



# History and impact of a bean (*Phaseolus* spp., Leguminosae, Phaseoleae) collection

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**Abstract:** This work explains the reasons why a bean collection was established in 1973 at the International Center of Tropical Agriculture (CIAT) near Palmira in Colombia. It shows the impact of the collection on plant breeding and in agricultural development through the distribution of germplasm to the center's bean breeding program, to successively find resistances to pests and diseases, adaptation to low phosphorus and drought, and more recently higher content of iron and zinc in seeds. The collection was also used to progress knowledge in biological sciences, as shown by a dozen of examples. A reason behind these successes was foresight and focus on diversity *per se* in the collection. The paper ends with a number of suggestions for the way ahead for the genetic resources conservation and management of these bean crops, and possible take-home lessons for curators in charge of other similar collections.

**Keywords:** distribution, yield, biotic stress, abiotic stress, breeding, *Phaseolus*

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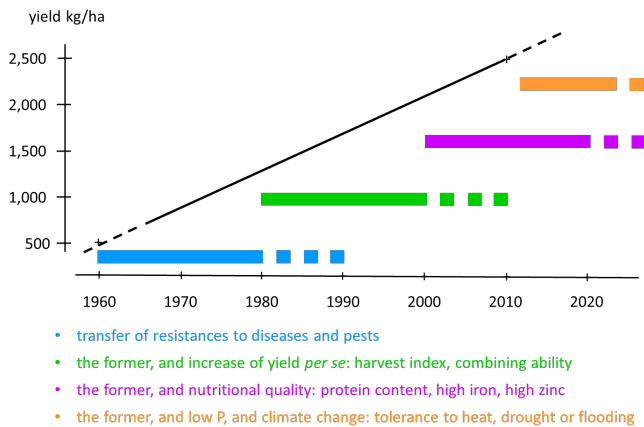
## The purpose for establishing a collection of genetic resources at CIAT

Created in 1967, the International Center of Tropical Agriculture (CIAT for its Spanish acronym) was the third international center of agricultural research whose mandate was to increase the agricultural productivity in the tropics. Because of population growth a sure food availability crisis was anticipated and yields of key staple crops had to increase (Kastner *et al*, 2012) and, fortunately, this actually happened, namely in Asia (Evenson and Gollin, 2003). Although CIAT was originally designed to improve agricultural systems in the lowland tropics (the Center had a couple of animal production programs), it became clear that the level of human talents, physical and financial resources required for such a task was beyond the donors' capacity and time frame, and these limits indicated to re-focus instead (Lynam and Byerlee, 2017). After the successful experience of the International Rice Research Institute

(IRRI) in Los Baños, Philippines, on rice and that of the Centro Internacional para el Mejoramiento del Maíz y Trigo (CIMMYT) in El Batán, Mexico, on wheat, and as an outcome of international conferences (Hernández-Bravo, 1973; Rachie, 1973; Voysest-Voysest, 1983), CIAT moved from a Food Legumes Production Systems Program into a program focused on common bean, *Phaseolus vulgaris* L. (Hidalgo, 1991); the Bean Program initiated in January 1974 (Voysest-Voysest, 2000).

Given the production problems faced for this crop (Hernández-Bravo, 1973; Singh, 1992), very often managed by small-holder farmers with limited access to inputs (Broughton *et al*, 2003), the next strategic decision was to increase productivity by transferring resistance to diseases and pests into target varieties. By then, the most severe diseases, out of more than one hundred affecting the crop (Zaumeyer and Thomas, 1957; Singh, 1999), often caused a 70-100% loss in yield (Sanders and Schwartz, 1980; Singh, 1999). The first cycle of breeding (which took about 8-10 years in beans in the 1960s) aimed at securing the potential yield of the landraces (Rachie, 1973). Thus, farmers would have a secure food stock at home and a surplus for

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**Figure 1.** Evolution of the breeding strategy in bush common bean in the tropics over the last decades.

sale in local markets. This strategy was likely to work because in subsistence agriculture beans were planted in mixtures to where resistant genotypes would lower the disease pressure for the total crop (Clawson, 1985), and in market-oriented agriculture with fewer genotypes under cultivation a higher part of the production would be saved for sale.

It was envisioned to tackle the next most limiting factor to productivity in a cumulative way, through the production and distribution of elite varieties, with the active participation of the national partners, who then would work with extension services for the diffusion of such a technological package. That participation was critical for impact, given the high number and regional variation of commercial seed types (Voysset-Voysset, 1983; Voysset and Dessert, 1991). Figure 1 shows how this strategic approach has worked for common bean over five decades. With each breeding cycle tackling a new challenge, the strategy had to be cumulative, because the entire production chain and the final users would hardly accept to go backwards. In this regard, it is worth noting that after fifty years, diseases and pests continue to be among the highest priorities of bean breeding, especially in Africa (Assefa et al, 2019).

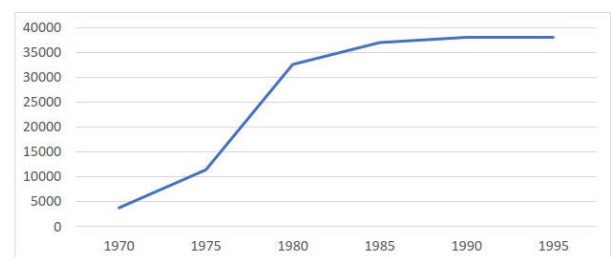
While the first breeding cycle was under way, improvements were introduced to agronomical practices, taking into account planting density, planting date versus water availability versus solar radiation/photoperiod, minimum of nitrogen-phosphorus-potassium fertilization, or pH correction by lime application (Thung, 1991). Once these improved agronomical practices were implemented, it was clear that progress in yield had to come from plant breeding (Borlaug, 1983), but there was a critically important assumption for the whole strategy to work: the immediate availability of well characterized and evaluated genetic resources, which would be the ultimate source of all desirable genes. Practically, because there were none at the Center, this meant assembling large collections of genetic resources of beans and evaluating such collections by multidisciplinary teams. In the early years of CIAT, that assumption had to quickly become reality for the effi-

ciency and impact of the breeding efforts. The need for multiple sources for disease and pest resistance and abiotic stress tolerance was also related to the wide diversity of conditions of deployment in the many countries benefiting from that technology. Note that apart from assembling collections, it was also the time of setting the founding principles of genebank management (Allard, 1970; Frankel and Hawkes, 1975).

### How the *Phaseolus* collection was assembled

With the establishment of the CIAT Bean Program, the first introductions of bean collections from other institutes (e.g. United States Department of Agriculture [USDA], Pullman, USA; Instituto Nacional de Investigación Agrícola, Chapingo, Mexico; Instituto de Ciencias y Tecnología Agrícola, Chimaltenango, Guatemala; Centro Agronómico Tropical de Investigación y Enseñanza [CATIE], Turrialba, Costa Rica) (Hernández-Xolocotzi, 1973; Vieira, 1973) were made thanks to the constant cooperation of the Instituto Colombiano Agropecuario, Palmira, Colombia on plant quarantine matters (Figure 2). Accessions were registered as Germplasm numbers (e.g. G4017 for ‘Carioca’, perhaps the most planted bean variety in the world; Voysset-Voysset (2000). Thanks to the support of the International Board for Plant Genetic Resources (IBPGR), Rome, Italy (established in 1974), several collecting missions were organized for landraces and wild species. Before the entry into force of the Convention on Biological Diversity (CBD), these crop genetic resources were considered as common heritage of humankind, and there was free exchange of genetic resources for breeding and agricultural research purposes. After December 1993, acquisition by introduction of copies of germplasm collections and explorations came to a halt (as experienced in other genebanks of the Consultative Group on International Agricultural Research (CGIAR); Halewood et al (2020). But in recent years, target explorations were carried out under the legal framework set by the International Treaty on Plant Genetic Resources for Food and Agriculture (FAO, 2002), for example in Costa Rica.

