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RESEARCH

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Developing country demand for crop germplasm conserved by the U.S. National Plant Germplasm System

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Abstract

Background: Future food production depends on the availability of crop varieties with more resistance to pests and diseases, temperature extremes, irregular moisture, and saltier soils. Plant breeders will need diverse germplasm to create improved varieties, especially in developing countries. The U.S. National Plant Germplasm System (NPGS) supplies germplasm to users worldwide.

Methods: To assess the demand for NPGS germplasm, we used: (1) distribution data from the Genetic Research Information Network; and (2) information collected directly from recipients of NPGS materials. Data collected included user characteristics, types of germplasm requested and received, the purpose of requests, the usefulness of materials received, and expectations for future use.

Results: For ten major crops, the NPGS distributed approximately 100,000 samples to users in developing countries during 2011–2015. NPGS germplasm ranged from final cultivars to crop wild relatives. These respondents requested proportionately more cultivars than are present in the NPGS. In developing countries, nearly all samples were received by scientists (98%). The most frequent purpose for requesting samples was basic research, followed by adding to collections, evaluating for specific traits, and breeding/prebreeding. These respondents found 38% of samples useful in breeding or in other ways. Another 38% of samples were still being evaluated. Previous research indicates the usefulness of samples is partially dependent on the data accompanying them. Compared with results from an earlier study, more samples had useful data. Finally, 64% of respondents in developing countries expected their use of the NPGS to increase, while only 8% expected their use to decrease.

Conclusions: The NPGS supplies significant amounts of crop germplasm to developing countries. The use of NPGS samples for basic research increased in developing countries. These respondents found more samples useful than those from an earlier study. NPGS samples were more likely to have useful data than in the past, which may enhance their usefulness. Finally, respondents in developing countries were more likely than other users to expect constant or increasing use of NPGS germplasm, underscoring the importance of NPGS materials for developing countries.

Keywords: Genebank, Crop diversity, Climate change, Plant genetic resources, Plant breeding, Agricultural productivity, Food security, Developing countries, Germplasm exchange, National Plant Germplasm System

Background

Genetic improvement is used to adapt varieties to meet production challenges, maintain farm profitability, and deliver affordable, nutritious food (Reynolds and Ortiz 2010; Byrne et al. 2018; Khoury et al. 2021). Crop varieties are developed to resist biotic (or living) stresses such

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Fig. 1 Centers of origin for selected crops

as pests and diseases. Because pests and disease evolve, the yield of a variety will decline over time without new sources of resistance. Therefore, readily available diversity is needed simply to maintain current yield levels. Climate change is expected to exacerbate pest and disease pressures (Galluzzi et al. 2020). Likewise, as overall temperatures rise and farmers see increased extreme weather events, crops will also need greater tolerance to temperature, moisture, and salinity stresses (termed abiotic stresses, i.e., not caused by living organisms). Other desirable attributes include improved yield and quality (such as properties desired by consumers or processers). Developing countries are likely to face the most extreme effects of climate change (Reynolds and Ortiz 2010).[1] Because available arable land is limited, increasing the yield and adaptability of crop varieties will be required to meet global food demand (Bohra et al. 2021).

All crops descend from wild and improved genetic resources (also called germplasm). The term "center of origin" refers to the area in which a crop was originally domesticated (see Fig. 1). Genetic diversity is often highest near those centers. Countries and international research centers routinely exchange germplasm because no nation has the desired spectrum of genetic resources within its borders. The international exchange of plant genetic resources (PGR) increased global food security (Mekonnen and Spielman 2018).

