Malawi	27,971
Iraq	26,239
Peru	25,670
China, mainland	10,789
Taiwan	10,789
Venezuela	8,226
Jamaica	6,756
Côte d'Ivoire	4,759
Egypt	319
Barbados	291
French Polynesia	171
Total across all countries	1,884,465

¹A significant proportion of the string beans produced and consumed in China and India as well as other SE Asian countries are Asparagus or Yard-long (*Vigna unguiculata*) beans. FAO combines *Vigna* and *Phaseolus* species in their estimates. Exact proportions are unknown.

crops (Zhang et al. 2014). Beans also play an important role in crop rotations. For example, in California, lima bean enters in rotation with crops such as cotton, maize, safflower, wheat, rice, alfalfa, tomatoes, sunflower, and cucurbits, and, more recently, young orchards (Long et al. 2010, 2014).

Phaseolus beans are also an important human nutritional asset (Hayat et al. 2014; Myers and Kmiecik 2017). They provide a diet high in protein (22-25% seed nitrogen) (Delaney et al. 1991a,b), mineral elements like iron and zinc (Castro Guerrero et al. 2016), dietary fibers (Brick and Thompson 2016; Moghaddam et al. 2018), antioxidants such as polyphenolics (Yang et al. 2018), and certain vitamins (e.g., folate). Although beans are low in sulfur amino acids like methionine and cysteine (Gepts and Bliss 1984), they are rich in lysine; thus, when combined with cereals like maize in a 3 maize:1 beans ratio (Bressani 1993), they provide a complementary source of essential amino acids that enhances its protein quality. As a grain legume, *Phaseolus* beans also mitigate chronic diseases, like heart disease, obesity, and diabetes (Thompson et al. 2017; Thompson 2019). Notably, they reduce the post-prandial glycemic index in adults, decreasing the risk of type-2 diabetes and cardiovascular disease (Thompson et al. 2012). Tantalizing evidence also suggests that *Phaseolus* beans may reduce breast cancer (Thompson et al. 2009). String beans (or snap beans, when the variety is devoid of pod fibers) contain approximately 2% protein and 7% carbohydrates, and are rich sources of vitamin C, carotenoids, and vitamin K (Myers and Kmiecik 2017).

Nevertheless, despite the many positive nutritional attributes, beans also harbor some antinutritional traits (Bressani 1993), some of which can be eliminated by heat treatment, like seed phytohaemagglutinins or lectins. Other negative traits include phytates, which limit the bioavailability of iron, zinc, and calcium (Campion et al. 2009; Blair et al. 2012b). It is also good to remember that there is genetic variation for these nutritional or anti-nutritional factors (Ramirez-Cardenas et al. 2008).

Culturally, *Phaseolus* beans have come to occupy a central position in the human diet of many regions of the world, principally in Latin America and Eastern and Southern Africa (see above). Archaeological, ethnobotanical, and biological data confirm the dietary role of beans in ancient Mesoamerica (Zizumbo-Villarreal and Colunga GarcíaMarín 2010; Zizumbo Villarreal et al. 2012, 2014). Although no comparable analysis exists for the Andean domestications of common and lima beans yet, the analyses of Zizumbo-Villarreal et al. illustrates active utilization and concurring selection that took place for cooking and dietary characteristics resulting in a very diversified diet that supported the development of Mesoamerican civilizations.

Further selections for adaptation, cooking, and dietary traits have no doubt taken place when *Phaseolus* beans were dispersed to other regions in the Americas before 1492 and other continents post-1492. Dispersal to regions of higher latitudes required selection for decreased sensitivity to photoperiod, including the sensing of night length and temperature. Beans became integrated into the cooking traditions of countries around the world (and sometimes acquired an important role as a national dish), like 'Gallo Pinto'

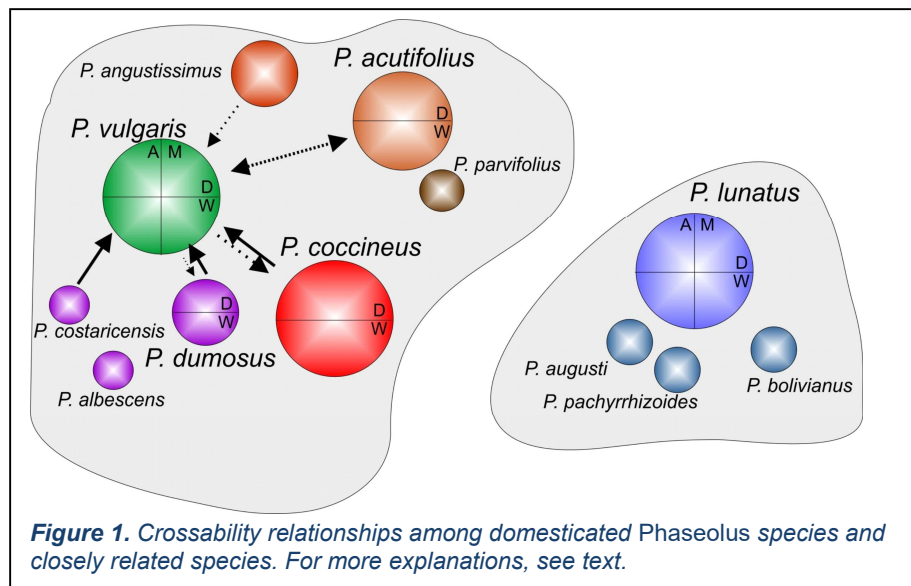
of Central America, 'Feijoada' in Brazil and other former Portuguese colonies, 'Cassoulet' of France, 'Fagioli all'uccelletto' of Italy, 'Lobio' of Georgia, and 'Jajangmyeon' in Korea, not mention Boston baked beans. This implies human selections for seed types (color, size, shape, grain texture, and broth density), accounting for the extraordinary diversity of seed types that sets apart from many other crops. In turn, these adaptations have shaped the diversity in the *Phaseolus* genome.

The genus *Phaseolus* encompasses no less than seven domestications in five species that differ in their life histories, reproductive systems, adaptations, and degrees of domestication. This feature raises scientific issues such as the extent of convergent evolution among domesticated species, the type of genes affected by domestication, whether structural genes or transcription factors, their location in the genome and the extent of linkage disequilibrium surrounding them, the evolution of genetic diversity, the role of gene flow, and any parallelism in genetic diversity in associated organisms like pathogens (Gepts 2014a,b; Hufford et al. 2019). Information from these studies can be applied to the conservation of genetic resources and their use in breeding (Kelly et al. 1998, Miklas et al. 2006; Gepts 2006; Acosta-Gallegos et al. 2007; Kelly 2018). Climate change will have a major impact on production of *Phaseolus* beans, greatly changing biotic and abiotic stresses that plants experience. The increasing wealth of genetic knowledge about the genus will be critical for developing varieties that suit the needs of these changing circumstances. The wealth of inter-specific diversity in *Phaseolus* has only recently begun to be explored. The transfer of useful alleles between species will be a major step in ensuring the continued productivity of this important genus as is the use of all the domesticated species in their own right as individual staple crops.

2.2. *Origin and Diversification of Phaseolus sp.*: T. Parker, P. Gepts

Phaseolus sp. is a member of the **Fabaceae (Leguminosae) family and the subfamily Papilionoideae**. Within the latter, *Phaseolus* spp. belongs to the warm-season phaseoloid/millettioid clade, which includes the Phaseoleae tribe (Gepts et al. 2005). The Phaseoleae tribe, and the genus *Phaseolus* in particular, constitute a domestication hotspot. This tribe also includes the closely related *Vigna* genus [e.g., cowpea *Vigna unguiculata* (L.) Walp.] from Africa; mung bean *Vigna radiata* Wilczek from Asia), soybean [*Glycine max* (L.) Merr.], hyacinth bean [*Lablab purpureus* (L.) Sweet], and pigeon pea [*Cajanus cajan* (L.) Hutt].

The **genus *Phaseolus***, in its current definition (Maréchal et al. 1978), originated some 5-6 million years ago (Delgado Salinas et al. 2006) and consists of some 70-85 species distributed exclusively in the Americas, with a particular focus on Mexico (Cerdeña-Hurtado et al. 2018), although several species of the genus are distributed outside Mexico in areas ranging from the northeastern U.S. and Canada [e.g., *P. polystachios* (L.) Britt., Sterns & Pogg.] to northwest Argentina (e.g., wild *P. lunatus* and *P. vulgaris*) and on some of the islands close to the American continent (e.g., *P. mollis* Hook. in the Galapagos, *P.*



lignosus Britton in the Bermudas) (Freitag and Debouck 2002; Delgado Salinas et al. 2006; Ramírez-Villegas et al. 2010; Debouck 2015; Dohle et al. 2019). Within this range, they inhabit ecozones from sea level to mountain highlands. Many species show specialization to particular habitats and temperature ranges, with unique species, for example, in arid regions, lowland tropics, and tropical highlands. *Phaseolus* species are highly variable in mode of pollination, with some species highly autogamous and others strictly allogamous. They also differ in perenniality, spanning from perennial to strongly annual (Bitocchi et al. 2017).

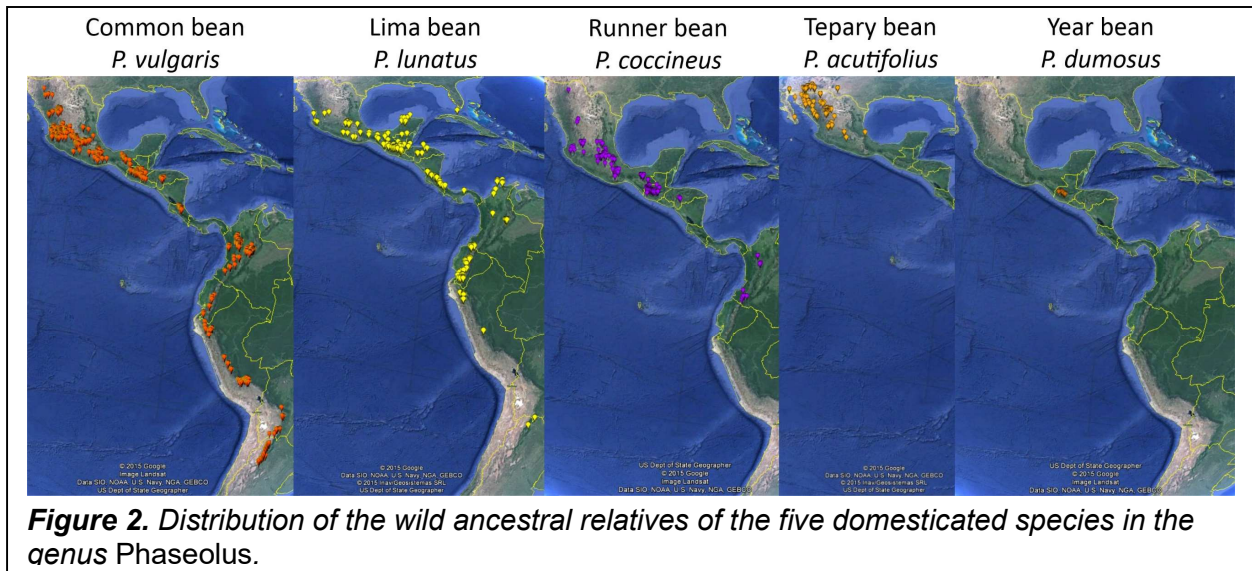
They can be divided into a hierarchy of gene pools based on the extent to which groups can be hybridized (Harlan and de Wet 1971). For common bean, other members of *P. vulgaris*, including wild types, are in the primary gene pool. The secondary gene pool includes *P. dumosus*, *P. coccineus*, and several wild species, such as *P. costaricensis* Freitag and Debouck (e.g., Mendel 1865, Butare et al. 2012); the tertiary gene pool includes *P. acutifolius* (e.g., Thomas and Waines 1984, Waines et al. 1988), and more distantly related species such as *P. lunatus* are in the quaternary gene pool (Fig. 1). This means that alleles from three of the five domesticated species can be exchanged fairly readily (Smartt 1970, Singh 2001, Singh et al. 2001, Mina-Vargas et al. 2016, Rendón-Anaya et al. 2017a). The gene pools relative to other *Phaseolus* domesticates have also been resolved (Dohle et al. 2019).

Delgado-Salinas et al. (2006) used the chloroplast loci *matK* and adjacent *trnK* intron sequences, combined with ribosomal internal transcribed sequences (ITS) in the nuclear genome, to develop a molecular phylogeny of the genus. They identified two major groups, known as the A and B clades in the genus, which diverged some 5-6 million years ago. They contain similar numbers of species but vary strongly in their breadth of their distribution. The A clade is found almost exclusively in Mexico, with a small number

of species extending into the Southwestern United States and Central American countries south to Panama. They are not found in oceanic islands and are confined to a relatively narrow highland elevational range. In contrast, the clade B species are native to every country from Canada to Argentina (except the Guianas, Brasil, Uruguay, Paraguay, and Chile), inhabit much wider elevational ranges, including numerous species found at low elevations and on oceanic islands. They also show much greater tolerance to environmental variability and stresses, such as frost and disturbed soils (Delgado-Salinas et al. 2006). This broad adaptability may have served as a pre-adaptation to the complex and variable conditions of the cultivated environment during and after domestications. *Phaseolus* spp. includes no less than five species that have been domesticated (see above). Domestication occurred in only two species groups of the genus, the Lunatus group (with two domestications) and the Vulgaris group (five domestications), both groups belonging to clade B; no domestication took place in clade A species. Two of these species were domesticated twice in geographically distinct regions of the Americas. These two species have the most extensive distribution in the genus: *P. lunatus* and *P. vulgaris* (Fig. 2). The five domesticated species show contrasting characteristics (Table 5).

Lima bean (*P. lunatus*) is the earliest diverging domesticated *Phaseolus* species. It is native to both North and South America and oceanic islands adjacent to the American continent, where it inhabits a wide range of elevations (0-1600m). In Mexico, it is the species with the broadest adaptation, being distributed in all 14 major vegetation types recognized by Rzedowski (1990), in contrast with runner bean (10), common bean (9), tepary bean (8), and year bean (1) (Delgado Salinas and Gama López 2015). In addition to Mexico, wild populations of lima bean are also distributed in Central America (Guatemala, Belize, Honduras, El Salvador, Costa Rica, and Panama) and the Andes of South America (Colombia, Ecuador, Peru, and Argentina). These wild populations are structured into three gene pools, two Mesoamerican (MI and MII) and one Andean (AI; Serrano-Serrano et al. 2010). The MI gene pool is distributed in west-central Mexico and the MII gene pool in southern Mexico, Central America, and South America. Two of these gene pools were domesticated (Gutiérrez Salgado et al. 1995, Motta-Aldana et al. 2010, Andueza-Noh et al. 2015, Chacón-Sánchez and Martínez-Castillo 2017): MI gave rise to Mesoamerican domesticates, either cv.-group ‘Potato’ (small, rounded seeds) or cv.-group ‘Sieva’ (medium-sized, flat seeds) and AI led to Andean domesticates, with large seeds (Mackie 1943, Baudet 1977; Lioi 1994).