Because beans as a staple are often associated with maize, collections of bean germplasm have been established across the tropics and subtropics, particularly in Latin America (e.g. in Chapingo in Mexico, Medellín in



**Figure 2.** Increase in size of the bean collection introduced into the CIAT genebank.

Colombia or Campinas in Brazil) (Vieira, 1973), which could be introduced into CIAT. It was not rare for a maize breeder to pick up seeds of local bean landraces when visiting a farmer or a local market and give them to colleagues in charge of bean breeding. As a general practice in Latin America the maintenance of bean germplasm collections was a side activity of the bean breeders. Given this kind of attention, it is no surprise that the landraces of the market classes worked on by the breeders were well represented in the respective collections. Retrospectively, this is positive because some of these collections were made in the 1940-1960s, just before massive rural transportation blurred the origins of many local landraces. By that time, the varieties selected or bred over the last decade were starting to replace many landraces. This replacement was seen in small black and red-seeded bean varieties of Central America. Consequently, the most original genetic variation in landraces that existed in the 1940s is by now either in genebanks or lost. Collecting today will only result in duplicates or in samples of bred materials.

The focus on common bean and the need to find resistances for several market classes of beans as final targets influenced the makeup of the collection (Table 1). As the Bean Program was working with Central American countries and Brazil (Voysesst-Voysesst, 1983), many small-seeded collections were introduced, but because CIAT also worked together with Andean countries, large-seeded collections were included as well (both collections but particularly the last ones were important for Africa: Martin and Adams (1987). Cultivated *P. vulgaris* makes up the biggest part of the collection, the other cultivated species follow, with a total of 32,183 landraces and 2,797 improved varieties. The wild forms of the cultivated species and the wild species are represented by over 2,000 accessions (Table 1).

The number of country depositors is 110. The top five countries that have contributed most are: Mexico (6,237 accessions), Colombia (3,927 accessions), Peru (3,798 accessions), Guatemala (2,853 accessions) and the United States (1,863 accessions), followed by Brazil, Ecuador, Turkey, Malawi and Costa Rica (with around 1,000 accessions each). Restoration of national bean diversity has been done for Bhutan, Chile, Costa Rica, India, Iran, and Mexico, based on institutional agreements.

After partial safety duplications at CATIE and Centro Nacional de Pesquisa de Recursos Genéticos e Biotecnologia, Brasilia, it was decided in 1996 to make a complete backup at CIMMYT because extra space was kindly offered by Bent Skovmand then in charge of the wheat collection. This included a check for viability and absence of diseases of quarantine importance. By 2019, 92% of the bean collection had been safely duplicated at CIMMYT. When the Global Svalbard Seed Vault (GSSV, Longyearbyen, Norway) was opened in February 2008 (Fowler, 2016), a second safety backup was implemented there. By 2019, 94% of the bean

**Table 1.** Accessions of the in-trust *Phaseolus* collection kept at CIAT Palmira (information also available in Genesys: <https://www.genesys-pgr.org/a/overview/v2ZW8lQwlep>)

Species	Biological status	No. accessions
<i>P. vulgaris</i> , common bean	cultivated (landraces, commercial varieties)	30,571
	wild and weedy forms	1,804
<i>P. lunatus</i> , Lima bean	cultivated (landraces, commercial varieties)	3,031
	wild and weedy forms	274
<i>P. coccineus</i> , scarlet runner	cultivated (landraces, commercial varieties)	760
	wild and weedy forms	198
<i>P. dumosus</i> , year-bean	cultivated (landraces)	475
	wild and weedy forms	15
<i>P. acutifolius</i> , tepary	cultivated (landraces, commercial varieties)	161
	wild and weedy forms	165
Other species (41 <sup>1</sup> )	wild forms only	484

<sup>1</sup> This figure represents half of the number of species of the genus (Debouck, 2021).

collection was safely duplicated at GSSV. In addition, CIAT safeguards in its vault the seed backups of the food legume collection of the International Institute of Tropical Agriculture (IITA), Ibadan, Nigeria, and the tropical forage legumes of the International Livestock Research Institute (ILRI), Addis Ababa, Ethiopia.

## The diversity in the bean collection and its use

Given the breeding priorities (Figure 1), the bean collections were evaluated by multidisciplinary teams in multiple locations in Colombia, first in Palmira, in Quilichao since 1977 and in Popayán since 1978 (Cuellar, 2003). Resistances to several highly damaging diseases (e.g. anthracnose, angular leaf spot (ALS), bean common mosaic virus (BCMV), rust) were found (Table 2) and transferred as their mode of inheritance was progressively defined (Singh, 1992; Beebe et al, 1997; Beebe, 2012). However, bean breeders soon realized that further genetic progress would be obtained only by screening the diversity outside the respective market classes, and that for many traits (e.g. *Ascochyta* blight, bean golden mosaic virus (BGMV), bean golden yellow mosaic virus (BGMV), common bacterial blight, halo blight, web blight, white mold, bruchids and leafhoppers) there were very few or no sources of workable resistance (Miklas et al, 2006; Singh and Schwartz, 2010; Beebe, 2012). In a copy of the USDA collection there were a few accessions of wild common bean from Mexico collected in the 1960s by Howard Scott Gentry in which, later on, César Cardona and his team found bruchid resistance associated with a particular seed protein (Osborn et al, 1988). The screening for the right variants of that protein by electrophoresis

opened the way for marker assisted selection (Kelly and Miklas, 1999), widely applied in breeding for BGYMV resistance (Broughton et al, 2003), anthracnose resistance (Kelly, 2004) and other traits. The wide secondary gene pool (e.g. *P. coccineus*, *P. costaricensis*, *P. dumosus*) has just started to be evaluated, and has already shown promise against *Ascochyta* blight (Schmit and Baudoin, 1992), angular leaf spot (Mahuku et al, 2003) and white mold (Singh et al, 2013). Such resistances were expected because the species of the section *Phaseoli* thrive in montane humid forests (Debouck, 2000) where these fungi diseases are frequent selection pressures (Cattan-Toupance et al, 1998) and have likely been present over hundreds of thousands of years, given the age of these species (approximately 1 million years) (Delgado-Salinas et al, 2006; Rendón-Anaya et al, 2017).