Facilities for ex situ conservation, such as genebanks, are the most cost-effective way to conserve large quantities of PGR (Li and Prichard 2009). Moreover, they provide materials that are more accessible to breeders and other crop scientists than those held in situ. According to the U.N. Food and Agricultural Organization (FAO 2010), in 2010, there were 1750 genebanks worldwide, many of them national genebanks. PGR conservation has "public goods" components (Fu 2017). Public goods have two classic characteristics: non-rivalry (use of a resource does not reduce the amount available to others) and non-excludability (others cannot be prevented from using a resource once it is made available). PGR are easily transported and replicated; it can be difficult for an individual country or firm to exclude others from their use (especially in the absence of enforceable intellectual property laws). Many PGR are not eligible for any intellectual property protection. As a result, research discoveries often "spill over" to other scientific enterprises. This lack of exclusivity reduces returns to investment, thus reducing the incentives for a company to conserve PGR. Moreover, the conservation of PGR requires capital to construct facilities to house materials and sufficient funds for the initial acquisition of germplasm, long-term

[1] For this study, development status was based on *World Development Indicators* from the World Bank (2018), which used Gross National Income. Only high-income countries were classified as developed. See Additional file 1 for more details on development status designations.

storage, regeneration, and viability testing. Savings are sizable when facilities are centralized and excessive duplication is avoided (Koo et al. 2004). Many developing countries cannot afford to create national collections containing all the germplasm they may need now and in the future; therefore, they rely on outside sources.

We conducted a case study of one such source, the U.S. National Plant Germplasm System (NPGS), a collaborative network of collections holding 600,000 living accessions[2] of genetic resources of 43 crop groups. (Accessions are uniquely-identified seeds or plant material conserved in a genebank; samples are reproduced accessions used for distribution.) The NPGS has a five-fold mission: (1) acquiring crop germplasm; (2) conserving crop germplasm; (3) evaluating and characterizing crop germplasm; (4) documenting crop germplasm; and (5) distributing crop germplasm.[3] The accessions range from improved crop cultivars currently produced to the undomesticated ancestors of crops. NPGS maintains highly detailed data using the Germplasm Resources Information Network (GRIN). The NPGS is the largest distributor of PGR globally (Byrne et al. 2018; Lusty et al. 2021). Over the past decade, the NPGS distributed approximately 250,000 samples of accessions yearly within the U.S. and internationally (Bretting 2020). The researchers, breeders, germplasm managers, and college-level educators who use the system receive samples free of charge from the NPGS. (For the most part, PGR are shipped without charging users for transport costs, unless the user requires rapid distribution via a courier service.) The NPGS provides PGR directly and through the multilateral system of the International Treaty on Plant Genetic Resources for Food and Agriculture, which governs the exchange of a selected group of crops.

For developing countries, the NPGS is by no means the only source of PGR. Some of the most important genebanks are the 11 collections of the CGIAR (Galluzzi et al. 2020).[4] Unlike the NPGS, the CGIAR genebanks are part of an international research system not located in a single country. More than 750,000 accessions are held in these genebanks for 25 crop and tree species. In addition to its genebanks, the CGIAR operates breeding programs. Some of these institutions, particularly the earlier ones, were founded with the explicit goal of crop improvement. Genetic resources flow from the genebanks directly and also as improved products of breeding efforts. The genebanks distributed roughly 1.1 million samples during 2010–2019 (Halewood et al. 2020).[5] Approximately 58% were sent to external users (46,000 in 2019, 38,000 of which were distributed to developing countries). Halewood et al. (2020) said CGIAR breeding programs distributed an additional 66% of samples. While the NPGS is the focus of this paper, we will note the role of CGIAR genebanks when relevant.

Gollin (2020) stated that one of the most constructive uses of economic techniques is to inform the prioritization of genebank functions. Because NPGS resources are such a critical input into the improvement of crop varieties, it merited a systematic assessment of demand for its resources. Yet, while NPGS distributions of materials rose in the past 20 years, and it has managed a growing collection, funding overall has been largely stagnant in real terms, i.e., corrected for inflation (Bretting 2020). Moreover, the literature suggests that scientists increasingly use PGR for research purposes rather than as direct inputs into breeding programs (Gollin 2020, Lusty et al. 2021). Khoury et al. (2010) said more diverse materials might be of special interest to researchers, genebank managers, and other users.

To better inform genebank managers and policymakers who must allocate scarce resources (Fu 2017; Bretting 2018), this paper characterizes recent and potential future demands for NPGS resources. To do so, we investigated who uses NPGS samples, the intended purpose for the materials NPGS users received, and the usefulness of those materials. The primary question we will address is how the developing world used the NPGS's germplasm.