Wild **teparty bean (*P. acutifolius*)** is found mainly in northwestern Mexico, as well as the states of Texas, New Mexico, and Arizona in the southwestern United States (Fig. 2). Several groups are close relatives of tepary beans, with disagreements on the relatedness between these based on sampling. The species has been traditionally divided into three subgroups, *P. acutifolius* var. *acutifolius*, *P. acutifolius* var. *latifolius*, and *P. acutifolius* var. *tenuifolius*; a *P. parvifolius* group is sometimes included within *P. acutifolius* or as a closely related species (Blair et al. 2012a). Several studies have



Species	No. of domestications	Presumed domestication locations	Reproductive systems	Life history	Adaptation
Common bean (<i>P. vulgaris</i>)	2	Central Mexico vs. Southern Andes	Predominantly autogamous	Annual (medium)	Mesic
Lima bean (<i>P. lunatus</i>)	2	Mexico vs. Ecuador & N. Peru	Mixed auto- and allogamous	Annual (long)	Hot, dry to humid
Runner bean (<i>P. coccineus</i>)	1	Mexico	Predominantly allogamous	Perennial	Cool and moist
Tepary bean (<i>P. acutifolius</i>)	1	N.W. Mexico (Jalisco, Sinaloa, Chihuahua)	Auto- to cleistogamous	Annual (short)	Hot and dry
Year bean (<i>P. dumosus</i>)	1	Guatemalan Highlands	Leaning to allogamous	Pluri-annual	Intermediate between runner and common bean

indicated that *P. acutifolius* var. *latifolius* is a misnomer and should be classified with *P. acutifolius* var. *acutifolius* (Pratt and Nabhan 1988, Blair et al. 2012a, Gujaria-Verma et al. 2016). Microsatellite data generated by Blair et al. (2012) supported a model of a genetic continuum between the core *acutifolius* types and the *P. parvifolius* types, which they classified as a separate species due to extremely limited gene flow with other groups. Intermediate between these are the *tenuifolius* types, which had previously been considered genetically indistinguishable from the core *acutifolius* group (Muñoz et al. 2006). The SNP-based analysis of Gujaria-Verma et al. (2016) came to essentially the

same conclusions as Blair et al. (2012a), with *parvifolius* forming a distinct group and *latifolius* comprising several groups of intermediates. Tepary beans are adapted to by far the hottest and driest conditions of the domesticated *Phaseolus* species and are exceptionally well suited to these conditions. The environmental conditions in its center of origin are not conducive for many bacterial and fungal pathogens. These pathogens therefore have not co-evolved with tepary beans, and the species is a source of resistance alleles to pathogens such as common bacterial blight (Drijfhout and Blok 1987, Singh and Muñoz 1999). Tepary beans are in the tertiary gene pool of all domesticates except *P. lunatus*, meaning that useful alleles from these wild populations can only be incorporated into *P. vulgaris*, *P. coccineus*, and *P. dumosus* through the use of advanced breeding techniques (e.g., congruity backcrossing: Haghighi and Ascher 1988, Muñoz et al. 2004), embryo rescue (Thomas and Waines 1984), other advanced techniques (Mejía-Jiménez et al. 1994), or bridging species and hybrids (Barrera et al. 2018).

Wild **runner bean (*P. coccineus*)** is found throughout the highlands of Middle America, spanning from northern Mexico through Guatemala and Honduras to Colombia (Fig. 2; Freytag and Debouck 2002, Chacón-Sánchez 2018). Within this distribution, it is found at high elevations, where it is semi-perennial. Two subspecies, *P. coccineus* subsp. *coccineus* and *P. coccineus* subsp. *striatus* have been recognized, although genetic and phenotypic evidence indicates that these are not evolutionarily differentiated (Guerra-García et al. 2017). The species is adapted to the coolest environments of domesticated *Phaseolus* (Bitocchi et al. 2017).

Year bean (*Phaseolus dumosus*) combines certain traits of *P. coccineus* and *P. vulgaris*. Like *P. vulgaris*, it has epigeal germination and anthers dehisce towards the stigma, but in seed size and environment of adaptation, the species resembles *P. coccineus* (Mina-Vargas et al. 2016, Bitocchi et al. 2017). *P. dumosus* has a root structure and perennality intermediate between these species, and displays strong, thickened storage roots that can lead to weak perennality, but which are not truly tuberous like those of *P. coccineus* (Schmit and Debouck 1991). The species arose through a complex network of cross-pollinations between ancestral populations of *P. vulgaris* and *P. coccineus* (Llaca et al. 1994; Mina-Vargas et al. 2016). *P. costaricensis* is similarly the polyphyletic result of crosses between this series of relatives (Mina-Vargas et al. 2016). The plastid genome of *P. dumosus* bears great similarity to *P. vulgaris*, while much of the nuclear genome is more similar to *P. coccineus* (Llaca et al. 1994, Mina-Vargas et al. 2016). This is likely the result of the partial incompatibility between the two species, in which successful hybridization requires *P. vulgaris* to be the maternal parent (Wall 1970, Shii et al. 1982, Hucl and Scoles 1985). Wild *P. dumosus* is found in an extremely limited range in the mountainous region of western Guatemala and southern Chiapas (Fig. 2). This contrasts with the much larger ranges of wild relatives of all other *Phaseolus* domesticates and may be responsible for the low diversity found in the species (Schmit and Debouck 1991, Freytag and Debouck 2002).

Unlike other domesticated *Phaseolus*, *P. dumosus* and *P. coccineus* are allogamous. This is related to their unique floral colors and morphologies (Schwember et al. 2017, Bitocchi et al. 2017). *P. dumosus* and *P. coccineus* are in the secondary gene pool of common bean (Fig. 1), and it is possible that the outcrossing nature of these species could be introgressed into *P. vulgaris* for hybrid seed production in the future. The compatibility of these crosses is highly dependent on parent choice, and careful selection of parents is important for introgression of characteristics between these species (Gepts 1981, Singh 2001, Schwember et al. 2017).

The range of wild **common bean (*P. vulgaris*)** is expansive, ranging from the state of Chihuahua in northern Mexico (e.g., G23463, collected at 28.3° N. Lat., -108.5° W. Long.) to the state of Córdoba in Argentina (Sirolli et al. 2015, -31.3° N. Lat., -64.6° W. Long.) over a distance of some 10,000 km (Fig. 2). Despite its widespread distribution, the species' ecological niche in the wild is restricted by several variables. Among these, it is adapted only to middle-elevation areas, and is not found below approximately 600m in elevation. It also requires a dry period to allow pod shattering and seed dispersal. Common bean is adapted to relatively moderate temperature and rainfall conditions, which may be a factor favoring its widespread cultivation by humans. These ecological factors are not found in many regions of the Neotropics, leading to a disjointed distribution with several geographically and genetically distinct populations. Gaps in the distribution of wild common bean are found in the isthmus of Tehuantepec, the isthmus of Panama and the neighboring region of Chocó in Colombia, and three locations throughout the Andes. Dispersal between these regions is believed to be the result of rare long-distance migrations by seed-eating birds like doves, as suggested by the local name for wild beans 'frijol de paloma' (dove or pigeon bean; Debouck et al. 1993, Ariani et al. 2018).

The earliest divergence within the common bean gene pool separates a population found in Ecuador and northern Peru from all other members of the species. This is believed to have occurred approximately 373,000 years (Ariani et al. 2018) or 260,000 years ago (Rendón-Anaya et al. 2017a). This population is unique in that it has the type I ("Inca") phaseolin lacking tandem direct repeats of 15 bp in the fourth exon and/or 27 bp in the sixth exon, found in phaseolin types of wild and domesticated accessions of the Middle American or Andean gene pools (Slightom et al. 1985). The absence of tandem direct repeats is significant because it represents an ancestral state as duplication generating repeats is more likely than deletions that precisely excise one of the members of the duplication. Further evidence for the ancestral nature of the I phaseolin types is their presence in two of the most closely related taxa to *P. vulgaris*, *P. coccineus* and *P. dumosus*. Additional data suggesting the uniqueness of the I phaseolin population include nucleotide divergence superior to that separating the Middle American and Andean gene pools, a position in a separate clade, sister to all *P. vulgaris* genotypes both for nuclear sequences and a chloroplast DNA fragment, an early split of the I phaseolin population compared to the Middle American and Andean gene pools, and a distinct metabolome, reproducing the phylogenetic separation based on nuclear sequence data (Rendón-

Anaya et al. 2017a). Hybridization experiments have shown that there is a partial loss of fertility in crosses between this earliest diverging population and the core Middle American and Andean common bean populations (Koinange and Gepts 1992). On this basis, the I phaseolin group from Ecuador and Northern Peru has been re-classified into a separate, sister species, *P. debouckii* (Rendón-Anaya et al. 2017b).

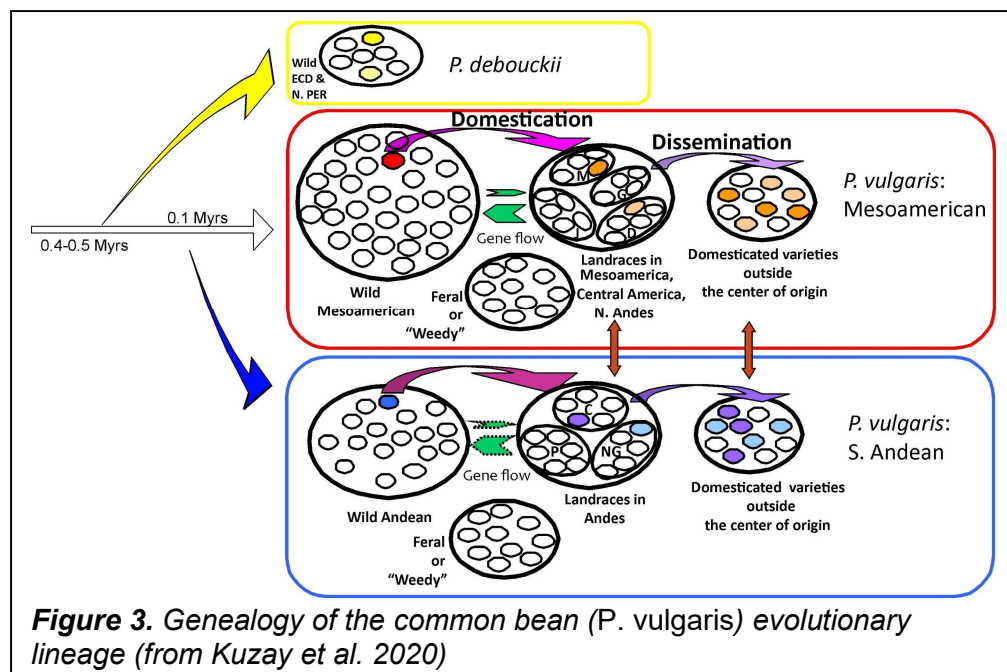
A second major divergence occurred later, separating Middle American wild common beans and those of the southern Andes. This is predicted to have occurred roughly 87,000 (Ariani et al. 2018), to 110,000 (Mamidi et al. 2013), to 165,000 years ago (Schmutz et al. 2014). *Fst* values between the populations have been repeatedly estimated at 0.34, indicating strong population differentiation (Schmutz et al. 2014, Ariani et al. 2018). The wild southern Andean gene pool is divided into two geographically distinct groups, one found in central Peru and the other ranging from southern Bolivia to Argentina. Although these two southern Andean populations are disjunct today and can be genetically distinguished, multiple studies have determined that they are closely related and therefore must have diverged recently (Koenig and Gepts 1989; Kwak and Gepts 2009, Bitocchi et al. 2012, Rodriguez et al. 2016, Ariani et al. 2018). The Andean population has allele frequency patterns that indicate it underwent a major pre-domestication bottleneck which reduced its genetic diversity, consistent with its origin in a rare long-range dispersal event (Ariani et al. 2018); this dispersal event was followed by a later population size expansion that continues to the present (Rossi et al. 2009, Bitocchi et al. 2012, Mamidi et al. 2013, Schmutz et al. 2014, Ariani et al. 2018). In contrast, there does not appear to have been a major bottleneck in the wild Middle American population. The genetic differentiation between these gene pools leads to hybrid lethality in some cross-pollinations, due to autoimmune effects of specific allele pairs of complementary genes, one of Mesoamerican origin (*Dominant Lethal-1* or *DL-1*) and the other of Andean origin (*Dominant Lethal-2* or *DL-2*; Shii et al. 1980, Gepts and Bliss 1985, Koinange and Gepts 1992; Hannah et al. 2007).

Genetic diversity of wild common bean varies by gene pool and by the type of marker used. Numerous studies have indicated that the wild Middle American population of common bean is highly diverse relative to all other wild and domesticated groups (Chacón-Sánchez et al. 2007, Kwak and Gepts 2009, Schmutz et al. 2014, Rodriguez et al. 2016, Ariani et al. 2018). Most of these studies have determined that the Andean wild population has less than half the genetic diversity as the Middle American population. These studies have determined that the ancestral Inca-phaseolin gene pool of Ecuador and northern Peru (*P. debouckii*) has a level of diversity intermediate between the Middle American and Andean wild populations (Kwak and Gepts 2009, Bitocchi et al. 2012, Schmutz et al. 2014, Ariani et al. 2018). The greater diversity of the Middle American wild population may be related to its greater geographic extent than other wild common bean groups, as it is distributed both latitudinally and longitudinally north of the Isthmus of Tehuantepec in Mexico. The fact that the distribution of Mesoamerican gene pool spans from northern Mexico to the northernmost Andes in Colombia, implies an additional dispersal event from Mesoamerica through Central America into the northern Andes.

Thus, the current distribution of wild common bean is the result of at least three major dispersal events between Middle America and the Andes of South America.

The diverse Middle American wild populations of common bean can be divided into several subgroups, which vary slightly based on sampling (e.g., Bitocchi et al. 2012, Rodriguez et al. 2016, Ariani et al. 2018). In general, at least three subgroups are recognized. One of these is endemic to the central Mexican states of Guerrero, Morelos, Puebla, and the state of Mexico. This population has relatively low diversity, which may be the result of the region's unique climate, volcanic soils, or other factors (Rodriguez et al. 2016). A different subpopulation predominates in all other areas to the northwest of the isthmus of Tehuantepec, from Chihuahua to northern Michoacán, and also in Oaxaca in the south. This genetic-geographic pattern clearly mirrors that of teosinte, the wild ancestor of maize (Moreno-Letelier et al. 2020). To the southwest of the isthmus of Tehuantepec, another subpopulation is found in southern Mexico, Central America, and Colombia. Its broad geographic range covers greater ecological diversity than other wild groups (Rodriguez et al. 2016). Despite this, the subpopulation cluster has similar levels of diversity to other Mesoamerican wild *P. vulgaris* groups.

Thus, the genealogy of the major gene pools of *P. vulgaris* can be presented as follows (Fig. 3). In keeping with the Middle American origin of the genus *Phaseolus*, an ancestral evolutionary lineage existed at one time in Mesoamerica which would ultimately evolve into *P. vulgaris*. From this lineage, a long-distance dispersal event – most likely bird-mediated - around 0.4-0.5 M years transported wild seeds from this region of origin to the western Andean region, now occupied by Ecuador and northern Peru. A subsequent long-distance dispersal event, also bird-mediated, conveyed seeds around 0.1 M years ago to the region encompassed by southern Peru, Bolivia, and northwestern Argentina. In the meantime, the original Mesoamerican ancestral lineage evolved into the



contemporary wild Mesoamerican *P. vulgaris* gene pool. Two geographically distinct domestications then took place, one in Mesoamerica and the other in the southern Andes (*P. debouckii* was never domesticated). Subsequent to each domestication, ecogeographic differentiation led to the existence of three to four races (Singh et al. 1991a) in the two main geographic, partially genetically isolated gene pools. One to two ecogeographic races were then disseminated to different continents, thus achieving the worldwide distribution common bean is known for nowadays.