Once disease resistances were transferred to the preferred varieties in the different market classes, yield came as the next challenge, in order to keep bean as a competitive (mono-)crop as compared to soybean, cowpea or sorghum. An early approach, in line with the spirit of the Green Revolution in wheat (Donald, 1968), was to optimize the ideotype under favorable environments (Adams, 1973). That breeding effort on plant architecture continued (Kelly, 2001), although with limited success in the tropics (Beebe, 2012). An important outcome, however, has been the rise of growth habit 2 or bush erect indeterminate (race 3 of Evans (1973) for mechanical harvesting in bean improved germplasm, little present in traditional landraces of Latin America. This also offered opportunities to enrich the collection (Hidalgo et al, 1992). Another breeding goal was to combine the productivity of the small-seeded varieties with the grain size of the large-seeded ones, many of them demonstrated to be of Mesoamerican and Andean origin, respectively (Evans, 1976). Thus came the works evidencing the two major gene pools (Gepts et al, 1986; Singh et al, 1991b; Kwak and Gepts, 2009; Bitocchi et al, 2013), and the races within them (Singh et al, 1991a; Beebe et al, 2000b; Blair et al, 2007, 2012). The presence of races was a bit unexpected in an autogamous crop but could be explained by the role of outcrossing during early domestication (Chacón-Sánchez et al, 2021). Some genetic isolation and poor recombination have been shown to exist between the two major gene pools (Singh and Gutiérrez, 1984) and since the wild state (Koinange and Gepts, 1992). But significant heterosis was demonstrated to exist (Nienhuis and Singh, 1986; Bannerot, 1989), especially between races (Singh et al, 1993; Singh and Urrea, 1995), while genetic disorders between races were sometimes observed (Singh and Molina, 1996). The significant interactions with the environment, however, have resulted in a narrow commercial applicability of this approach (Gutiérrez and Singh, 1985; Nienhuis and Singh, 1986). Another strategy inspired from the quantitative developments in tomato breeding (Tanksley et al, 1996) was the advanced back-

cross QTL analysis using a wild form. The accessions of wild *P. vulgaris* G12947 (Acosta-Gallegos et al, 2007), G19892 (Buendía et al, 2003), G24404 (Blair et al, 2006) and G24423 (Kelly, 2004) were found to contribute a significant QTL for yield (a 27% increase as compared to the recurrent parent in the last example). In some cases, the use of weedy types would help reduce the number of backcrosses needed to recover the appropriate seed size (Acosta-Gallegos et al, 2007). Another innovative approach has been the use of lines coming from crosses with the year-bean (for transfer of high iron in the grain) or with tepary (for transfer of bacterial blight resistance) in order to bring more monocarpism into common bean (Klaedtke et al, 2012; Mejía-Jiménez et al, 1994). The bean crop with exceptions in growth habits 1 and 2 still has the ancestral trait of continuing shoot production and lateral flowering, while the first pods already enter into maturity. In the wild it makes all sense, but not in a crop aimed at mechanical harvesting. The desert ephemerals of the genus such as *P. acutifolius* A. Gray, *P. filiformis* Benth, or *P. microcarpus* Mart. (Freitag and Debouck, 2002) invest much less in profuse branching but soon move all photosynthesis products into their seeds. Thus, under heat or drought stress, it makes sense to quickly redirect such products to the only part that will be harvested (Rao et al, 2013; Suárez et al, 2020).

One outcome of the increase in size of the collection and the first phase of germplasm evaluations at CIAT was the establishment of core collections (along the concept introduced by Frankel and Brown (1984)). The CIAT common bean core collection was established by use of Geographic Information Systems maximizing the environmental diversity of landraces, and a few morpho-agronomic descriptors (Tohme et al, 1995a). The core collection, consisting of 1,556 accessions, has been used for the identification of germplasm tolerant to low phosphorus (Beebe, 1997) or containing high levels of micronutrients (Islam et al, 2002). For both traits less than 10% of the total collection had been evaluated at that time (Beebe et al, 2000b,a), explaining the recourse to the core collection. Using core collections was, in part, the consequence of internal duplication or redundancy in general collections, which for cultivated common bean has been estimated at 50% across the major genebanks (Lyman, 1984). This figure is perhaps on the high side but reflects the amount of commercial and breeding materials kept in genebanks as compared to primary sources of variation (landraces, wild species). As mentioned, the management of germplasm collections was often a side activity of bean breeders who would hesitate to eliminate all variants close to the target market class. Given the cost of keeping accessions versus the cost of tracking down internal copies (this was then achieved by multi-site characterization, in addition to passport data) (Koo et al, 2004), the problem was not given high priority in the past. With the development of SNP genotyping technology, this issue should be revisited,



**Table 2.** Bean accessions from the CIAT collection used as sources of resistance to diseases and pests.

Trait	Material used	References
<b>Diseases</b>		
angular leaf spot	G10613 from Guatemala interspecific hybrids with <i>P. coccineus</i> ; G4691	Pastor-Corrales <i>et al</i> (1998) Pastor-Corrales <i>et al</i> (1998); Islam <i>et al</i> (2002); Mahuku <i>et al</i> (2003)
angular leaf spot and anthracnose	G3991 from Costa Rica	Schwartz <i>et al</i> (1982)
anthracnose	Aliya G02333 Kaboon G1588; Cornell 49-242 G5694 interspecific hybrids with <i>P. coccineus</i> G35252	Young and Kelly (1996) Melotto and Kelly (2000) Mahuku <i>et al</i> (2002)
<i>Ascochyta</i> blight	<i>P. dumosus</i> G35369 from Costa Rica <i>P. dumosus</i> G35182 from Guatemala	Schmit and Baudoin (1992) Garzón <i>et al</i> (2011)
bacterial wilt	wild <i>P. vulgaris</i> G12883 from Mexico	Urrea and Harveson (2014)
Bean Golden Yellow Mosaic Virus (BGYMV)	<i>P. coccineus</i> G35172 from Rwanda	Beaver <i>et al</i> (2005)
Bean Common Mosaic Virus (BCMV)	Porillo Sintético G04495, Royal Red G04450	Singh <i>et al</i> (2000)
beet curly top virus	California Pink G06222, Red Mexican G05507 Porillo Sintético G04495, Burtner, Tio Canela 75	Larsen and Miklas (2004) Singh and Schwartz (2010)
common bacterial blight	interspecific hybrids with acutifolius VAX4, MBE7	Zapata <i>et al</i> (1985); Singh and Muñoz (1999); Michaels <i>et al</i> (2006); Navabi <i>et al</i> (2012)
halo blight	Montana No. 5; PI 207262 Montcalm G06416, ICA Tundama G14016 Palomo G12669 Pinto US 14 G18105 Wis HBR 72 G03954	Miklas <i>et al</i> (2003, 2006) Beaver (1999) Schwartz (1989) Singh and Schwartz (2010) Taylor <i>et al</i> (1996)
<i>Fusarium</i> root rot	Porillo Sintético G04495; wild <i>P. vulgaris</i> G12947	Beebe <i>et al</i> (1981); Acosta-Gallegos <i>et al</i> (2007)
<i>Pythium</i> root rot	PI 311987 G02323	Beebe <i>et al</i> (1981)
<i>Rhizoctonia solani</i> rot	N203 G00881	Beebe <i>et al</i> (1981)
rust	Compuesto Negro Chimaltenango G05711 Ecuador 299 G05653 Redlands Pioneer G05747 PI 260418	Stavelly (1984) Stavelly and Pastor-Corrales (1989) Liebenberg <i>et al</i> (2006) Singh and Schwartz (2010)
web blight	BAT 93; Flor de Mayo G14241	Beaver <i>et al</i> (2002)
white mold	<i>P. coccineus</i> PI 175829 from Turkey <i>P. dumosus</i> PI 417603 from Mexico interspecific hybrids with <i>P. coccineus</i> G35172 interspecific hybrids with <i>P. costaricensis</i> G40604	Abawi <i>et al</i> (1978) Hunter <i>et al</i> (1982) Singh <i>et al</i> (2009) Singh <i>et al</i> (2013)
<b>Pests</b>		
<i>Acanthoscelides</i> weevil	wild <i>P. vulgaris</i> from western Mexico G12952; QUES	van Schoonhoven <i>et al</i> (1983); Zaugg <i>et al</i> (2013)
<i>Apion godmani</i> pod weevil	Amarillo 154 G03982; G03578	Beebe <i>et al</i> (1993); Garza <i>et al</i> (2001)
<i>Empoasca</i> leafhoppers	Turrialba 1 G03712 California Dark Red Kidney, from USA G17638	Galwey (1983) Schaafsma <i>et al</i> (1998)
<i>Ophiomyia</i> bean fly	<i>P. coccineus</i> G35023 and G35075, and interspecific hybrids	Kornegay and Cardona (1991)
whiteflies Aleyrodidae	DOR 303	Blair and Beaver (1992)
<i>Zabrotes</i> weevil	wild <i>P. vulgaris</i> from Chiapas, Mexico G24582	Acosta-Gallegos <i>et al</i> (1998)