Because the improvement level of PGR affects how they are used and the length of time they need to be assessed, we evaluated the types of materials demanded (Lusty et al. 2021). Generally speaking, materials that have been selected using post-Mendelian methods are easier to incorporate into breeding programs because breeders have used generations of parental crosses to remove undesirable traits (Khoury et al. 2010; Galluzzi et al. 2020). Less improved materials, such as landraces and wild relatives, often have polygenic traits that may reduce yield and include characteristics less suited for final varieties (Byrne et al. 2018). However, this material is more diverse than modern varieties and lines. Crop wild relatives can be the most diverse germplasm type (Dempewolf et al. 2014). Therefore, while more challenging to incorporate into final varieties, these materials can have considerable benefits, especially as sources of tolerances to biotic and abiotic stress (Khoury et al. 2010; Galluzzi 2020).

[2] The NPGS also holds thousands of "inactive" accessions that exist as data only, mostly early ex situ material that was lost over the decades.

[3] The NPGS is managed by USDA's Agricultural Research Service, with additional support from universities and state agricultural experiment stations.

[4] Formerly the Consultative Group for International Agricultural Research.

[5] Some of these transfers were through repatriation programs.

Another factor affecting both the demand for and the usefulness of genebank material is whether it includes data about accession itself. For example, NPGS samples can be accompanied by passport information (e.g., species name, country of origin, acquisition date), characterization (morphological and molecular), and evaluation data. The presence of such data varies by accession, i.e., a widely utilized accession may have all of this information, whereas there may be very little data for accessions of the "unknown" type. Gollan et al. (2000) demonstrated that better information about accessions can speed up the process of searching a genebank for desired traits.

In the past two decades, technologies to manage and utilize PGR management have changed significantly. Bretting (2018) said that innovative networks of PGR managers and users have stimulated innovation in PGR distribution. For example, a PGR requestor in Africa can now use a mobile device to search for and request samples through GRIN. Historically, phenotyping (that is, assessing the physical properties of genetic resources) was a lengthy process, but now the use of genomic methods can speed the discovery of physical traits (Swarup et al. 2021; Lusty et al. 2021; see also Gollin 2020). Gene editing allows a breeder to change a single gene related to a desirable trait, without the problems associated with wider crosses of PGR (Lusty et al. 2021). Halewood et al. (2018) described an "ongoing revolution" in applying big data to the use of PGR. Genomic data allows users to search for materials with desirable traits.

Climate change is likely to increase demand for genetic diversity (Dempewolf et al. 2014; Galluzzi et al. 2016, Fu, 2017; Lusty et al. 2021; Swarup et al. 2021). Developing countries may face disproportionate challenges from the effects of changing climates, increased population, and shifting dietary consumption patterns (Galluzzi et al. 2020). More diverse genetic resources expand options for scientists developing varieties adapted to a broader range of conditions (Cox et al. 1988; Swarup et al. 2021; Khoury et al. 2021). Lusty et al. (2021) stated that because future challenges are so unpredictable, there is latent demand for PGR in developing countries. Dempewolf et al. (2014) said that finding sufficient temperature tolerance will be particularly important for African countries. Therefore, we explored what resources scientists expect they will need in the future from the NPGS.

Methods

The primary source of information on the use of the NPGS system is produced by the National Germplasm Resources Laboratory (NGRL) using the GRIN information management system. The NGRL records each sample distributed from the NPGS. Such records include the accession requested, the date and volume of the distribution, the institutional affiliation of the user (e.g., public or private), their locations, and the type of material requested (i.e., the improvement level). These data allow us to establish who uses the germplasm, their location, and what types of material they use, but they only capture broad reasons for requests and do not indicate whether the users found samples useful. To answer these and related questions, we collected information directly from users.