3. Urgency and extent of crop vulnerabilities and threats to food security

3.1. Genetic uniformity in the “standing crops” and varietal life spans: C. Urrea, J. Osorno, P. Gepts, J. Myers, J.D. Kelly, M. Brick

Dry beans

There is a concern about genetic vulnerability of the bean crop in the U.S. and the lack of adequate genetic diversity to meet specific eventualities. Although commercial production is relatively isolated across a dozen geographically separate areas across the U.S., there is a potential threat from localized genetic vulnerability within specific production regions. The tradition of growing only one or a few market classes within a geographic region, coupled with genetic similarities among cultivars of a class increases the problem. However, market class diversification has occurred in Michigan in the last few decades. Navy beans that once dominated the acreage in **Michigan**, now only constitute 32% of the acreage; blacks occupy 49% of the acreage, while small reds account for 10%. The navy class is dominated (90%) by two cultivars, Merlin and Medalist, whereas the black bean class is dominated by Zorro and Zenith, each having about 50% market share. Both Medalist and Merlin trace back parentage to the early upright navy bean cultivars, Mayflower, Mackinac, Avanti and Vista, whereas Zorro is a parent of the Zenith black bean cultivar. Acreage of the large seeded cranberry, light, and dark red kidney bean classes has decreased over the past 20 years, with a small increase in the white kidney bean class. Breeding progress in the dark red kidney class has been limited, with two cultivars Montcalm (released in 1974) and Red Hawk (released in 1998) dominating the acreage. The vulnerability situation in Michigan has improved in recent years with the shift away from Seafarer and Sanilac navy cultivars that constituted 90% of the acreage for over three decades and a much shorter life span among current cultivars. In addition, black, small red, dark red kidney, light red kidney, white kidney, and cranberry bean cultivars that possess unique genetic backgrounds from navy beans have expanded to 68% of the acreage in Michigan.

During the past ten-year period dry bean production has fallen in **Colorado**, with production stabilized at 45,000 to 60,000 acres annually. Production remains at approximately 85% pinto 10% kidney, 3% yellow, and 2% Anasazi beans. The variety mix for pinto has shifted to more upright cultivars with public cultivars Croissant, Longs Peak, Montrose, and Othello on less than half the acreage and private cultivars Windbreaker,

Sinaloa, Monterrey, Santa Cruz, Medicine Hat and others sharing the remaining acreage. Most of these cultivars share a fairly narrow genetic base from the Durango race of the Mesoamerican gene pool. New pinto cultivars such as Centennial, Twin Falls, and others have recently been introduced that were developed by introgression of genes from outside the pinto market class. Growers are seeking better resistance to white mold, bacterial pathogens such as common bacterial blight, halo blight, and brown spot, as well as more upright architecture and early maturity to facilitate direct or near direct harvest using the MacDon swather. These traits will require introgression of genes (mostly from marker-assisted selection) for non-market types and unadapted germplasm to achieve the highest level of resistance or plant architecture. In recent years, slow darkening pinto beans are becoming important, but have not penetrated the market in any sizable portion at this time. Growers continue to desire higher yield and improved seed size, color and cooking quality. An interest in health benefits of dry beans steadily increases by consumers and will require the introgression of novel germplasm sources.

Nebraska was first in great northern, second in pinto and light red kidney, and fourth in black bean production in the United States in 2016. Approximately 138,000 acres were planted in 2016, with an average yield of 2,776 lb acre⁻¹ and a production value of \$77 million. In 2015, there was a high incidence of common bacterial blight (CBB), a major disease of common bean, caused by the seed borne bacterium *Xanthomonas axonopodis* pv. *phaseoli* and the brown pigmented variant *X. axonopodis* pv. *phaseoli* var. *fuscans* (Xapf), in western Nebraska. Both species produce the same symptoms on bean leaves and infest the seed internally and externally affecting negatively the seed quality. The great northern cultivar 'Coyne' which was bred specifically for adaptation to the common bean growing conditions of Nebraska and for enhanced resistance to CBB, was negatively affected by a disease resembling CBB in 2015. However, the brown-pigmented variant Xapf was isolated from Coyne's leaves and pod samples. There is now a need to identify sources of Xapf resistance. Bacterial wilt, caused by *Curtobacterium flaccumfaciens* pv. *flaccumfaciens*, has been detected from more than 400 fields throughout the Central High Plains in 2011. The pathogen has apparently become well established in Nebraska. Bacterial wilt reduces seed quality and is considered an A2 quarantine pest for Europe where it is subject to phytosanitary regulations in some countries and some states in the U.S. Very few sources of bacterial wilt resistance have been reported. The development of improved varieties and germplasm with high yield potential, resistance to multiple diseases, greater water use efficiency, and better seed quality must continue to maintain market competitiveness for the Nebraska bean industry.

North Dakota and Minnesota (MINDAK) is the largest producing region of dry beans in the U.S. Approximately 650,000 acres of dry beans are grown every year in North Dakota, which is equivalent to almost 40% of the U.S. total production. Main market classes in North Dakota are pinto, navy, and black, accounting for almost 90% of the total area. Other minor classes include great northern, pink, small red, and yellow. Contrastingly, the neighbor state of Minnesota is the largest producer of kidney beans in the U.S., accounting for almost 50% of the total production. Navy and black market

classes are also of economic importance in Minnesota. For pinto beans, six varieties are the most commonly grown while for the rest of market classes have no more the four or five main cultivars covering most of the production. The dry bean crop in the MINDAK region is vulnerable to biotic stresses, mostly fungal and bacterial diseases such as rust, white mold, anthracnose, root rots, and bacterial blights are the main production constraint. In addition, abiotic stress such as flooding at early stages, drought during reproductive stages, and frost at final stages are the main problems. Finally, since most production is rainfed, water use efficiency is an important component for productivity. Genetic diversity may have been narrowed significantly by the recent interest in upright cultivars that allow direct harvest, especially in pinto and great northern market classes.

More than 80% of dry and snap bean seed production in the U.S. takes place in the **PNW (ID, OR, WA)**, for shipment throughout the U.S., Canada and globally. This means that many different cultivars are grown within the region, and consequently, genetic variability is likely the highest in the nation. Seed-borne diseases introduced from elsewhere as well as natural disasters could strongly affect the supply of bean seed. The dry climate in combination with disease quarantines limits the spread of bacterial and fungal diseases, but the conversion of irrigation systems from gravity fed (furrow or rill) to overhead center pivots has increased the risk from diseases. Drought resulting from reduced snow pack in the mountains, the primary source of irrigation water, poses the greatest climatic risk factor, but thus far there has never been a regional crop failure. Approximately 80,000 acres of commercial dry beans and 20,000 acres of seed beans are produced in the PNW. While the seed acreage is genetically diverse, the commercial acreage relies on relatively fewer cultivars. No specific cultivar dominates the acreage planted for any given market class, but as in the Midwest and elsewhere, cultivars with improved upright architecture are favored. Of total commercial bean acreage grown in 2016, 30% were pintos, 18% were small reds, 10% were pinks, and 10% were blacks.

California is the sixth-leading producer of dry beans, producing about 5 percent of the U.S. crop in 2006-08. California's climate is favorable for most types of dry beans, with a wide variety produced annually. However, four bean classes dominate (accounting for 86 percent of output). These include baby limas (*P. lunatus*; 27 percent of California's crop), large limas (*P. lunatus*; 25 percent), black-eyed peas/beans (*Vigna unguiculata*; 21 percent), and garbanzo beans (*Cicer arietinum*; large chickpeas) (13 percent). Production is concentrated mostly in the Central Valley (both the Sacramento and San Joaquin Valleys), with Stanislaus (18 percent), San Joaquin (14 percent), and Sutter (12 percent) counties the major producers. Common bean production is small and of limited significance compared to the other four classes and that in other states. Large lima bean production is unique to California. Vulnerability is limited by the existence of three different bean genera, the existence of two planting seasons (winter for garbanzos vs. summer for lima bean and blackeyed peas), crop dispersion among other field and orchard crops, and varietal diversity originating in two distinct domestication areas (Mexico for small-seeded limas vs. Ecuador for large-seeded limas). On the other hand, overall in-field varietal diversity is limited compared to the available diversity in gene banks.

Snap beans

In attempting to assess the vulnerability of **U.S. snap beans**, the problem appears less acute initially for several reasons. Snap beans are a minor crop with less than a quarter of a million acres planted across ten states. In those states with relatively high concentration of bean acreage, Wisconsin, Oregon, Florida, Georgia, and New York, there is intercrop buffering and dispersion of relatively small bean fields of several different cultivars. It is unlikely that horizon-to-horizon plantings of single snap bean cultivars will occur as with wheat, corn, or soybean production, in part due to the small acreage, but also due to the diversity in cultivars developed specifically for the canning, frozen, and fresh market.

Unlike dry beans where most cultivars are produced by public breeding programs, only three part-time public programs breed snap beans, with the majority of cultivars being bred by a half-dozen seed companies for U.S. and European markets. With increased use of intellectual property protection, exchange of germplasm between the public and private sector, as well as among companies has become increasingly rare. Nearly all snap bean cultivars developed privately are protected with utility patents and “bag tag” licenses that prohibit use of cultivars in research. Such a pattern of intellectual property protection impacts genetic vulnerability in two ways: 1) companies become “inbred” in their in-house genetic base because little exchange happens outside of each company’s base material, and 2) Seeds of cultivars protected with utility patents are not placed in the USDA-NPGS W6 repository upon release, which are made publicly available after the patent expires. The U.S. Patent and Trademark Office does require that seeds of a patented cultivar be deposited in a repository to show “reduction to practice”, but the repositories that companies typically use are not easy to identify and access, and there is no guarantee that the seeds will be saved beyond the 20 year life of the patent.

There is a well-regulated seed production industry for snap beans and a wide geographic separation of basic seed stocks in the arid western states from the major Midwestern and/or eastern production states. This separation of seed stocks and commercial production greatly reduces the likelihood of buildup of seed-borne pathogens. This system of seed production, however functional for snap beans, has been utilized less with dry beans in Michigan and North Dakota.

Recent molecular evidence suggests that snap beans possess similar or even greater genetic diversity than dry beans (Weeden 1984; Haley et al., 1994a; Skroch and Nienhuis, 1995; Wallace et al., 2018). A STRUCTURE analysis of snap bean with reference to known races of dry bean found eight distinct groups within snap bean (Wallace et al., 2018). Snap bean mirrors dry bean in having two centers of domestication as would be expected for multiple derivations from dry beans at different times and in different places. Some snap bean types may have been developed by Native Americans in both Middle American and Andean centers, but the majority of cultivars were probably developed in Europe after the Colombian exchange. Another characteristic of snap beans that distinguishes them from dry bean is that has been a high degree of mixing across

racial and centers of domestication boundaries, compared to the rather distinct boundaries found in dry beans.

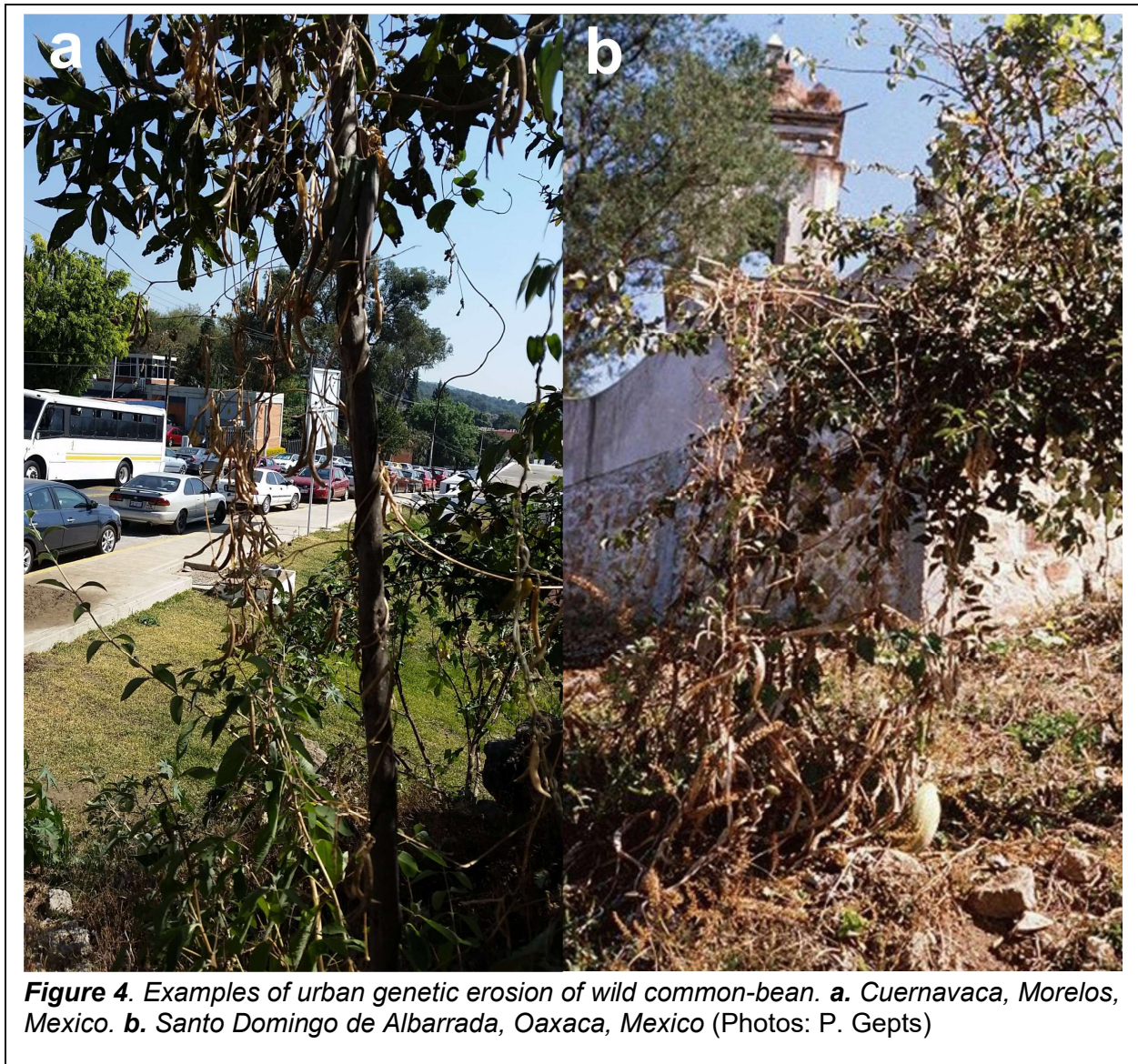
Another assessment of the relative genetic vulnerability differences exhibited by **snap and dry bean cultivars** is demonstrated by their respective reactions to different races of the rust fungus. Stavely (pers. comm.) reported in 1989, that 66 bush snap bean cultivars and 15 bush wax beans had the same reaction to rust races 38 to 70, similar to one of the original processing type snap bean cultivars, Early Gallatin. In addition, similar reactions were exhibited by the majority of commercial light and dark red kidney cultivars. This similarity of reaction to rust was exhibited by many of the PI lines originated from the Andean domestication center. The host cultivar's reaction to these races indicated greater genetic diversity in U.S. dry bean cultivars than in U.S. snap bean cultivars. In recent years new snap and dry bean cultivars have been released that confer resistance to races of rust in the U.S. The resistance genes utilized by cultivars released in the past 15 years has been dominated by the *Ur-3* allele in dry beans and *Ur-4* allele in snap beans. Resistance provided by the *Ur-3* gene has now broken down in MI and ND.