with the merging of near identical accessions and the review of the core collection (as already suggested for the USDA core collection by Kuzay *et al* (2020)). The most significant costs ahead are likely to be about regeneration and evaluation, not the chasing of internal copies helped by robotics!

### Distribution of the bean collection

Since being established in August 1977 as an internal service unit (Hidalgo, 1991), the genebank has distributed to the Bean Program and the Biotechnology Research Unit of CIAT a total of 318,148 samples (or 69.4 % of the total distributed) (Figure 3). Externally, the genebank has distributed 140,109 samples (or 30.6% of the total) to users in 105 countries. The total distributed was 458,257 samples of 37,657 accessions, or 99% of the bean collection. These figures indicate that: i) the collection has been studied and used initially by the scientists of CIAT, ii) the number of countries benefiting from the conservation work through distribution almost matches with the number of country depositors, and iii) the collection has been distributed almost entirely (this percentage could be even higher since some accessions have not been distributed due to lack of seeds). One should note that apart from CIAT programs, the most important users were national agricultural research services, universities and research institutes. The shares of farmers, commercial companies and non-governmental organizations in the distribution were low in comparison. Assuming farmers are aware of the existence of germplasm collections, reasons for the low number of requests might be related to the farmers' access to on-line request processes (mail requests were honored), as well as the capacity to deal with phytosanitary regulations in the respective countries. As dry bean breeding has been mostly carried out by public institutions, requests of genetic diversity by the private sector were few, often related to specific sources of variation for snap bean breeding (e.g. sources of resistance to anthracnose).

The purposes of distribution have generally followed the breeding priorities shown in Figure 1: interest in resistances to diseases and pests, nutritional quality and more recently tolerance to abiotic stresses such as drought and high temperature. As discussed below and shown in Figure 4, a significant part of the distribution has been for the purpose of advancing knowledge. In Figure 4, breeding activities (38.9%) and applied research (e.g. in pathology or entomology: 37.1%) were the top purposes for seed requests, followed by agronomy (11.7%) and basic research (e.g. in genetics or evolutionary studies: 9.6%). The variation in number of distributed samples from one year to another can be significant, namely if the core collection with over 1,500 accessions was requested and sent. The peak in distribution in the period 1978-1996 practically matches with that of the activities of CIAT Bean Program (Voyses-Voysest, 2000). For the period 1973-2019, the top five recipient countries were:

USA (26,093 samples), Colombia (18,444 samples), Brazil (9,198 samples), Guatemala (7,430 samples) and Mexico (6,787 samples). The term 'samples' is preferred over 'accessions' as a country recipient could ask for a specific accession more than once.

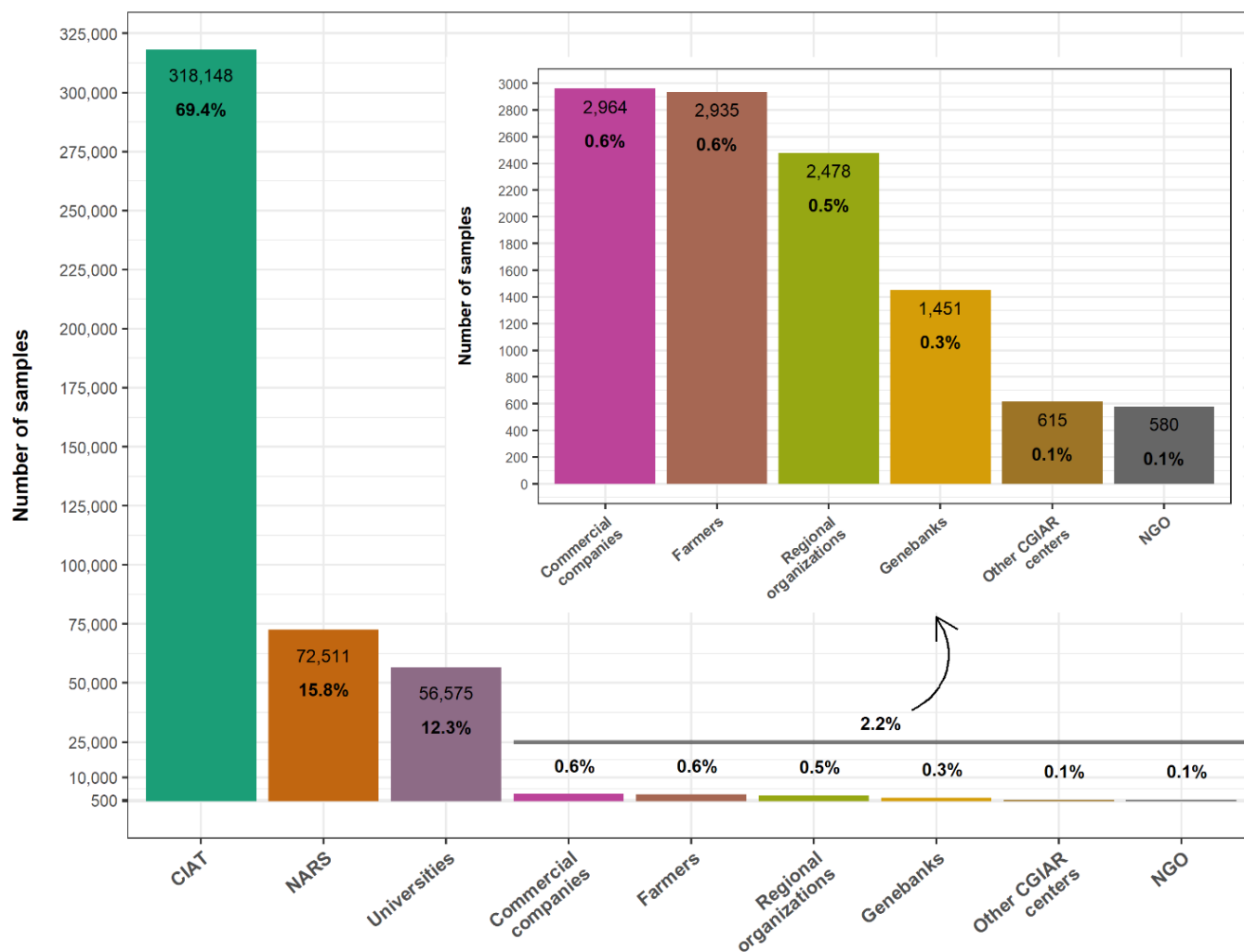
Apart from germplasm, the genebank also distributed information related to the in-trust collections. An indicator of this service is given by the number of consultations of the genebank website (<https://ciat.cgiar.org/what-we-do/crop-conservation-and-use/>) to have access to data (Figure 5).

Statistics about access to genebank information and services in recent years show that most of the visitors (81%) reach the genebank website directly, indicating a user knowledge and confidence that relevant information can be found there, while 19% of visitors find the website through a browser search or are referred to it through another link. Users also benefit from specialized technical information currently consisting of 658 documents (including articles, book chapters, conference proceedings, germplasm exploration reports, posters and presentations). These documents can be accessed through the genebank website or the institutional document repository CGSpace (<https://cgspace.cgiar.org/handle/10568/35697>), that registered 27,278 downloads in 2017-2019.

### Impact of the bean genetic resources collection

The 225 varieties released in 17 countries of Latin America and the 88 varieties released in 14 countries of Africa in 1974-1999 by the Bean Program (Voyses-Voysest, 2000), the check of BGYMV in Central America (Beebe, 2012), as well as the yield gain from 688 kg/ha to 782 kg/ha in eastern Africa (Lynam and Byerlee, 2017) eventually have their origin in the CIAT genebank. Once the interesting traits were identified (Table 2); (Hidalgo and Beebe, 1997), through different breeding schemes, elite varieties were produced, tested and released via international nurseries such as the International Bean Yield and Adaptation Nursery (Voyses-Voysest, 1983; Beebe, 2012), generating significant economic and social benefits (Johnson *et al*, 2003). In this last work, over the period of analysis, and because of the varieties involved, some countries of Latin America and the Caribbean were net beneficiaries (Argentina, Brazil), while others were net contributors (Mexico, El Salvador). Overall, and over the duration, however, it seems that all countries benefit from conservation and unrestricted international exchange of germplasm (Johnson *et al*, 2003).

As an example of changing context over time, the gene gy. originating from Peru and conferring an intense and sustained yellow color (Bassett *et al*, 2002) was used since 1978 in northwestern Mexico (Lépiz-Ildfonso and Navarro-Sandoval, 1983), because it gave a premium price as compared to the fading color in yellow-seeded traditional landraces. It ended up in the variety 'Azufrado Peruano 87' (Voyses-Voysest, 2000) and also



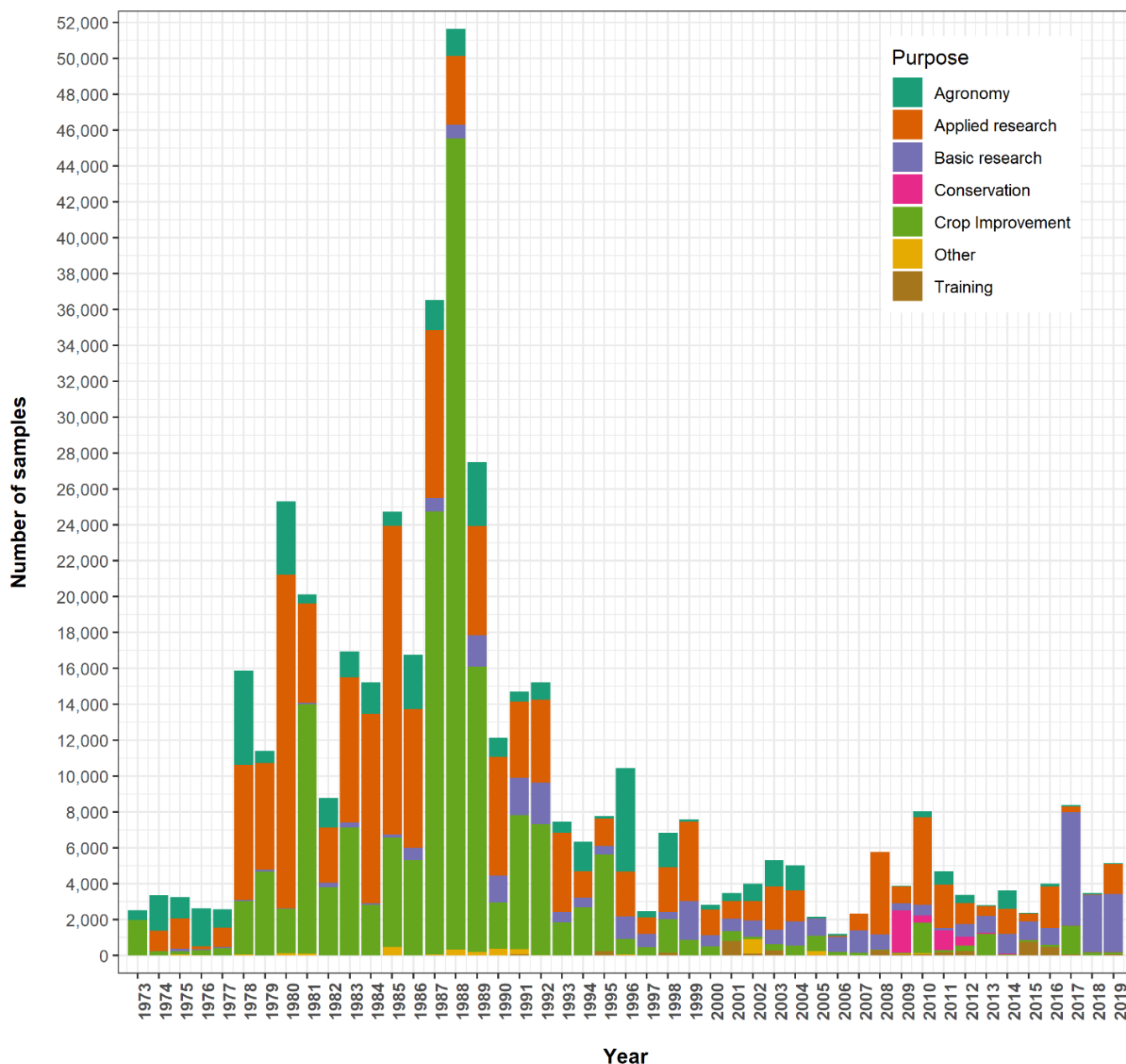
**Figure 3.** Number of samples distributed in the period 1973-2019. Important recipients were the Bean and Biotechnology Programs of CIAT, the national agricultural research services (NARS), universities and research institutes.

an undue patent granting (genetically dissected in great detail by Pallottini *et al* (2004)). It is because the in-trust collection was rich in yellow-seeded accessions from Mexico and Peru, and because the CIAT genebank kept past records such as old catalogs of varieties (Hedrick, 1931), it was possible to demonstrate ample prior art, and the patent was turned down in 2008.