3.2. Threats of genetic erosion in situ: A. Delgado Salinas, D.G. Debouck, J. Acosta Gallegos, P. Gepts

There have been significant reductions in the genetic diversity *in situ* of domesticated *Phaseolus* in Latin America. In addition to the *milpa* agroecosystem (associated cropping of beans, maize, and squash), in itself a telling example, the Jalisco eco-geographic race of *P. vulgaris*, is affected by erosion because few people still plant the climbing lines associated with maize cultivation. In the sierra of Jalisco and Nayarit towards the Bajío region, it is very difficult to obtain labor, especially for harvest. Hence, the bean crop has been subjected to **changes in bean production systems**, which have affected its genetic composition (e.g., Martínez-Castillo et al. 2012).

The bean crop migrated to the north and northeast (e.g., Zacatecas state), became mechanized, and adopted new varieties with different growth habits. There was a similar situation in 1985-1987 in the highlands of Chimaltenango and Quezaltenango in Guatemala. It was more profitable for smallholder farmers to plant horticultural crops of cool climates for sale in cities or for export than to continue growing the traditional milpa with *chomborotes* (*P. coccineus*). The key species of the cropping system – maize – had been changed from landraces to less robust F1 hybrids or corn-on-the-cob varieties, which were not strong enough for associated cropping with beans. There has been a wholesale substitution of landraces by uniform/homogeneous improved varieties, mainly in the Center-North states (Chihuahua, Durango, Zacatecas, San Luis Potosí, Guanajuato, and Querétaro) and Pacific Coast states (Sinaloa, Nayarit). Thus, the changes with regard to genetic resources have involved both substitutions of varieties and replacements of entire agro-ecosystems.

In the case of wild *Phaseolus*, **changes in land use** have been an important factor. **Expansion of urban zones** is very relevant here (e.g., Fig. 4), with a complete replacement of the original vegetation. One can cite specific populations (with collector name and number) that have been lost (see “Cuadernos de Faseología” of D. Debouck at CIAT). Examples include a population of *P. maculatus* collected by Edward Lee Greene in 1880 in Silver City, several populations of *P. polystachios* in Florida (collectors Curtiss and Rugel), a population of *P. coccineus* (collector: Bourgeau) where there is now a metro station of Mexico City, and the type population of *P. bolivianus* (Holway 411) where there is now a neighborhood of Cochabamba in Bolivia. Many additional examples can be mentioned. For example, the hills surrounding the city of Querétaro, it is still possible to observe isolated plants of *P. acutifolius*, *P. vulgaris*, *P. coccineus*, and mainly *P. microcarpus*. Nevertheless, construction of new housing in these hills has changed the environment considerably and it is highly probable that these wild plants will disappear



completely in 2-3 years.

Agriculture itself has been a cause of loss of genetic diversity, with its use of herbicides or the clearing of land where previously there was natural vegetation. In the basin of Rio Grijalba in the state of Chiapas, Mexico, the boost in the cultivation of coffee, sugarcane, and fruit crops, together with the use of herbicides eliminated wild populations of *P. vulgaris* and other *Phaseolus* species from milpa fields, where wild *P. vulgaris* was tolerated and consumed, together with the domesticated beans. Higher coffee prices in Costa Rica have favored expansion of the coffee crop; this has affected populations of *P. costaricensis*, *P. lunatus*, *P. tuerckheimii*, and *P. vulgaris*. Similarly, national parks in Panama face pressure from encroaching crop (Debouck and Rodriguez-Quiel 2020).

Migration away from the land to urban centers in Mexico or other countries like the U.S. have led to the abandonment of rainfed fields, such as in the center and southwest of the state of Guanajuato, Mexico. There are also an estimated 4 million goats that pasture in vegetation close to villages and cities and constitute a threat to natural vegetation in general, and *Phaseolus* population more specifically.

In addition, **global climate change** will affect *Phaseolus* in situ genetic resources, especially with an increase in temperature of 1-2 °C in various parts of the distribution of wild *Phaseolus* species. This effect may affect not only the plants themselves but also their pollinators. Even though several wild *Phaseolus* species are self-fertilized, Charles Darwin had already demonstrated in 1858 the beneficial effect of Apidae pollinators on seed production. Reduced fitness will ultimately lead to extinction. It is possible that wild populations will increase in altitude. For tall peaks like the Colima Volcano or the Orizaba Peak, there is a theoretical possibility of an altitude increase. However, in Central America, the smaller volcanoes provide a more limited opportunity for altitudinal escape, which may affect several populations of *P. dumosus* and *P. vulgaris*, such as the Agua, Fuego, and Acatenango volcanoes near Antigua, Guatemala, and *P. anguciana* in the Fila Cruces range in southeastern Costa Rica (Debouck et al. 2018).

Another factor is the change in precipitation patterns, for example in the south of the state of Coahuila, Mexico, although wild populations from arid regions have been exposed to this type of rainfall changes for several thousands of years.

In the majority of archaeological ruins, wild species of *Phaseolus* are often observed. When these ruins become **tourism** attractions, upkeep of the land at and surrounding these sites results in wild populations being eliminated.

3.3. Current and emerging biotic, abiotic, production, and dietary threats and needs

3.3.1. Biotic Stress: M.A. Pastor-Corrales, A.V. Karasev, C. Estévez de Jensen, J.K. Brown, J.R. Myers, T. Porch, J.S. Pasche, J.R. Steadman, J.S. Beaver

Common bean (*Phaseolus vulgaris* L.) production is affected by numerous types of pathogens and insect pests. This discussion will be limited to the genetic vulnerability of

beans to the most important diseases and pests worldwide. Host resistance, reviewed in great detail in other references (Kelly et al 2003; Kelly and Vallejo 2004; Miklas et al. 2006; Singh and Schwartz 2010; Singh and Miklas 2015), is an important component of most management strategies for the dynamic complex of biotic constraints encountered in various bean cropping systems throughout the world (Schwartz et al. 2005). In addition to incorporating genes from *P. vulgaris*, disease and pest resistance genes have been introgressed from secondary and tertiary gene pools (Abawi et al 1978; Kusolwa and Myers 2011; McElroy 1985; Mahuku et al 2002; Schwartz et al. 2006; Scott and Michaels 1992; Singh and Munoz 1999).

Viral diseases

Bean common mosaic virus (BCMV) and *Bean common mosaic necrotic virus* (BCMNV), both seed-transmitted potyviruses, are the most important viral diseases in common bean (Drijfhout and Morales 2005). Genetics of resistance to both BCMV and BCMNV in common bean is governed by the same five genes, one dominant (*I*) and four recessive (*bc-u*, *bc-1*, *bc-2*, and *bc-3*) (Drijfhout 1978; Drijfhout and Morales 2005). The two recessive genes, *bc-1* and *bc-2*, control systemic movement of both BCMV and BCMNV in common bean plants, but often confer partial or incomplete resistance if present alone (Feng et al. 2017, 2018). The *bc-3* gene is very effective against BCMNV; however, an isolate of BCMV that overcomes *bc-3* was identified (Feng et al. 2015). The *I* gene is the most widely used and provides complete immunity against all strains of BCMV, but expresses a systemic necrotic reaction in common bean when infected with BCMNV; this systemic necrosis can be prevented if any of the recessive genes, *bc-1*, *bc-2*, or *bc-3* are present. The best strategy for breeding for resistance to these two important viruses is to date is to combine the *I* and *bc-3* genes. There are several common bean cultivars from different market classes that combine the *I* and *bc-3* genes (Beaver et al, 2015; Beaver et al; 2020; Pastor-Corrales et al, 2007).

The genus *Begomovirus* (Geminiviridae) has long been problematic in the Americas where common bean is widely cultivated (Bird et al. 1973, Brown, 1990; Brown and Bird, 1992; Morales and Jones, 2004). They are transmitted variably by certain members of the whitefly *Bemisia tabaci* (Genn.) cryptic species. No begomovirus infecting bean endemic to the American Tropics has been reported to be seed transmitted. Several are experimentally transmissible by mechanical inoculation. Among bean-infecting begomoviruses, several species were described from bean and are considered the core bean-infecting species in part because of they were the first begomoviruses identified from common bean and additionally, because their host range is restricted to bean and/or may also include one or several leguminous wild hosts. This latter observation suggests these viruses would likely become extinct in the landscape if bean ceased to be cultivated in these locales where the core begomoviruses are endemic, in that their nearly exclusive host-association with common bean, *Macroptilium* spp., *Calopogonium* and wild *Phaseolus* spp. (Morales and Jones, 2004) has either resulted from an inherent narrow host range and/or selection against a possibly once broader host range that apparently

has precluded them from expanding their extant host range. These viruses are *Bean golden mosaic yellow virus (BGYMV)* (Caribbean Basin, including Dominican Republic, Mexico, and Puerto Rico), *Bean dwarf virus (BDV)* (Colombia), *Bean golden mosaic virus (BGMV)* (Brazil and elsewhere in South America), and *Bean calico mosaic virus (BCaMV)* (Mexico, southwestern U.S.) (Brown et al. 1999). Phylogenetically, the core bean-infecting begomoviruses are evolutionarily divergent from one another, each belonging to a distinct clade among the New World begomoviruses. Also reported from the Caribbean Basin, Central America, and/or are several begomoviruses are endemic in wild legume (Fabaceae) hosts that occur throughout much of the American Tropics, and although they have been identified from naturally-infected common bean, they have not been considered economically important. These include two species from *Macroptilium lathyroides* (L.) Urb. endemic to the Caribbean Basin and Mexico, *Macroptilium golden mosaic virus (MGMV)*, identified from *M. lathyroides* in Cuba and Mexico (J.K. Brown, unpublished) and from *Wissadula amplissima* in Jamaica (Collins et al. 2010), and *Macroptilium mosaic virus* (Brown, 2010; Brown et al. 2011; Idris et al., 1999, 2003). Two others associated with the wild legume, *Rhynchosia minima* (L.) DC are the broad-host range *Rhynchosia mild mosaic virus* (Brown and Idris, 2009) and the recombinant *Rhynchosia yellow mosaic Yucatan virus* (Hernández-Zepeda et al. 2010) reported in Florida, USA, Mexico, and Puerto Rico. The latter viruses are likely widely distributed throughout the Caribbean region and Central America, and although they infect common bean neither has been reported to be economically important despite their apparent wide co-distribution where BGYMV also occurs. Many begomoviruses are known to naturally or infect bean as a secondary host and their economic importance has not been evaluated. Among these viruses are *Cotton leaf crumple virus* (western US and Mexico) (Brown et al., 1986), the *Squash leaf curl virus* complex comprising four species (*Cucurbit leaf curl virus*, *Melon chlorotic leaf curl virus*, *Squash leaf curl virus*, and *Squash mild leaf curl virus* (US, Mexico, Caribbean) (Isakeit et al. 1994, Brown et al., 2001, 2002, 2011, Idris et al., 2008), and *Tomato yellow leaf curl virus-Israel (severe, TYLCV-IL)* (Papayiannis et al., 2007).

In particular, BGYMV has been the focus of most attention with respect to breeding because it has long been known to cause significant yield reduction in dry and snap beans in the Caribbean, Central America, Mexico, and Southern Florida (Singh and Schwartz, 2010). Significant progress in BGYMV resistance breeding has been achieved in Puerto Rico with cultivars and germplasm developed in the Mesoamerican, Andean, Durango, and snap bean market classes through use of key sources of *P. vulgaris* and *P. coccineus* resistance (reviewed by Beaver et al., 2020). Breeding has been facilitated by use of existing and development of new molecular markers for MAS for resistance genes including *bgm-1*, *bgm-2*, *bgm-3*, *Bgp-1*, *Bgp-2*, and the QTL SW12. As the climate warms, incorporation of BGYMV resistance in snap beans will become increasingly important in Florida, while currently there is little incidence of BGYMV in Puerto Rico.

Fungal diseases

The most damaging fungal foliar diseases of dry bean in the Americas and Africa include anthracnose, caused by *Colletotrichum lindemuthianum* (Sacc. & Magnus) Briosi & Cavara, rust, caused by *Uromyces appendiculatus* (Pers.) Unger, and Angular leaf spot, caused by *Pseudocercospora griseola* (Sacc.) Crous & Braum. These three pathogens are known for their extensive and changing virulence diversity that includes hundreds of virulent strains or races. However, co-evolution in these pathosystems has resulted in the races of these three pathogens generally separating into two groups that correspond to the Middle American and Andean gene pools of common bean. Andean races most commonly infect beans of the Andean gene pool. Conversely, Mesoamerican races have broader virulence diversity and although they tend to infect common beans from the Middle American gene pool, they also infect beans from the Andean gene pool (Pastor-Corrales, 1996; Balardin and Kelly, 1998). Infection by each of these pathogens can result in up to 100% yield loss under conditions favoring high disease development (Kelly and Vallejo 2004; Mahuku et al. 2002). To date, approximately 20 single and mostly dominant anthracnose resistance genes, identified by the *Co*-symbol, have been reported. Only the *co-6* gene is recessive. In addition, Multiple alleles are present at the *Co-1*, *Co-3*, *Co-4*, and *Co-5* genes (Kelly and Young, 1996, Valentini et al., 2017). Similarly, 10 single and dominant genes rust resistance genes have been named, mapped and tagged with molecular markers. Five genes (*Ur-3*, *Ur-5*, *Ur-7*, *Ur-11*, and *Ur-14*) are present on common bean accessions of the Middle American gene pool and three genes (*Ur-4*, *Ur-6*, *Ur-9*) are on common beans of the Andean Gene Pool. In addition, The gene has been reported as a Mesoamerican gene present in an Andean (Redlands Pioneer) while the *Ur-12* gene is a gene, present in Andean common bean common bean (Pompadour Checa 50 or (PC 50) is a gene associated with adult plant resistance and abaxial leaf pubescence (Hurtado-Gonzales et al., 2017; Jung et al., 1998). Angular leaf spot is an important yield-reducing common bean disease throughout the Tropics and particularly in South and Central America, as well as in the Caribbean, Mexico and multiple countries in Eastern, Central and Southern Africa (Nay et al., 2019). Changes in weather patterns may favor development of this disease in higher latitudes. Five major loci, *Phg-1* to *Phg-5*, conferring ALS resistance have been named, and markers tightly linked to these loci have been reported. Quantitative trait loci (QTLs) have also been described, but the validation of some QTLs is still pending at the time of this publication. The *Phg-1*, *Phg-4*, and *Phg-5* loci are from common bean cultivars of the Andean gene pool, whereas *Phg-2* and *Phg-3* are from beans of the Mesoamerican gene pool (Nay et al., 2019). Combining disease resistance genes from Andean and Mesoamerican centers of domestication in single common bean cultivars has been a successful strategy to combat these pathogens (Beaver et al. 2015; Kelly et al. 1998; 2001; Pastor-Corrales et al., 2007). However, numerous races have been described for all three pathogens, some of which overcome resistance genes integrated into currently grown cultivars (Balardin et al. 1997; Damasceno E Silva et al. 2007; del Rio-Mendoza et al. 2003; Goswami et al. 2011; Guzmán et al. 1995; Kelly et al. 1994; Markell et al. 2009; Pastor-Corrales et al. 2010).

Sources of resistance have also been identified in the secondary gene pool of *P. vulgaris*, namely *P. dumosus* and *P. coccineus* (Mahuku et al. 2002)

White mold, caused by *Sclerotinia sclerotiorum* (Lib.) de Bary, affects hundreds of agricultural crops, including *Phaseolus* beans. In common bean, snap beans are even more susceptible than dry beans. Disease avoidance associated with varying environmental conditions and modification in plant architecture make phenotypic evaluations in the field difficult and greenhouse protocols do not always accurately correspond to field evaluations. However, improvements to methodologies to identify resistant cultivars under greenhouse conditions have been more successful (Schwartz and Singh 2013; Viteri et al. 2015). Numerous major effect QTL have been identified for resistance to the white mold pathogen, largely of Andean origin and from the secondary gene pool (*P. costaricensis*) (Jhala et al. 2015; Kolkman and Kelly 2003; Singh et al. 2013). Recently, consensus QTL were identified using meta-analysis (Vasconcellos et al. 2017). This relatively novel approach has the potential to accelerate resistance breeding.