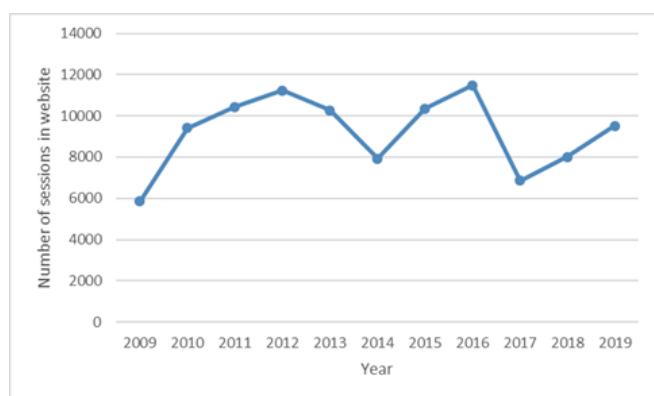
Legumes have been called the 'meat of the poor' (Heiser, 1990) and in many parts of Latin America (e.g. Brazil, Mexico, Cuba) people with low income eat beans daily. Similarly, the highest consumption rates per capita are currently registered in eastern Africa (OECD, 2015). Given this, it was becoming evident that improved varieties should also fight the 'hidden hunger' or the deficiency in minor minerals such as iron and zinc where the diet is not sufficiently diverse. Using the core collection, the evaluation to find accessions with high iron and zinc was expanded (Islam *et al*, 2002), and good sources were identified (G21242, G23818, G23834) (Blair *et al*, 2011), primarily from the Andean region. Nothing on the seed aspect indicates high values in these micronutrients. Likewise,

G14519, an old landrace named 'Hickman Pole Bean' from the United States and belonging to the Mesoamerican gene pool, also has shown potential (Blair *et al*, 2010). From the start, the genebank had interest in assembling variation for any future need, and this is precisely the wide scope that made biofortification possible thirty years later and with a lasting impact where it is today most needed, e.g. in East Africa (Sellitti *et al*, 2020).

With changing context of bean production over the last forty years, for example, common bean being pushed towards the west in the Plains of the USA or in the Canadian prairie, the northwest in Mexico and the northeast in Brazil (Singh, 2001), new challenges like drought, cold, heat or low phosphorus are set for breeding. Some drought tolerance can be found in the 'Durango' race (Singh, 2007; Beebe *et al*, 2013), in other landraces such as G21212 (Beebe *et al*, 2008) and in wild forms (Cortés and Blair, 2018). Root architectural and physiological traits identified in an Andean landrace, G19833, may contribute to phosphorus acquisition (Beebe *et al*, 2006).



**Figure 4.** Number of samples distributed annually to users in the period 1973-2019, according to the purposes of requests.



**Figure 5.** Number of consultations of the CIAT genebank website (<https://ciat.cgiar.org/what-we-do/crop-conservation-and-use/>) in the period 2009-2019.

The impact of the bean germplasm collection has also been through the direct adoption of genebank accessions by farmers after the screening of international nurseries. No less than thirty-four accessions have been registered in national catalogs of varieties in thirty-eight countries in 1974-1999 (Voysset-Voysset, 2000), or 13% of the total of improved genetic materials distributed by CIAT. This figure may not look impressive, but bean varieties produced by breeding have been released in the same geographic areas since the 1940s. That said, it is anticipated that apart from the use of landraces for specific niche markets (see popping beans below), for specialized studies for example in pathology (e.g. disease differential sets) or for servicing gardeners, a significant coming impact of genetic resources will materialize through libraries of genetic stocks (van



Treuren and van Hintum, 2014), targeted diversity panels (Cichy *et al.*, 2015; Moghaddam *et al.*, 2016), and sequence tagged traits (Lobaton *et al.*, 2018). But in order to allow the ‘molecular’ breeder to do advanced searches throughout the collection substantial changes must be brought to databases (McCouch *et al.*, 2012; Byrne *et al.*, 2018). Learning from experience, the design should be for use by non-database experts, modular and scalable, moving from passport data into accession traits and ending into annotated genes. Somehow, this focus re-emphasizes the role of genebanks as keepers of the primary genetic variation, and perhaps less of all allelic combinations of that variation (i.e. the sister lines of simple crosses), since tools now exist to recombine that variation to better meet human needs or agricultural contexts (towards precision agriculture for instance). Appraising that variation by curators might be difficult (what should be kept in the genebank remains a cornerstone and recurrent question), although they will be helped by sequence information. From a pragmatic perspective genebanks may keep interest in old landraces since these have been tested over long durations in farmers’ fields. For similar efficiencies in breeding, genebanks might be interested in keeping recombinants between gene pools, for example from southern Europe (Gioia *et al.*, 2013), part of the Guarani area in Brazil (Burle *et al.*, 2010) or the northern Andes (Chacón-Sánchez *et al.*, 2021), especially if they represent novelties in agronomic or nutritional attributes.

### The other impact: the contribution to knowledge

The in-trust collections, because of the open access set forth by FAO in the early years and then the facilitated access approved by the parties to the International Treaty (FAO, 2002), have helped increase knowledge in many fields of biological sciences (Dudnik *et al.*, 2001). Conversely, the increased knowledge contributed tremendously to the efficiency of the breeding and varietal deployment efforts. This was particularly applicable to the mandate crops of CIAT, since with the exception of rice, not much basic biology and genetics was known in the late 1960s when crop improvement efforts were launched. For instance, the ancestry of common bean became firmly established at a time not far away from the founding of CIAT (Burkart and Brücher, 1953; Gentry, 1969). The double domestication of common bean became obvious only in 1986 (Gepts *et al.*, 1986), and that of Lima bean in 1989 (Debouck *et al.*, 1989), and the existence of a fifth case of domestication in the genus was clarified as late as 1991 (Schmit and Debouck, 1991)!

Such increased knowledge also helped to better define what should be conserved in genebanks; for example, studies on the founder effect due to bean domestications have stressed the importance of wild forms for accessing the total genetic diversity of three bean crops (Sonnante *et al.*, 1994; Martínez-Castillo

*et al.*, 2015; Mina-Vargas *et al.*, 2016). As expected, that founder effect was less marked in the scarlet runner (Guerra-García *et al.*, 2017). That knowledge also helped in the development of disease indexing methods for the safe movement of germplasm (Kumar *et al.*, 2021). Some examples are provided in Table 3 (by tracking accessions distributed in 1973-2019). The breadth of disciplines, evidenced by the diversity of peer-reviewed journal titles and linked to genebank accessions, is striking but just reflecting the diversity of the collection. No less important are the opportunities of scientific collaborations around ‘problems’ set up by the bean crops and materials provided by the genebank, as reflected by the institutions and countries of authorships.