Root-rotting soilborne pathogens producing root and stem rot, include several fungi such as *Rhizoctonia solani* Kühn and *Fusarium solani* (Mart. Sacc.) and fungal-like organisms (numerous *Pythium* spp.). *Fusarium* root rot (*Fusarium* foot rot, dry root rot) of beans occurs in most bean-growing regions throughout the world. Root rots usually cause little damage in unstressed plants. However, under conditions of reduced root growth caused by drought, soil compaction, soil saturation (oxygen stress), or low soil fertility, root rot can nearly destroy a bean crop. Even the highest available levels of resistance are overcome by the pathogens when fields are flooded or roots are deprived of oxygen for short periods (e.g., 24h). Resistance to these pathogens is described as quantitative in nature and is not well understood. Sources of resistance have been identified, but the environment and agronomic practices play large roles in the expression of resistance. Additionally, these pathogens are nearly always found in a complex under field conditions, further complicating the introgression of resistance into improved germplasm (Abawi and Pastor-Corrales 1990; Schwartz et al. 2005). Germplasm with Andean backgrounds generally are more susceptible to root rotting pathogens. The transfer of resistance from the Middle American gene pool is ongoing but has been met with challenges. Recent breeding efforts have focused on incorporating vigorous root systems in an attempt to tolerate pathogen infection (Oladzad et al. 2019; Zitnick-Anderson et al. 2020). Appropriate crop management practices can reduce root rot disease pressure and improve the performance of bean cultivars with moderate levels of resistance (Abawi and Ludwig, 2002; Abawi and Widmer, 2000).

Charcoal rot, also known as ashy stem blight, caused by *Macrophomina phaseolina* (Tassi) Goid. (Mph), infects beans in all growth stages resulting in poor emergence and yield reductions. Charcoal rot is influenced by abiotic factors especially high temperature, drought stress and plant age. Genotypes are more susceptible during the vegetative stage than during the reproductive stage. No commercial cultivars with resistance to Mph are available. Resistance to Mph isolate PRI16 in 'Badillo' was

conferred by a single recessive gene, whereas the resistance of 'PC-50' was controlled by two independent complementary recessive genes. Segregation patterns between lines derived from the cross 'A 195 x PC-50' suggested that a single dominant gene conferred resistance to Mph isolate PRI16 (Viteri and Linares, 2019).

Bacterial diseases

Common bacterial blight (CBB), caused by *Xanthomonas axonopodis* pv. *phaseoli* (Smith) Dye (Xap), halo blight, caused by *Pseudomonas syringae* pv. *syringae* (van Hall), brown spot, caused by *Pseudomonas syringae* pv. *phaseolicola* (Burkh.) and bacterial wilt, caused by *Curtobacterium flaccumfaciens* pv. *flaccumfaciens* (Hedges) Collins & Jones, are the four main bacterial diseases that affect dry bean production worldwide. For CBB, resistance is quantitative, affected by the environment and pathogen strains, and originates in three different species, common bean, runner bean, and tepary bean (e.g., Singh and Muñoz 1999).

Marker-assisted selection has proven useful to develop CBB-resistant, improved germplasm from a broad range of resistance sources. The SU91 marker is used for a source of resistance was derived from tepary bean (Singh and Schwartz, 2010). Zapata et al. (2010) identified a dominant gene associated with the SAP6 marker that confers moderate levels of resistance to CBB. Using the SAP6 and SU91 markers, Urrea et al. (2019) were able to develop an improved Great Northern cultivar. Zapata et al. (2004) released five common bean germplasm lines with high levels of resistance to common blight derived from *P. coccineus*. Miklas et al. (1999) also developed and released common bean germplasm lines with enhanced levels of common bacterial blight derived from *P. coccineus*. The common blight resistant pinto bean germplasm line TARS-PT03-1 (Smith et al., 2005) was derived from a cross with the interspecific *P. vulgaris* x *P. coccineus* germplasm line TARS VCI-4B. The white-seeded common bean cultivar Bella combines resistance to CBB with resistance to BCMV and BCMNV, and to BGYMV (Beaver et al., 2018).

Numerous resistance genes have been identified to control halo blight; however, race 6, possibly the most prevalent race, overcomes all of these genes (Taylor et al. 1996). QTL have been recently identified that provide good control of race 6 (Tock et al. 2017) but these have yet to be integrated into cultivars (González et al. 2016). Bacterial wilt is not as widespread as the other bacterial diseases of dry beans. Resistance to bacterial wilt is thought to be quantitative by limiting bacterial colonization in the xylem tissue (Maringoni et al. 2015; Valentini et al. 2011). Little research has been performed on bacterial brown spot, but some resistant lines have been identified (Muedi et al. 2015). Like the other bacterial diseases, resistance to brown spot is heavily dependent on the environment.

Pests

In addition to pathogens, insect pests are extremely damaging to common beans. The potato leafhopper, *Empoasca fabae* (Harris) is an important source of economic loss

to beans produced in the U.S. and Canada east of the Rocky Mountains. Brisco et al. (2014) identified a novel QTL (LH2.2) for *E. fabae* nymph counts that is possibly associated with antibiosis resistance. They reported fourteen QTL associated with resistance to *Empoasca* spp. that explained up to 66% of phenotypic variation. The authors concluded that marker-assisted selection may be a useful approach to breed beans for leafhopper resistance (Brisco et al. 2014), while a pinto bean germplasm resistant to both *E. fabae* and *E. kraemeri* was recently released (Porch et al. 2020). The bruchid species *Acanthoscelides obtectus* (Say) and *Zabrotes subfasciatus* (Boheman) cause significant post-harvest loss to seed quality and germination of beans produced in the tropics. Resistance found in tepary bean has been introgressed into Andean common bean (Kusolwa and Myers 2011; Kusolwa et al. 2016) and Middle American common bean (Beaver et al. 2016) and has been deployed in Africa.

The current strategy in breeding for resistance to most pathogens and pests of dry beans is to pyramid known resistance genes to lengthen the usefulness of the resistance. Virulence patterns need to be monitored to identify the most effective combinations of resistance genes. Concomitantly, breeders, geneticists and pathologists need to identify new sources of resistance in common bean germplasm and from related gene pools.

3.3.2 Abiotic Stress: T. Porch, C. Urrea, J. Osorno, J. Beaver

The largest common bean production in the U.S. is in North Dakota, with most of the current production in the Northern U.S. and West of the Mississippi, and in Michigan. As a result of a rapidly changing climate, even these Northern areas of the U.S. are frequently experiencing heat waves with higher temperatures and longer duration during the sensitive flowering and pod fill stages, while drought stress is becoming more widespread in the West, and excess rainfall or flooding is a recurrent event in U.S. Northern Great Plains. Common bean is one of the most drought-sensitive crops among the grain legumes (Daryanto et al., 2015), it is highly sensitive to high ambient temperatures especially during reproductive development (Gross and Kigel, 1994), and it is intolerant to low soil fertility (Singh et al., 2003) and flooding (Soltani et al., 2017; 2018). Increases in CO₂ levels, from greenhouse gas emissions, have been shown to increase C3 crop yields, however most studies show that these benefits can be offset by the detrimental effects of warming, drought, and increased competition from weeds and greater disease and pest pressure. Warming can also increase the length of the frost-free crop production season, however, drought and high temperatures can shorten the crop cycle resulting in a contraction of developmental phases, such as seed fill, resulting in reduced yield potential and lower seed quality. In addition, breeding for abiotic stress tolerance is challenging due to the polygenic nature of these traits and high genotype x environment interaction (Beebe et al., 2009).

Heat

In temperate regions worldwide, excessive temperatures during reproductive development are predicted to occur with increasing frequency and intensity (Teixeira et

al., 2013). Heat spells during production are regularly exceeding the common bean ceiling temperatures of 30/20°C maximum (daytime/nighttime) in key production regions in California, Colorado, Idaho, Nebraska, Oregon, and Washington State and can result in significant seed yield reduction and/or in split pod sets in dry beans and snap beans (Myers and Baggett, 1999). In the Middle American gene pool, progress has been achieved through selection under high temperature lowland tropical sites, such as the Pacific Coast of Honduras (Rosas et al., 2000) and Puerto Rico (Roman-Aviles and Beaver, 2003) and through introduction of heat tolerance from tropical germplasm. The Mesoamerican race (black, small red and navy beans), having evolved at lower altitudes, are also inherently more heat tolerant, which may have led to their extensive adoption in the tropics. Medium seeded pinto beans of the Durango race with a prostrate type III architecture have been cultivated and selected under semi-arid conditions in the highlands of Mexico and have higher levels of drought tolerance as compared to heat tolerance. Long-term use of the Winter nursery program in Puerto Rico by U.S. breeding programs has likely contributed to increased tropical adaptation (Beaver et al., 2020), including tolerance to moderately high nighttime temperatures, in the Durango race, however, upright type IIa pinto beans require significant improvement for heat tolerance.

In areas that have experienced continuous and long-term selection under high temperature stress, such as under the high daytime temperatures of the Central Valley of California, heat tolerance has been improved (Shonnard and Gepts 1994), such as in the Andean kidney cultivars 'Sacramento' (Soltani et al., 2019) and 'CELRK', as well as in other more recent kidney bean germplasm releases selected for heat tolerance under high temperature greenhouse conditions (Cornell 105) and in Puerto Rico (PR9920-171 and TARS-HT1), among others. The Indian subcontinent landrace Indeterminate Jamaica Red has been a crucial source of heat tolerance in the highly heat sensitive Andean gene pool. Among other U.S. Andean market classes, such as cranberry and yellow, little heat tolerance has been found, however, current breeding efforts are directed at increasing the diversity of the Andean market classes through incorporation of diverse germplasm, using the bulk breeding method, from the characterized Andean Diversity Panel (ADP; Cichy et al., 2015a).

Drought

The Western U.S. may currently be experiencing an extended and historic period of reduced precipitation, or a megadrought, resulting in a major impact on agricultural productivity in the Western U.S. and Northern Mexico (Park Williams et al., 2020). Worldwide, an estimated 70% of common bean production area is affected by drought (Beebe, 2012). Depending on the target environment, improvement efforts focus on breeding for productivity under terminal (Frahm et al., 2004) or intermittent (Beebe et al., 2013) drought stress. Evidence suggests there is significant interaction with the environment under drought stress (Ramirez-Vallejo and Kelly, 1998), thus requiring selection under target production environments. The diversity of production environments in terms of soil types, rainfall patterns, relative humidity, photoperiod, and biotic and abiotic constraints makes breeding for broad production areas challenging, however

identification of mega-environments for selection can increase breeding efficiency (Katuuramu et al., 2020). Introgression and pyramiding of multiple mechanisms of drought tolerance has been effective, as well as the use of exotic germplasm and sister species (reviewed by Beaver and Osorno, 2009). Due to the complexity of drought and the challenges of trait dissection, high quality phenotyping is needed for effective genetic mapping, marker assisted selection (MAS), and breeding progress (Trapp et al., 2016; Berny Mier y Teran et al. 2019a,b, 2020). Long-term breeding efforts in pinto beans has led to the pyramiding of multiple disease resistance, and tolerance to drought, low soil fertility and compaction (Brick and Grafton, 1999; Miklas, 2000; Singh, 2007, Brick et al., 2008). Current breeding and trait dissection efforts pursue specific combinations of diverse germplasm, such as the Mesoamerican and Durango races (Frahm et al. 2004; Terán and Singh 2002), the use of shuttle breeding between temperate (Nebraska) and tropical (Puerto Rico) environments (Porch et al., 2012), and through the use of high-throughput phenotypic methods (Sankaran et al., 2018; Parker et al. 2020c).

Flooding

A study on the impact of natural disasters on agriculture showed that ~60% of crop losses are due to flooding, followed by storms (22%) and drought (16%) (FAO, 2015). In some bean growing regions (i.e. U.S. northern Great Plains), total rainfall amounts have not changed significantly; however, rainfall distribution across the growing season has shown dramatic shifts. Heavier rainfall events are more common now than ~20 years ago, causing significant flooding in the region. This is exacerbated by heavy clay soils that can retain water for long periods of time. Common bean is one of the most sensitive crops to flooding, especially at early developmental stages (germination, emergence, and establishment). During the growing season of 2016, ~167,000 acres (28% of the total dry bean farmlands in North Dakota) were negatively impacted by excess water (Knodel et al., 2017). Tile drainage is often used as a solution, but it is expensive. Therefore, the use of genetic tolerance may be a more efficient and a less expensive option to cope with flooding stress assuming there is genetic variation for tolerance within the bean germplasm. Previous research has shown that significant variability for flooding tolerance in common bean germplasm (Soltani et al., 2017; 2018). A handful of genotypes have been found to be flooding tolerant, with genotypes belonging to the Middle American gene pool being more tolerant than those in the Andean gene pool. However, different tolerance mechanisms appear to be present in both gene pools. Overall, white beans tend to be more susceptible than colored beans, suggesting that the flavonoids may play an important role. Since some of the wild and cultivated *Phaseolus* species naturally grow in regions with high precipitation, there is a need to continue screening and identifying new potential sources of tolerance and perhaps different physiological mechanisms of flooding tolerance.

Edaphic constraints

Deficiency in major and minor soil nutrients are critical constraints to common bean production worldwide, especially in regions lacking resources for fertilizer inputs or in

organic production systems. Nitrogen and phosphorus (Rao, 2001; Hergert et al., 2015) are particularly important macro nutrients in production environments, while alkaline soils in North Central U.S. and California/Arizona experience Zn (Hacisalihoglu and Kochian, 2003) and Fe micronutrient deficiencies (Hergert et al., 2019). The major dry bean breeding programs and seed production in the High Plains in the U.S. are on high pH soils (Kelly and Cichy, 2013). Low fertility constraints result in poor seedling germination and development, reduced biomass, delayed flowering, later maturity, and reduced yield (Singh et al., 2003). The effects of low nutrient fertility can be exacerbated by inadequate rotations, intensive bean production, and compaction. Multiple deficiencies and toxicities can be present in the same production environment, and they can interact with abiotic and biotic stress. High levels of N fertilization of kidney beans on sandy soils in MN can threaten water quality. Optimum levels of fertilization needed to maintain productivity and reduce production costs. Symbiotic nitrogen fixation (SNF) can alleviate soil N deficiencies (reviewed by Bliss, 1993) and increase a plants access to water resources, however, few breeding programs incorporate this important objective because of its complexity (Miklas et al., 2006) and common bean has poor SNF compared to other legumes (Herridge et al., 2008). Long-term selection under lower fertility conditions in carefully managed nurseries and through use of approaches such as recurrent selection have led to increases in tolerance to low fertility both in temperate (Miklas, 2000) and tropical (Dorcinvil et al., 2010) U.S. production environments.