### Knowledge often overlooked, although associated with crop germplasm for millennia

Because germplasm collections were assembled at CIAT primarily in relation to breeding, traditional knowledge associated with specific accessions was rarely documented. As the first phase of breeding was focused on resistance to diseases and pests, with systematic inoculation of known strains, there were often no incentives for a time-consuming effort to document vernacular names, culinary and other folk practices. One such example is that of popping beans consumed toasted (National Research Council, 1989). That group of landraces still exists in the Andes, from Cajamarca in Peru down to Chuquisaca in Bolivia (Tohme *et al.*, 1995b). Elder farmers in the countryside will tell which variety can pop, while migrants to urban areas one generation after will simply process them all in water cooking, even with a slight increase in digestibility (van Beem *et al.*, 1992). Documenting this property by the genebank is doubly important. First, consumer preferences change over time (Voysest-Voysest, 2000) and, in contrast to the 1960s, there is a renewed interest nowadays in local gastronomy that can provide a better income to mountain farmers (Zimmerer, 1992). Second, water and fossil energy might become expensive inputs to food processing or transportation, as it is still the case in many parts of rural eastern Africa. In pre-ceramic times in the Andes, these two inputs (excepting fire) were either difficult to carry or to access. Producing a hot surface with the help of solar energy might not be an excessively difficult or expensive technology to implement in the Andes or in eastern Africa. In altitude, this kind of germplasm and the unique way to make it ready for human consumption may also contribute to reduce deforestation for fuel wood, while montane forests usually occupy a small acreage (National Research Council, 1989). Finally, it is worth noting that this group has a high number of phaseolin types (Tohme *et al.*, 1995b), indicating a high diversity in contrast to other Andean landraces (Beebe *et al.*, 2001). Evaluation of popping beans is continuing in Peru (Cruz-Balarezo *et al.*, 2009) and Colombia (Otálora *et al.*, 2006), while

**Table 3.** Examples of impact of CIAT bean in-trust collection for the advance of knowledge.

Field	Output, problem solved	References
Botany	new species described	Salcedo-Castaño <i>et al</i> (2011)
Plant taxonomy	taxonomic status of bean species re-assessed	Schmit <i>et al</i> (1996)
Agricultural botany	review of the genus and species	Freytag and Debouck (2002)
	founder effect of bean domestication	Schinkel and Gepts (1988)
Crop evolution	definition of a 3 <sup>rd</sup> gene pool in Lima bean	Motta-Aldana <i>et al</i> (2010)
Phylogeography	fifth case of domestication in the genus	Schmit and Debouck (1991)
Plant breeding	recombination between gene pools	Gioia <i>et al</i> (2013)
Plant pathology	past trans-isthmic migrations of wild bean	Chacón-Sánchez <i>et al</i> (2007)
Plant virology	gene pools/ races of common bean defined	Singh <i>et al</i> (1991a)
Entomology	inheritance of ANT/ALS resistance genes	Gonçalves-Vidigal <i>et al</i> (2011)
Plant genetics	coevolution of ALS in bean gene pools	Guzmán <i>et al</i> (1995)
	resistance to Clover yellow vein virus	Hart and Griffiths (2014)
Plant biotechnology	resistance to bean bruchids	Cardona <i>et al</i> (1990)
	resistance to bean weevil	Kamfwa <i>et al</i> (2018)
Plant physiology	common bean genomic map	Schmutz <i>et al</i> (2014)
	common bean genome history & evolution	Rendón-Anaya <i>et al</i> (2017)
Plant root physiology	inheritance of pod dehiscence	Parker <i>et al</i> (2020)
	inheritance of leaf mutation	Garrido <i>et al</i> (1991)
Plant microbiology	genetic transformation in tepary bean	Dillen <i>et al</i> (1997)
	flowering response to daylength	White and Laing (1989)
Human nutrition	identification of phosphorus-efficient genotypes	Beebe <i>et al</i> (1997)
	low phosphorus tolerance in bean	Rao (2001)
Archaeology	variation in photosynthetic activity	Lynch <i>et al</i> (1992)
	tolerance to NaCl salinity in early growth	Bayuelo-Jiménez <i>et al</i> (2002)
Intellectual Property Protection	coevolution of <i>Rhizobium etli</i>	Aguilar <i>et al</i> (2004)
	content in micronutrients such as iron	Beebe <i>et al</i> (2000a)
Intellectual Property Protection	phaseolin type and digestibility	Montoya <i>et al</i> (2008)
	crop domestication and ancient diet	Piperno and Dillehay (2008)
	rebuttal of an undue crop utility patent	Pallottini <i>et al</i> (2004)

the inheritance of the trait is being investigated (Campa *et al*, 2011; Yuste-Lisbona *et al*, 2012).

### Serving the breeders community and beyond

As shown in Figure 3 and Table 3, distribution has been significant to a high diversity of users, going beyond CIAT breeding activities in Colombia and in eastern Africa. The trend that in some countries dry bean consumption is declining (Khoury *et al*, 2014) (contradictory to health and global environment benefits: Foyer *et al* (2016) may mean fewer requests for that kind of germplasm but an increased interest into snap bean, often of Andean origin (Myers and Baggett, 1999). With the development of urban gardening, snap bean might be on the rise, either through the planting of old heirloom varieties (Kaplan and Kaplan, 1992; Zeven, 1997) or new ones. In CIAT, the priority was on dry bean, little on snap bean for the tropics, but with possibilities of using a wide range of resistance sources developed for the former commodity (Silbernagel *et al*, 1991). The changing fate of the popping beans, even

in countries of origin over the last forty years, shows the ever-changing nature of markets. Thus, examples of unpredictability abound, indicating for the genebank to focus on diversity *per se*, independently from immediate and local interests.

This example of success brings a strong message to focus scarce resources, at a time when there is risk of repeating previous work because many disciplinary continuums have been broken. Thus, it seems of paramount importance to document at accession level what is already known: phaseolin type, alleles of allozyme, RAPD markers, SCARs, SSRs, also evaluation data (trait, location, strain as applicable). Individual accessions should be linked with references and supporting documents. Keeping in mind that one third of the collection has not been evaluated, there is still a lot of work for pathologists, entomologists and virologists. Evaluations were done on up to 23,000 accessions only for anthracnose, angular leaf spot and common bacterial blight; for the other limiting pests the figures are much lower (Hidalgo and Beebe, 1997). The reaction should be reported at each accession level, and not restricted to the best performers. Evaluation

should obviously capitalize on knowledge generated by previous protocols. For example, on bruchids, it is likely that evaluation of the rest of cultivated common bean germplasm will lead to nowhere (van Schoonhoven and Cardona, 1982), because domestication occurred elsewhere (Chacón-Sánchez *et al.*, 2005; Bitocchi *et al.*, 2013; Kwak *et al.*, 2009). But the right arcelin can be picked by screening for the protein or the gene(s) involved instead of testing thousands of accessions in contact with the insects.

From previous experience, it seems likely that genebanks will face periodic shortages in skilled, highly specialized staff (a challenge also mentioned by Fu (2017). This is a recurrent limitation for germplasm evaluation (thus resulting in limited use of the collection in the future). Sending the core collection or more accessions abroad for specialized evaluations is an option, although perhaps not as fast as having it evaluated by a multidisciplinary team as done at CIAT in the 1970s. Incidentally, blocks of resistance genes (Gonçalves-Vidigal *et al.*, 2020) that can be traced by molecular markers are giving an unexpected support to that approach. But in view of complex traits such as heat or drought tolerance, for which just a fraction of the entire collection has been evaluated, multi site evaluation of thousands of accessions seems extremely time-consuming and expensive. New evaluation schemes have to be designed and are a true challenge at the organ level (Zhao *et al.*, 2019), but not impossible when focused for example on pulvini-caused movements of leaflets in relation to solar radiation avoidance (Thomas *et al.*, 1983).