Traits

Plant architecture, determinacy, days to flowering, and harvest maturity are key components in plant response to abiotic stress. The combine-friendly erect architectures of most modern cultivars tend to have deeper taproots with better water mining ability; however, indeterminate prostrate types tend to be better adapted to intermittent drought (Beebe et al., 2013). Root architecture needs to carefully balance the mining of nutrients and water while excessive root biomass can result in reduced harvest index and yield. The plastic response afforded to indeterminate types can increase yield stability under stress (Rao et al., 2016) through avoidance of short periods of stress during reproductive development, followed by the production of new flowers and pod set. More stable and higher yields in type IIa pinto beans in the U.S. has been major success (Soltani et al., 2016; Vandemark et al., 2014). Early maturity is an effective method to escape abiotic stress through avoiding the increasing stress associated with terminal drought and through avoiding heat spells during a prolonged reproductive development (Beebe et al., 2013). However, a shorter crop cycle has reduced yield potential. The distinct and non-reversible switch from vegetative to reproductive development, characteristic of some early maturing genotypes, is often associated with improved yield under drought and heat and should be further pursued. Longer growing seasons in North Dakota and Minnesota, due to climate change, could result in higher yielding, later maturity cultivars and/or impact where beans are produced. Increasing temperatures result in increases in evaporative demand, and in an increased vapor pressure deficit (VPD), thus resulting in faster changes in plant water status. Higher VPD with climate change results in reduced

stomatal conductance, when plants close their stomata to reduce water loss, which in turn leads to reduced transpirational cooling and increased leaf temperatures, and to reduced photosynthesis and plant growth. In common bean, the association of VPD with leaf temperatures was higher in heat tolerant germplasm, indicating their increased transpirational cooling ability (Deva et al., 2020).

Any combination of abiotic stresses can result in complete yield loss. For example, the combination of heat and drought stress in the U.S. Midwest has been blamed for recent broad yield reductions in crops (Hatfield et al., 2018). Increasing temperatures and drought can also lead to increasing incidence of certain diseases such as common bacterial blight, ashy stem blight, and to higher insect pressure, such as the leafhopper pest. Disease interaction can also take on different forms with a warming climate as is the case with *Bean common mosaic necrosis virus*. Genotypes absent the *I* and *bc-3* gene combination (for example) are susceptible at temperatures > 30 °C (Singh and Schwartz, 2010).

Wild *P. vulgaris* and the related domesticated species, *P. acutifolius* and *P. coccineus*, still remain a relatively untapped novel source of useful traits for dry and snap bean improvement in the area of abiotic stress tolerance. Ongoing efforts to introgress abiotic stress tolerance (Barrera et al., 2020) and biotic stress tolerance from tepary bean (*P. acutifolius*) hold great promise. The usefulness of interspecific populations could be maximized by screening them against many different biotic and abiotic stresses through circulating the interspecific materials among many programs for screening in different environments. The introgression of key abiotic stress tolerance from tropical photoperiod sensitive dry beans into day neutral lines for evaluation and utilization in temperate environments will improve genetic diversity and allow for the pyramiding of stress tolerance mechanisms. Introgression of desirable agronomic traits like drought tolerance from wild *P. vulgaris*, require observations of specific phenotypic traits and genotyping of the wild accessions for efficient introgression into the domesticated gene pool (Berny Mier y Teran et al. 2018, 2020; Cortés and Blair 2018).

3.3.3. Dietary and cooking needs: K. Cichy, J. Myers

Compared to other staple foods, such as rice and corn, beans require long cooking times to become palatable. This is often a deterrent to greater utilization by consumers. Cooking time of beans is influenced by the age of the seed, seed growing and storage conditions, and genotype. Freshly harvested beans generally cook 2-4 times faster than beans stored for six months (Coelho et al. 2007). Storing beans at high temperature and high humidity induces 'hard-to-cook' syndrome where cooking times are greatly prolonged (Reyes-Moreno et al. 1993; Liu and Bourne 1995).

Wide genetic variability for cooking time has been documented. Under optimal growing, storage, and cooking conditions, cooking time of over 200 dry bean lines of the *P. vulgaris* Andean Diversity Panel ranged from 16.5 to 90 min (Cichy et al. 2015a,b). Cooking time varies among market classes such that on average white kidney beans

cook faster than light and dark red kidney beans. However, there is also significant genetic variability for cooking time within a market class. For example, within the dark red kidney class, cooking time was evaluated on 14 North American commercial cultivars grown in Montcalm, MI, for two seasons: the cooking times ranged from 28 to 63 minutes. This within-market-class genetic variability is a challenge for consumers, as beans are not sold as single varieties, and mixtures of varieties within a package will have uneven cooking times. Consumer demand for beans would likely increase if fast cooking beans were commercially available and marketed as such with reliable specific cooking instructions were available on packages. Therefore, cooking times should be evaluated during the breeding process and/or prior to variety release.

Some bean market classes are susceptible to seed coat after-darkening. This is most prevalent in beans with cream-brown colors, such as pinto and cranberry beans, but it is also a problem in pink and light red kidney beans. Unfavorable environmental conditions, delayed harvest, and poor storage conditions all may contribute to accelerated darkening, thereby making seed appear to be older than they are (Beninger et al. 2005). Darkened seed is perceived to be older seed of inferior quality and, therefore, fetch a reduced price in the market. Two genes have been found to influence after darkening. The *J* locus controls whether a genotype will darken (Elsadr et al. 2011). The *sd* allele (slow dark), of the *P* gene on Pv07, influences the rate of darkening; slow darkening is recessive to regular darkening (Junk-Knievel et al. 2008; Felicetti, 2011; Islam et al. 2020). Slow darkening has been deployed in commercial pinto cultivars, including ND-Palomino (Osorno et al. 2017).

Research is needed to understand how climate change, including rising CO₂ levels, increased temperatures, and drought will influence the end use quality and nutritional composition of beans (e.g., Jones and Boulter 1983). Based on the few studies that have been conducted in this area, it appears that composition and quality will be impacted differently depending on the specific stress. In soybean, elevated CO₂ resulted in decreased levels of seed zinc and iron (Myers et al. 2014) and a similar outcome would be expected for *P. vulgaris*. In common bean drought stress reduced seed iron concentration, but increased protein, zinc, and phytate levels (Hummel et al., 2018). Hot, humid growing conditions can also contribute to increased cooking times (Berry et al., 2020; Cichy et al., 2019). The potential for climate change to induce prolonged cooking times is of great concern as a barrier to bean consumption. The *P. vulgaris* germplasm collection is an important resource to identify germplasm with fast cooking times and favorable nutrient composition when grown under adverse climatic conditions.

When green pods are consumed as a vegetable, the pods have high moisture content (90% vs. 67% for dry beans when cooked), with green pods containing about 1.9% protein and 8% carbohydrate, and significant quantities of vitamin C, carotenoids, and vitamin K, which dry beans are low in or lack. Cooked snap bean pods also have more calcium and zinc on a per unit basis than dry beans.

4. Status of plant genetic resources in the NPGS available for reducing genetic vulnerabilities

4.1. *Germplasm collection*: B. Hellier, L. Wallace

Holdings

The NPGS Phaseolus collection is maintained at the Western Regional Plant Introduction Station (also known as the Plant Germplasm Introduction and Testing Research Unit) in Pullman, WA and currently has 17,653 accessions in 57 taxa with 13,175 accessions available (75%) and 13,054 accessions backed-up (74%) at the National Laboratory for Genetic Resources Preservation (NLGRP), Fort Collins, CO. Table 6 has the total number of accessions, number available and backed-up for the species with the largest number of accessions per taxa in the collection: *P. vulgaris*, *P. lunatus*, *P. coccineus*, *P. acutifolius*, *P. dumosus*, *P. leptostachyus*, and *P. filiformis*.

Gaps

The geographic distribution of sample origins of the *P. vulgaris* collection is heavily weighted towards the Americas with 39% of the collections originating from Central and South America where the highest genetic diversity is found (Table 7). Europe, Asia, Africa, and Oceania account for approximately 17%, 20%, 5%, and 0.2%, respectively, of the *P. vulgaris* collection. *P. lunatus* is also heavily weighted towards the Americas with 65% of the collection obtained from Central and South America where the highest genetic diversity is found. At 12%, Africa is the second largest source of sample origins for *P. lunatus* after the Americas with all other geographic regions being negligible in size. The next largest species collection is that of *P. coccineus*. Sixty-one percent of this collection originates from Central America where it has the highest genetic diversity. Europe, Asia, and Africa account for 14%, 14%, and 1%, respectively, of the *P. coccineus* collection. Finally, the remaining two domesticated *Phaseolus* species (*P. acutifolius*, and *P. dumosus*) have negligible sample origins outside of the Americas. Wild *Phaseolus* species are not examined as they are not found outside of their natural range in the Americas. The strong emphasis in all these collections for the center of domestication where the highest genetic diversity is found indicates that no significant gaps exist. The low number of African accessions in the *P. vulgaris* collection may indicate a gap considering the high level of bean consumption in East Africa and the extended historical use of bean landraces there, but the available evidence for genetic diversity in Africa shows that it is not a secondary center of domestication for the species but rather reflects the diversity already present in Central and South America.

A wild species of *Phaseolus*, *P. debouckii*, has recently been identified and characterized (Rendón-Anaya et al. 2017b). This newly identified species is a close sister line to *P. vulgaris* that may possibly represent a primary or secondary gene pool for the improvement of the crop. Its absence from the NPGS collection is a gap that could readily

Table 7. Distribution of sample origins among *Phaseolus* species. Shown are a count of accessions followed by the percentage of that collection. A United Nations geoscheme was followed in demarcating geographic regions.

Sample Geographic Origin	<i>P. vulgaris</i> (incl. var. <i>aborigineus</i>)	<i>P. lunatus</i>	<i>P. coccineus</i>	<i>P. acutifolius</i>	<i>P. dumosus</i>
Northern America	2,278 (17%)	288 (13%)	35 (7%)	198 (41.3%)	0 (0%)
Central America	3,681 (26.9%)	430 (18.9%)	294 (61.0%)	263 (54.8%)	93 (96%)
South America	1,654 (12.1%)	1,057 (46.5%)	8 (1.7%)	2 (0.4%)	3 (3%)
Caribbean	136 (1.0%)	21 (0.9%)	0 (0%)	0 (0%)	0 (0%)
Europe	2,334 (17.0%)	8 (0.4%)	67 (13.9%)	0 (0%)	0 (0%)
Asia	2,707 (19.8%)	40 (1.8%)	67 (13.9%)	0 (0%)	1 (1%)
Africa	639 (4.7%)	283 (12.5%)	6 (1.2%)	7 (1.5%)	0 (0%)
Oceania	29 (0.2%)	0 (0%)	0 (0%)	0 (0%)	0 (0%)
Uncategorized	241 (1.8%)	146 (6.4%)	5 (1%)	10 (2.1%)	0 (0%)
Totals	13,699 (100%)	2,273 (100%)	482 (100%)	480 (100%)	97 (100%)

be filled through cooperative sharing with the Centro Internacional de Agricultura Tropical (Cali, Colombia) collections where examples of this species are held. *P. polystachios* is another wild species with a gap in the NPGS collection. This species is the most northerly species of *Phaseolus* with the potential for unique disease and climate adaptations to the North American environment where it is found. *P. polystachios* is also a tertiary gene pool member to *P. lunatus* with potentially valuable traits for crop improvement. This wild bean is only found within the United States of America and it is unlikely that another country will sponsor its collection. The states of Florida and Georgia, which appear to be a center of diversity for the species based on the distribution of its subspecies, remain largely unsampled for this species. Plans are underway to collect *P. polystachios* from these areas.

Still another gap in the collections is the minimal representation of diversity panels utilized in genetics research in the NPGS collections. Several panels are currently utilized by researchers, such as the Diversity Panel for Andean Bean Improvement (Cichy et al. 2015a) or the Middle American Diversity Panel (Moghaddam et al. 2016), but nearly all

these contemporary panels are derived from the federally funded Bean Coordinated Agricultural Project (BeanCAP) diversity panel. The BeanCAP diversity panel was conceived of as an important advance in translational genetics and genomics that would facilitate the development of markers for marker assisted selection for all the traits under improvement by breeders. These markers would be identified through mapping methods, such as Genome Wide Association Studies, for which these panels are ideally suited. Currently, only 56% of the BeanCAP diversity panel is represented in the NPGS, and the available accessions are ambiguously identified with duplicate names or names that do not precisely match the names found in the BeanCAP diversity panel. This should be remedied by including all the BeanCAP diversity panel into the NPGS and clearly identifying them as such. This may be augmented in the future by adding other diversity panels of importance to the research community into the NPGS collections.

Acquisitions

The NPGS *Phaseolus* collection has a long history. The oldest active accession in the collection, PI 90758, was donated in 1930. Material has been added via donation and collection since that time. The last NPGS sponsored explorations outside the U.S. targeting *Phaseolus* were from 2002 – 2004 in Honduras which added 83 accessions of wild species and landraces. From 2004 onward, the material collected outside the U.S. has been landraces from Central Asia, Greece, and Ukraine. New material has also been added which was collected in the U.S. Wild species were collected in Arizona in 2003 and 2004 and *P. polystachios* was collected across its range from 2010 to 2018.

Adding additional germplasm from the primary centers of origin is difficult as Mexico and the Central and South American countries are not contracting parties to the International Treaty on Plant Genetic Resources. For the near future, filling gaps in the collection for *Phaseolus* species occurring in the U.S. will be the primary goal along with adding important cultivars used in research.

Regeneration

All *Phaseolus* regenerations are done in two greenhouses on the campus of Washington State University and two at the Western Regional Plant Introduction Station Central Ferry Farm. Only greenhouse regeneration is used to prevent BCMV infection spread among accessions. Currently, approximately 400 accessions are regenerated per year with low seed quantity or low viability used as the selecting criteria for regeneration. Seed from each accession is direct seeded into pots, watered with drip irrigation and hand harvested. Species requiring pollinators for seed production are hand pollinated. Both IPM and conventional pest control, with a zero tolerance for aphids, are used in all the greenhouses. Photoperiod-sensitive accessions can only be grown from the end of September to mid-March in part of one of the greenhouses at WSU and both of the greenhouses at Central Ferry. With the additional of the 2 Central Ferry greenhouses (first used in 2019), there is adequate regeneration space to maintain the *P. vulgaris* photoperiod-sensitive accessions, but we lack personnel to maintain the *P. coccineus*

photoperiod sensitive accessions. Due to a lack of personnel, the BCMV testing and elimination program has been halted.

Distribution

The *Phaseolus* collection is distributed as seed to both domestic and international requestors. There continues to be strong interest in the collection. From 2015 to 2019, an average of 285 requests were received and 7,079 seed packets distributed per year. Requests are received via the GRIN-Global website. For all international orders, export phytosanitary requirements are obtained from the USDA Animal and Plant Health Inspection Service (APHIS). If a phytosanitary certificate is needed the seed is sent to the National Germplasm Resources Lab, Beltsville, MD for APHIS inspection. The European Union and several other countries require certification that seed exported from the U.S. be free of *Xanthomonas axonopodis* pv *phaseoli*. This limits the distribution of the NPGS *Phaseolus* collection to these countries as the resources, both financial and personnel, are lacking for this testing.

4.2. Associated information: L. Wallace

4.2.1. Web site

GRIN-Global is has become a well-respected standard for public databases of germplasm around the world. The International Maize and Wheat Center (CIMMYT) and the germplasm collections of several nation states have taken advantage of the free and unfettered licensing of the GRIN-Global software to manage and access their own collections. Its use by several countries is a testament to its usefulness. Nevertheless, upgrades and improvements are needed. In particular, the ability to seamlessly integrate genomic data into the passport data for an accession is a need that is becoming more acute with the accelerating capacity for high throughput whole genome sequencing. This accelerating capacity is making genomic information more relevant as more research is done on it, but also increasing expectations by users of GRIN-Global that this relevant information will be provided.