For location-related abiotic stresses, geographical approaches (targeted towards the surviving germplasm where the stress has been present for thousands of years, and thus logically the wild forms) may help. But these GIS approaches did not pick up outstanding wild forms under low phosphorus stress (eighteen accessions tested, Beebe *et al.* (1997), while there seems some promise for drought tolerance (eighty-six accessions tested, Cortés and Blair (2018). Internally, these approaches requires the genebank to be strict on passport data accuracy (van Hintum *et al.*, 2011). However, this is not always possible; for example, accession G40001 with promise for heat tolerance is from a market in Veracruz (Suárez *et al.*, 2020). Given some intrinsic limitations of common bean, coming heat and drought stress in the tropics and subtropics (Battisti and Naylor, 2009; Beebe *et al.*, 2011) may be the opportunity to re-balance the collection towards the tepary and Lima bean, more hardy crops in this regard (Freeman, 1913; Rachie, 1973), respectively). Eventually, bean breeders may realize that they have five crops instead of one, each one with a different ecological head start (Debouck, 1992). With the advances in marker assisted selection and genetic maps, it might be faster to correct a shortcoming in seed or growth habit in tepary than expecting the common bean to fully change its ecological background.

## Discussion

The afore-mentioned facts suggest the following points for discussion. **First**, one can ask whether this bean germplasm collection meets the expectations for which it was established. Many sources of disease resistance were found (Table 2), and one should note that in many cases the findings were unpredicted, and largely independent of geographic origin or gene pool. As well noted by Harlan (1978), page 351 “resistance is where you find it”. For those diseases where no good sources of resistance have been found, in the light of a similar experience with the USDA collection (e.g. the case of white mold: Schwartz and Singh (2013), it seems more a deficiency of the common bean crop species itself than a severe lack of representativeness. Thus, the breeders turned logically to the wild forms and the secondary gene pools (Debouck, 1999), where the collection provided some solutions but also means for the needed preliminary studies in taxonomy and wide crossing. This links with a **second** point: given the above evidence of return on investment and incompleteness of the task (Hidalgo and Beebe, 1997), it might be important to continue with evaluation, namely for abiotic stresses such as drought or heat caused by global warming, as these will impact on yield (Lobell and Gourdj, 2012; Beebe *et al.*, 2013). In view of the numbers of accessions and facing the need for developing novel evaluation schemes for abiotic stresses including a network of well characterized (climate, soil) experimental plots, it might be cost effective to cooperate with other bean germplasm repositories (e.g. Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Tepatitlán, Mexico; Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany; USDA, USA). Incidentally, this cooperation might also include a reciprocative safety backup and the development of a novel database because it is a shared concern. **Third**, to the question whether the genebank has made any impact, the answer came from bean breeding but also many actors in the global community. The figures of germplasm distribution for applied and basic research (Table 3 and Figure 4) have shown a vibrant research community worldwide adding value to the collection. They invite the genebank to a permanent capacity to respond to requests (because of the ‘on-line shopping syndrome’) but also to document these impacts. The question whether the collection will make any impact in the future should also consider technological innovations such as transgenesis and gene editing (e.g. using CRISPR-Cas9) (Doudna and Charpentier, 2014). These approaches of genetic engineering bring new light on using diversity, as they have the potential to add a new function such as herbicide tolerance or improve an existing one, such as seed protein quality, beyond the trait offer of the primary gene pool (Gepts, 2002). Transformation in common bean has proven to be particularly difficult (Jacobsen, 1999), and with limited success (Aragão *et al.*, 1998, 2002; Estrada-Navarrete *et al.*, 2007). Transformation seems

quite possible in tepary bean (Zambre et al, 2005), but apparently little exploited for tepary improvement. The CRISPR technology in soybean aims at editing genes involved in a biosynthetic pathway for seed oil quality, for herbicide tolerance, or changing photoperiod sensitivity (Bandyopadhyay et al, 2020; Xu et al, 2020). New technologies will continue to appear, but under currently available evidence and costs they seem likely to contribute to a wider and/or faster use of the collection rather than to replace it. **Finally**, in this context, in order to continue to meet the broader expectations of human societies, the genebanks should fill gaps which were identified early on, in terms of geography, e.g. the northern Andes: (Hidalgo and Beebe, 1997; Beebe and Debouck, 2019); or in terms of biological coverage (Ramírez-Villegas et al, 2010, 2020). Wild forms and wild species should thus be better represented in the collection, with due consideration to the regeneration capacity and disclosure of the potential. There are two points here: first, given the possibilities opened by comparative mapping in the Phaseoleae (Schmutz et al, 2014; Vlasova et al, 2016; Garcia et al, 2021; Moghaddam et al, 2021) and by gene editing (Bhatta and Malla, 2020; Ku and Ha, 2020), it may be time to think beyond direct interspecific hybridization for the use of alien germplasm. In that sense, species of clade A that may represent half of the genus (Delgado-Salinas et al, 2006; Porch et al, 2013; Debouck, 2021) may be opportunities of genes to imitate and/or to regulate differently instead of genes to transfer. But given the speed of the technological development in breeding (Hickey et al, 2019), the action should be initiated now with the most threatened habitats (Williams et al, 2007), species (Goettsch et al, 2021), or unpredictable conditions, or time-consuming work. This leads to a second point, as forsaking millenary crops (Mamidi et al, 2011) does not improve humankind's food security. The four other bean crops mean four more opportunities for plant breeding. Following the diversity criteria prevailing during the establishment of the common bean collection, similar efforts should be carried out for these bean crops. The change experienced by soybean from an oriental soy sauce in North America in 1767 into an animal feeding and agro-industrial crop in just one hundred years (Hymowitz and Bernard, 1991) is a strong message to not lose options. Along the concept of a societal insurance provided by crop genetic resources (Gepts, 2006), keeping more crops alive goes in line with productive, sustainable and locally adapted agriculture and, as a consequence, with reducing rural poverty and increasing appreciation towards indigenous cultures. More than ever before, genebanks should continue to be the reserve of all options.

### Concluding remarks

Figure 1 presented breeding challenges in Latin America in a time sequence, which were largely met by use of genetic resources assembled and evaluated over

the last fifty years. The same germplasm collections allowed inheritance studies and the improvement of bean breeding methods, when looking for combining ability, tolerance to abiotic stress or tagging a resistance. The coming storms in areas of bean production (e.g. increased demand due to demography in eastern Africa, extinction of crop wild relatives in Mesoamerica, drought in 60% of bean growing areas worldwide) are resetting the timing to meet all breeding challenges at once and soon, but they also involve the genebanks to have the genetic solutions ready on the shelf or on the screen (or both). The contributions of the bean collections to advance knowledge on the nature, structure and evolution of *Phaseolus* genetic resources can now help the genebanks to check two extinctions: the extinction of populations in the wild, and the extinction of knowledge about cultivated diversity. Buying time on these two fronts will be difficult for genebanks, but the continuing improvement of conservation methods and efficiencies will contribute to find and enable the human talents for these daunting tasks. The above history shows many ways forward to ensure global food security in uncertain times.

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### Author contributions

DGD conceptualized and wrote the paper. DGD collated the data about use and impact for the first period of the genebank, while MS covered the most recent period. LGS compiled the data about germplasm distribution. MS and LGS re-checked the data of accession numbers. All authors read, revised and approved the manuscript.



## Conflict of interest statement

The first author has been responsible of CIAT genebank, as Head of the Genetic Resources Unit (1996-2009) and as Leader of the Genetic Resources Program (2009-2016), with over seventy Staff members operating in five experimental stations and three labs, for three germplasm collections (bean, cassava and tropical forages) of over 67,000 accessions. The second author has been responsible for all genebank operations in 2017 to date, which include the regeneration of bean and tropical forages collections in the experimental stations and the conservation in the labs. The third author has been responsible since 2009 for all operations related to seed conservation of the bean and tropical forages collections, which include germplasm distribution.

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