4.2.2. Passport data

Species is given for the taxonomy portion of passport data on 17,516 (99.2%) of accessions. Nevertheless, there are 137 accessions that contain only a genus name without a species name. These accessions were generally submitted by the collector without a species name. This oversight can be remedied through a taxonomic reexamination of materials in the collection. There may be valuable germplasm that has yet to be properly categorized and integrated into the collections with its full significance registered in the passport data. For the minority of accessions that do not contain origin passport details (2.3% of accessions), there may be no remedy at this time, although genetic analysis may one day place them correctly in a geographic location. A key

passport detail that needs expansion is the seed description and a photograph of the seeds. Until genotyping of accessions becomes ubiquitous and provides an identity that can be verified, the seed description and a photograph of the seeds provides the best method available to verify the identity of the accession outside of a full evaluation in the field. Currently, 11,308 (64%) of accession passport details contain a seed description and 9,393 (53.2%) contain a photograph of the seeds. This deficit is being remedied with each regeneration of seed during which a photograph and seed description are added to the accession details.

4.3. Genomic and genotypic characterization data: P. McClean, P. Gepts

The NPGS *Phaseolus* collection has been screened phenotypically for multiple traits over the years. While this is useful when searching for variation among general phenotypes, it does not provide sufficient detail when selection based on overall genomic diversity is the goal. At the genomic level, the common-bean core collection was characterized using microsatellite markers (McClean et al., 2012), but, while using the state-of-art tools at that time, only 58 loci were surveyed. This does not provide a sufficient genomic survey. For a more complete analysis, and more importantly to make selection more accurate for germplasm with only limited variability, more marker loci need to be sampled. This has changed with the release of multiple reference and draft genome sequences of common bean. It is important to note that the *Phaseolus* collection was integral in the population genomics analysis that utilized the initial reference assembly of *P. vulgaris*.

More recently, the same core collection was genotyped with the BARCBear6K_3 BeadChip (n ~ 5,400 SNPs, see below) (Figure 3; Kuzay et al. 2020). Together with seed type (size, shape, and color) and phaseolin seed protein data of the Genetic Resources Unit at the Centro Internacional de Agricultura Tropical (Cali, Colombia), these SNP data allowed an assessment of the representativity of the core collection, which was one of the first core collections established in the world. Kuzay et al. (2020) recommend that a separate core collection be established for wild common bean and the domesticated common bean collection be supplemented with representation from races Peru and Chile from the Andean gene pool and races Jalisco and Guatemala in the Middle American gene pool.

G19833 (W6 36342) was selected to develop a representative reference genome for the Andean gene pool (Schmutz et al., 2014). The primary sequence data was collected from 454 reads (18.6x genome coverage) and augmented with 454 paired-end library read data. The assembly was based on 21x sequencing coverage. During the early stages of the project, an Illumina Golden Gate assay with 827 SNPs was developed (Hyten et al. 2010). The SNP depth was increased during the genome project through resequencing of a family of divergent genotypes and mapping to early scaffold assemblies. The product of that effort was an Illumina Infinium chip (Song et al., 2015) used to genotype the segregating populations derived from a Stampede x Red Hawk cross. The resultant genetic map (1,784 genetic loci) was an integral part of the assembly process. It contained 7,015 SNP and 261 SSR, along with 25 indel markers that were

used to anchor the map to the common bean linkage groups. The assembled contig data spanned 472 Mb (of the estimated 587 Mb genome; <http://www.kew.org/cvalues/>), while the assembled scaffold distance was 521 Mb. The L50 of the contig assembly was ~40 kb, while the L50 for the scaffolds was ~50 Mb. The chromosomal scale assembly represented 89% of the scaffold distance. 45.4% of the total assembly were repeat elements. The largest class of repeats, the LTR retrotransposons, make up 36.7% of the genome size. Gene modeling was based on RNA-seq data from 11 libraries representing multiple anatomical tissues sampled at different development stages. In addition, ~50k transcript assemblies based on available EST sequences in NCBI GenBank were developed. Standard homology-based prediction software packages were employed to develop gene models. These approaches defined 31,638 transcripts derived from 27,197 gene models. More recently, long-read PacBio sequences were collected for the same G19833 genotype. This data was used to develop a more complete genome assembly of 537.2 MB with scaffold N/L50 of 5/49.7 MB, and contig N/L50 of 73/1.9 MB. This assembly ranks as one of most complete among plant species.

BAT93 (PI 633451), a small-seeded breeding line developed by CIAT, was chosen to develop a draft genome of the Middle American gene pool (Vlasova et al., 2016). This line has multiple resistances to major bean diseases and is a parent of a historical mapping population (Nodari et al., 1993; Freyre et al. 1998). The bulk of the sequencing reads were obtained using the 454, SOLiD, and Sanger technologies. The primary reads represented 133x coverage of the bean genome. The total contig length was 428 kb (73% of estimated size; L50=18.1 kb), and the scaffold length was 495 kb (L50=0.43 Mb), while the physical distance of the chromosomes was 81% of the scaffold distance. The observation that 35% of the genome consisted of mobile elements was determined using multiple repeat predictors. The Class I LTR retrotransposons accounted for 29% of the genome size. Multiple transcript libraries were developed and sequenced using Illumina or 454 technologies. This was combined with publicly available transcript data for gene modeling purposes using standard gene prediction software. A total of 66,634 transcripts were discovered to define 30,491 protein coding gene models.

In turn, this BAT93 Middle American assembly (Vlasova et al. 2016) was used to investigate additional features of the *Phaseolus* germplasm (Rendón-Anaya et al. 2017a). These include 1) shallow (8-20x) sequencing of 29 *Phaseolus* genomes representing most of the species diversity (as defined by Delgado-Salinas et al. 2006), 2) a more detailed genomic characterization of five accessions of the intermediate, wild common-bean gene pool from Ecuador and Northern Peru based on re-sequencing and metabolomics, 3) gene flow intra- and inter-species in *P. vulgaris* and taxa closely related to it, and 4) shared and differential selections of genes by the Andean and Middle American domestications. Based on these detailed genomic analysis, the presence of ancestral sequences for phaseolin, and ecogeographic data, the intermediate gene pool was re-classified as *P. debouckii* to further draw the attention to the distinctness of this lineage, which separated from the main *P. vulgaris* lineage in Middle America some 0.26 – 0.4 Ma ago (Rendón-Anaya et al. 2017b, Ariani et al. 2018).

More recently, another reference assembly of the genotype Pinto UI 111 (PI 549535) was released. This genotype is three-way cross consisting of 50% Common Pinto, 25% Common Red Mexican (UI 34), and 25% Common Great Northern (UI 1). Thus, this genotype contains a genetic background of the three major market classes of race Durango (for ecogeographic race classification, see Singh et al. 1991a). Because phylogenetic analyses consistently have shown each *P. vulgaris* race to be distinct, a Durango reference genome assembly will be highly useful for race specific analysis aimed at improving the most widely grown ecogeographic race in US bean production fields. The reference assembly used the latest PacBio long-read technologies. The scaffold size of the UI 111 genome is 554.9 Mb while the contig size is 553.8 Mb demonstrating the value the improved PacBio long-read chemistry and sequencing hardware. The scaffold and contig N50/L50 are 5/51.0 Mb and 23/8.5 Mb, respectively. RNA-seq reads from triplicate samples of leaf, stem, root, and basal root tissue identified 65,104 RNA sequences. From that data, a total of 27,385 loci were identified that are associated with 36,018 transcripts. The assembly can be downloaded from https://phytozome-next.jgi.doe.gov/info/PvulgarisUI111_v1_1

Reference genome sequences of other domesticated species have been (lima bean: G27455, domesticated line of the Middle American gene pool from Colombia) or are being developed (teparty bean). The genotype of lima bean chose belongs to the 'sieva' cultivar group, based on its seed size and shape (Mackie 1943, Baudet 1977) The lima bean sequence is available online at https://phytozome-next.jgi.doe.gov/info/Plunatus_V1.

The BARCBean6K_3 BeadChip (Song et al., 2015) was the first tool developed directly from the Andean genome project. It quickly developed into an important research tool, especially for assessing genetic factors associated with important agronomic traits such as nitrogen fixation (Heilig et al. 2016), disease resistance (Nakedde et al. 2016), and pod characteristics in snap beans (Hagerty et al. 2016). From a germplasm evaluation perspective, the chip was instrumental in assessing genomic variation among the newly developed Andean Diversity Panel (n~350) that is being used to map important agronomic traits using association mapping techniques (Cichy et al., 2015). Another early tool developed from the sequencing and SNP development efforts was a set of 2,687 indel markers distributed across the genome that can assess not only inter-gene pool variation, but also intra-gene pool and even within market class variation (Moghaddam et al., 2014). Markers from this collection were instrumental in locating the WM7.1 and WM8.3 white mold tolerance QTL to narrow genomic regions (Mamidi et al. 2016) and providing gel-based markers for the *Co-1* anthracnose gene (Zuiderveen et al. 2016).

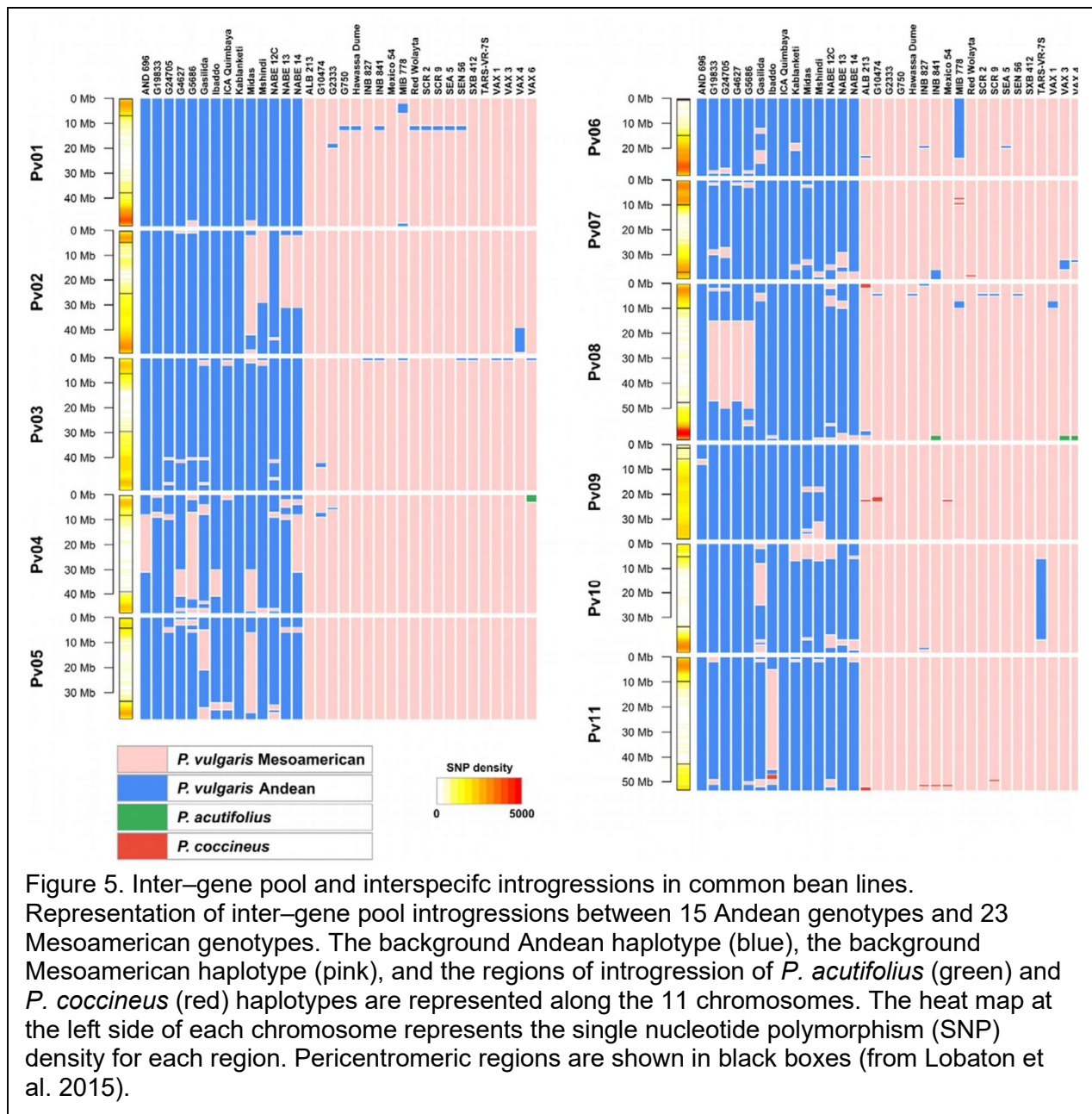
A richer SNP data set was created using low-pass sequencing (Schröder et al., 2016) to generate a set of ~150,000 SNPs for the BeanCAP Middle American Diversity Panel (MDP) (Moghaddam et al., 2016). The MDP is a collection (n~300) of historical and modern cultivars representative of US, Canadian, and Latin America breeding programs. This SNP collection was used to define the population structure of the MDP,

determine that linkage disequilibrium varies among Middle American races, chromosomes and even among various regions within a chromosome, and evaluate the genetic architecture of several agronomic traits (Mogghadam et al. 2016). Other SNP sets were developed such as the one reported by Ariani et al. (2016) that discriminates wild and cultivated bean genotypes and was used to track the migration history of wild common bean (Ariani et al., 2017). The richest SNP data sets, short of a complete genome sequence, are products of resequencing. Mamidi et al. (2016) applied resequencing at the level of ~2x per individual within pools of tolerant and susceptible white mold lines. ~1.5 million SNPs distinguished the two pools, and these SNPs were used to map tolerance to very narrow intervals. This approach, introgression mapping, can be applied to any mapping population, and the low-cost of pooled, rather than individual, resequencing makes this an attractive approach to rapidly mapping genetic effects to narrow intervals.

The significant genotype efforts are now being leveraged to develop a much larger set of SNP marker loci that are specific to each of the two gene pools. GBS reads (n=381,092,199) from multiple libraries (Oladzad et al., 2019) consisting of individuals with either MA (n=469) or Andean (n=325) parentage were pooled. Individual MA and Andean haplotype maps (HapMap) were developed after final SNP filtering and imputation. The Middle American HapMap contained 205,293 SNPs, and the Andean HapMap consisted of 260,670 SNPs. Given the large number of genotypes in each of the two HapMaps, researchers can now design experiments to capture phenotypic data from all or a subset of the genotypes in the HapMap populations and then perform GWAS analyses with a very large SNP dataset to discover important genetic factors controlling trait(s) of interest. Importantly, as additional GBS data is generated for a wider array of germplasm, it can be merged with this HapMap data set to create a denser SNP collection for those germplasm but also all germplasm that has been characterized at the genomic level.

Whole-genome sequencing, performed on a set of 37 domesticated lines belonging to *P. vulgaris*, *P. coccineus*, and *P. acutifolius*, identified some 40 million sequence variants and confirmed known structure of the *P. vulgaris* germplasm into the two major gene pools and domestication centers (Andean vs. Middle America). Several inter-gene pool (Andean vs. Middle American) and interspecific introgressions were identified or confirmed (Figure 5). In addition, SNP markers located within previously identified QTLs provided more precise tagging of anthracnose and angular leaf spot resistance loci (Lobaton et al. 2018).

Recent phylogenetic and domestication discoveries (Delgado-Salinas et al. 2006; Repinski et al. 2012; Kwak et al. 2012; McClean et al. 2018; Weller et al. 2019; Parker et al. 2020a,b) are pointing to the fact that common bean diversity assessments must be made within each gene pool or ecogeographic race at significant depth rather than taking a simple pan-species view at a narrow depth of genotyping. From the perspective of



developing evaluation panels, the unique LD structure within the two bean gene pools (Kwak and Gepts 2009) and the repeated observation that phenotypes are often controlled by different genetic factors in the two pools makes it important to evaluate distinct MA and Andean panels. It is important to remember that, as a species, *P. vulgaris* is unique in that the wild ancestor split into two wild gene pools, the Middle American and Andean, ~100k years ago (Gepts et al. 1986; Kwak and Gepts 2009; Mamidi et al. 2013; Schmutz et al. 2014). Only recently did these gene pools undergo independent domestications about ~7k years ago (Mamidi et al. 2011; Schmutz et al. 2014) in distinct locations to form two distinct domesticated clades.

Domestication within each of the clades involved between 748 (Andean) and 1748 (MA) genes, but only 59 of genes were shared between the two gene pools (Schmutz et al. 2014). Rendón-Anaya et al. (2017a) identified 599 gene models associated with domestication phenotypes that were shared between the Andean and Middle American domestications; 628 gene models were unique to the Middle American domestication. When the same gene is involved in the domestication, recent research has shown convergent evolution produced unique alleles in each gene pool that were associated with the domesticated phenotype (determinacy, *PvTFL1y* on Pv01: Repinski et al. 2012, Kwak et al 2012; seed and flower pigmentation: *P* locus, Pv07: McClean et al. 2018) or different, unlinked genes altogether (pod shattering, *PvPDH1* on Pv03 and MYB26 candidate gene on Pv05: Parker et al. 2020a,b; Rau et al. 2019. GWAS experiments are also revealing that adaptation to environmental stress conditions evolved differentially in the two gene pools as exemplified by the discovery that distinct genetic factors are associated with the response to flooding in the two gene pools (Soltani et al. 2017, 2018). These independent evolutionary paths have also affected marker development and deployment, most notably for disease resistance markers where quite often a specific marker is only diagnostic in a one gene pool (Miklas et al. 1993, 1996) while being monomorphic in the other pool regardless of whether the genotype is resistant or susceptible. This is the result of the strong population structure and distinct linkage disequilibrium (LD) arrangements in the two gene pools (Kwak and Gepts 2009).

4.4. Phenotypic evaluation data: L. Wallace

The predominant source of phenotypic evaluations of the NPGS *Phaseolus* collection is the regeneration of the germplasm and the associated observations obtained during the regeneration process. Sixty-four percent of scored traits are obtained in this manner based on method records. These observations are limited in scope to characterizing the seed, pod, flower, leaf, plant, and plant photoperiod. The most complete set of observations among these traits is that of photoperiod, which is found in 17,253 records out of 17,653 in total or 98% of the NPGS *Phaseolus* collection. The next most complete set of observations is that of seed weight, which is found in 15,349 records out of 17,653 in total or 87% of the collection. Descriptions of the seeds, such as color and pattern, cover between 62% to 63% of the collection or 64% if taken together. Observations of pod, flower, leaf, and plant are much less common and range from 1% of records to 53% of records containing this information. Nevertheless, these publicly available data (via GRIN) can be very useful for research as illustrated by the pod shattering data used by Parker et al. (2020a) in order to correlate them with molecular data and map genetic factors involved in the genetic control of this trait.

Dedicated trials to assess disease and pest susceptibility only represent about 23% of scored traits. The most prevalent observation among these dedicated trials is that of white mold susceptibility. There are 556 observations of white mold susceptibility among the 17,653 records or about 3% of records contain this disease information. The remaining disease and pest observations include trials of anthracnose, bacterial blight,

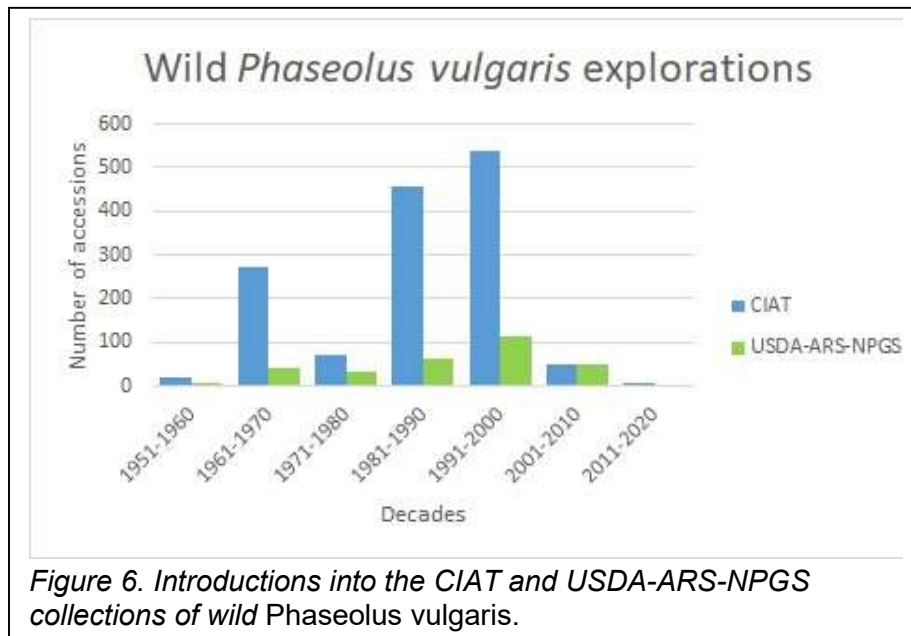
bacterial wilt, bean common mosaic virus, *Fusarium*, halo blight, *Pseudomonas*, rust, Mexican bean beetle, and potato leaf hopper. Each of these disease or pest susceptibility trials contributes observational data to 1% or less of the total records in the collection. An even smaller number of records include information from a dedicated trial of nutritional properties. Of 17,653 records in total, 113 records (0.6%) contain information on protein, antioxidants, and sugars.

Observations on disease resistance and nutritional quality traits are the most pertinent to plant breeders and to the health and safety of the food supply, yet they are the least frequent types of observation in the records of the NPGS. Unfortunately, funding for the evaluation of NPGS germplasm has remained flat for many years, so progress in adding these observations to the records of the NPGS has been slow.

4.5. Plant genetic resources research associated with NPGS: P. Miklas

The germplasm evaluation grants awarded by NPGS the past 20 years have been extremely useful for identifying novel and useful traits for managing pests, increasing climate resilience, and broadening genetic diversity to facilitate genetic gains. Funded proposals since 2018 include evaluating wild *P. vulgaris* for disease resistance and adaptive root traits, common bean landraces for resistance to soybean cyst nematodes, and wild and domesticated tepary bean for resistance to seed weevils. Other NPGS grants since 2010 included evaluations of lima beans, nuña popping beans, snap beans, an Andean diversity panel, and the Central and South American core collections for traits ranging from adaptation to temperate regions, disease resistance, nutritional components, and cooking quality. NPGS germplasm has also contributed significantly to recent diversity panels (Andean, Durango, Tepary, and Yellow bean panels; Cichy et al., 2015; Hart et al., 2019; Soltani et al., 2016) used for GWAS of economically important traits including plant architecture (Soltani et al., 2016), flooding tolerance (Soltani et al., 2018), anthracnose resistance (Zuiderveen et al., 2016), pod shattering (Parker et al. 2020a,b), and others.

The NPGS wild bean collection has supported the resurgence of mining wild crop relatives for traits supporting adaptation to extreme climate changes (Berny Mier y Teran et al. 2019). Many of the newly discovered traits above will soon be added to the list of success stories of evaluation, identification, characterization, and introgression of valuable traits from NPGS accessions into improved cultivars. A sampling of these success stories for bean include landraces and tepary bean PI lines contributing resistance to common bacterial blight (Singh and Miklas, 2015), PI150414 landrace contributing quantitative resistance to halo blight (Tock et al., 2017), landraces and *P. coccineus* accessions contributing novel resistance to *Sclerotinia* white mold (Schwartz and Singh, 2013), PI203598 landrace contributing root vigor and associated root rot resistance and drought tolerance to race Durango beans in the PNW (Miklas 2000), PI181996 contributing a gene for broad resistance to bean rust (Beaver et al., 2020), and wild common beans PI319441 and PI 417653 contributing higher yield under drought



stress (Berny Mier y Teran et al. 2020). NPGS funding of PCGC proposals have been and will continue to be a critical need for evaluating the *P. vulgaris* germplasm collection for novel traits useful to the bean research and breeding community.

4.6. *Phaseolus* explorations over time: P. Gepts

Progress in our understanding of the organization of genetic diversity in the genus *Phaseolus*, in general, and the domesticated species, specifically, has been stimulated by extensive explorations over several decades. An analysis based on introduction data of wild *P. vulgaris* (the most widespread and abundant wild relative) into the collections of the Genetic Resources Unit at CIAT (Cali, Colombia) and GRIN-Global (W6 Plant Introduction Station (Pullman, WA, USA)) shows that initial introductions were made in the 1950s and the majority of the introductions were made in two decades, the 1980s and 1990s (Figure 6). Since then, however, explorations have sharply decreased, in spite of the continued genetic erosion documented in section 3.2.

One can speculate about this decline. First, there may be a sense that most of the germplasm of wild *P. vulgaris* and landraces (let alone other *Phaseolus* species) has been collected. This is contradicted, however, by observations made by Zizumbo-Villarreal et al. (2009) in western Mexico and P. Gepts (Sierra de Penjamó, Guanajuato, Mexico), where limited sampling revealed additional wild populations that were unreported. Additional examples are provided by the Venezuelan Andes and several areas in Peru (e.g, Ayacucho) (D. Debouck, pers. comm.). Second, there may be a feeling that there is a need to more thoroughly evaluate and phenotype the existing accessions in the germplasm collections before embarking on additional explorations. Third, a change in generations is taking place with many of the collectors retiring and in need to be replaced by younger colleagues.

5. Priority issues and recommendations: P. Miklas, P. Gepts

The *Phaseolus* community has very much appreciated the dedication of the staff at the Western Regional Plant Introduction Station (WRPIS) over the many years since the inception of the NPGS *Phaseolus* collection. The staff has done its utmost to serve the

community and has facilitated many genetic studies and complemented breeding programs, which would not have been possible without its prompt and excellent contributions as illustrated by the many examples in this Crop Vulnerability Statement.

We offer these recommendations as a constructive effort to further improve the quality and function of the NPGS *Phaseolus* collection. These recommendations are based on the preceding text and our mutual experiences across a broad range of disciplines.

5.1. Need for adequate and permanent staffing, operating budget, and facilities (greenhouses)

The *Phaseolus* collection at the WRPIS in Pullman (WA) is one of the largest collections of NPGS with some 18,000 accessions. In addition, most of the materials are of tropical or subtropical origin, which presents challenges regarding regeneration due to thermo-photoperiod sensitivity delaying or preventing flowering under summer field growing conditions. Adequate maintenance, characterization, and distribution requires permanent staffing, an adequate operating budget, and sufficient greenhouses to conduct increases during the off-season to address the flowering issue.

5.2. Updating the *Phaseolus* collection: e.g., diversity panels, core collections, additional explorations

This statement has mentioned several gaps in the collection that should be filled. These include:

- a) Integration of the various diversity panels developed by the *Phaseolus* community (e.g., Middle American and Andean diversity panels, Moghaddam et al. 2016, Cichy et al. 2015a). Only some 55% of these panels are currently included in the collection. Additional panels have been developed, including for races Durango and Mesoamerica (P. McClean) and wild *P. vulgaris* (Berny Mier y Teran et al. 2018). Of additional interest is that these panels have been genotyped with SNPs.
- b) The core collection of common bean should be re-evaluated to be more representative. Additional materials should be introduced to include Andean gene pool materials from the ecogeographic races Jalisco and Guatemala, and Middle American materials of races Jalisco and Guatemala. In addition, a wild common-bean core collection should also be established (Kuzay et al. 2020).
- c) Explorations for additional wild types and additional landraces should resume, as they provide additional genetic diversity not present in the elite, domesticated gene pools (e.g., Berny Mier y Teran et al. 2020; A. Delgado-Salinas, pers. comm.; D.G. Debouck, pers. comm.).
- d) Continued reciprocal exchanges with the CIAT gene bank should be encouraged, especially to enrich the Western Regional Plant Introduction Station from the larger Colombian collection (D.G. Debouck, pers. comm.).

- e) Add specific germplasm addressing specific breeding needs: e.g., fast cooking germplasm to the collection, notably Manteca beans collected in marketplaces in Angola and yellow beans collected in marketplaces in Haiti (Beaver, J and Porch, T. collection trips) (components of the Andean Diversity Panel and Yellow Bean Collection) (Cichy et al., 2015a).
- f) The bean host differentials included in the collection for anthracnose, BCMV, halo blight, and rust should be updated as warranted and increased to meet demand. The differentials for angular leaf spot could be added as well.

Related to this point, future *Phaseolus* CGC meeting agendas could include a recurring item devoted to “special collections” in hopes to solicit new and updated germplasm of novel and useful value to the global research community. The goal would be to encourage researchers to donate useful materials from their personal “working collections” after vetting by the *Phaseolus* CGC before such valuable materials would likely be lost upon their retirements.

5.3. Genotyping of the collection and bioinformatic analysis to integrate phenotypic and genotypic data

Several thousands of *Phaseolus* accessions have been genotyped in several ways, from in-depth sequencing to develop reference sequences for different gene pools or ecogeographic races, to shallow genotyping-by-sequencing (GBS) or SNP genotyping using the BARCBear6K_3 BeadChip.

- a) An effort should be made to systematically genotype or sequence the collection in collaboration with the *Phaseolus* community worldwide using a platform to be determined (either by sequencing or SNP chip). This effort could be initiated with updated core collections and extended with diversity panels.
- b) The genotypic data should be combined with phenotypic data - via GRIN-Global? - to strengthen the link between the two types of data, in support of conservation and breeding programs (Gepts 2006).
- c) Climate change/warming data should be integrated into the planning for germplasm exploration, conservation, and utilization: e.g., Barrera-Sánchez et al. 2020

5.4. Emphasize the phenotypic evaluation of the collection

To increase the usefulness of the collection, evaluations should continue with the financial support of NPGS to stimulate these evaluations. These results should then be integrated promptly into GRIN-Global.

5.5. Establish links to microbial germplasm collections

Access to the pathogen differential strains/races are as important as the host differentials in order to maintain a common system for interpreting host - pathogen interactions. Many pathogen collections are maintained by individual researchers without a mandate for

preservation or sharing of strains. Often these pathogen collections are lost upon retirements or shifts in research focus. The ATCC maintains isolates for some pathogen but it can often be difficult to obtain and resuscitate needed strains relevant to *Phaseolus*.

- a) Many BCMV and BCMNV strains for the 8 pathogroups are scattered among research programs but given that the strains are seed borne they can be maintained for long periods in seeds harvested from purposely infected plants. Perhaps these infected seeds for specific differential strains can be stored as new accessions in a special BCMV collection and supplied to researchers upon request given proper permits are supplied.
- b) Perhaps other seed borne pathogens have a similar opportunity for preservation as a special germplasm collection. There are some national labs such as the Fusarium Center at Penn State that might be amenable to curating a collection of Fusarium strains relevant to *Phaseolus*.
- c) Relatedly, there is a national Rhizobium collection curated by USDA-ARS that should be utilized for establishing a comprehensive collection of Phaseolus symbiotic N-fixing bacteria.

5.6. Further improvements to GRIN-Global

The content of the GRIN-Global database should be further improved by integration of phenotypic data of the accessions and relevant links to external information (e.g., sequence or genotyping data at NCBI, Dryad, etc.) and other germplasm collections (e.g., CIAT, microbial collections, etc.).

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