There is precedent for collecting this information.[6] In 2000, the U.S. Department of Agriculture, led by the Economic Research Service, cooperated with the CGIAR's International Plant Genetic Resources Institute (IPGRI, now called Bioversity) and Auburn University to conduct a case study on demand for NPGS resources (Smale and Day-Rubenstein 2002; Rubenstein et al. 2006). Two sets of data were used in this case study, covering 1995–1999. A five-year period was chosen because Widrlechner and Burke (2003) found it important to use more than a single year of germplasm distribution data because of short-term fluctuations in demand. First, distribution data for ten major crops were obtained from GRIN. The crops were barley, cotton, maize, potato, rice, sorghum, soybeans, and wheat (the most economically important row crops in the United States).[7] In addition, beans and squash, two crops originating in the Americas, were included by IPGRI. Second, a mailed census instrument collected data from end-users of the NPGS's resources for the same ten crops, including the characteristics of NPGS users, the types of germplasm requested, the purpose of requests, the usefulness of samples received, the presence of useful data, and expectations for future use.

In 2018, we revisited the census of 2000. Again, we used two sets of data. As in the first case study, the first source of data for this case study was information for the ten original crops distributed during the five-year period of 2011–2015, provided by the NGRL using GRIN. For the second, we collected information from users who received samples from the NPGS via the Census of Users of the National Plant Germplasm System of 2018. We based this new census on that of 2000 as much as possible, using a nearly identical questionnaire so that we could compare the two periods of germplasm use and measure changes in demand for NPGS resources over time. The 2000 study used a mailed survey instrument. Postage for replies from international users could not be prepaid, and some international respondents did not

[6] Other related research includes Halewood et al. (2020), who surveyed CGIAR genebank managers about acquisitions between 2010–2019. Galluzzi et al. (2020) surveyed plant breeders in 19 developing countries about their use of PGR in the face of climate change.

[7] USDA categorizes alfalfa as a forage crop.

receive their invitations before the deadline to respond. The response rate for developing countries was relatively low. Therefore, in 2018 we used an electronic survey for the new census. The invitation was sent under the auspices of the NRGL, an entity familiar to users. A web-based instrument asked ten questions. Seven questions covered the respondents' experiences with each crop they requested, one question addressed their expectations about the future use of the NPGS, and two questions asked the respondents' professions and institutional affiliations. Some users requested multiple crops from the NPGS; others only a single crop.

To define the population of users from 2011 to 2015 for these ten crops, we initially adopted the NPGS institutional categories to classify individuals. The NPGS assigns each user of the NPGS one of the following institution categories:

U.S. institution categories

- Public
    - State Agricultural Experiment Stations and universities
    - USDA Agricultural Research Service
    - Federal agencies
    - Non-profit organization
- Commercial companies
- Individuals not assigned an institutional category, though these could provide an organizational affiliation

International institution categories

- Public
    - Universities and other non-profit organizations[8]
    - National genetic resource programs or genebanks
    - CGIAR research centers
- Commercial companies
- Individuals not assigned an institutional category (though again, these could provide an organizational affiliation)

The population consisted of users whom the NPGS classified as having an institutional affiliation and unaffiliated individuals who listed an institutional affiliation. Some unaffiliated users, such as gardeners and elementary school educators, received PGR even though they were not conducting research, breeding, or scientific education (Gerwin 2017). Many of these did not include institutional affiliations. Users are now screened more rigorously. Because the inclusion of these unqualified users would bias our assessment of legitimate demand for NPGS materials, unaffiliated users who did not provide an organization or institution were excluded. We used email addresses as an identifier for each user because it allowed us to combine users' requests across multiple years. The population included users of the ten crops with an email address. All members of the population were sent an invitation from the NGRL via SurveyMonkey, along with a unique link. A total of 5347 invitations were sent. The initial invitation was followed by three reminder messages containing the same unique link.

Respondents were given a list of professions to describe themselves, i.e., acquisition/curatorial activities; pre-breeding/evaluation activities; breeding; genetics/molecular biology; education; farming; or other. This was the only question that differed substantially from the version used in the 2000 census instrument because it added "genetics/molecular biology" as a profession. (The options offered on the 2000 instrument were breeding, acquisition activities, evaluation activities, education, farming, and other.) Respondents who selected "other" supplied text answers further describing their profession. Using these text answers, we classified the professions as follows:

- Acquisition/curatorial activities
- Breeding
- Pre-breeding/evaluation activities
- Genetics/molecular biology
- Scientist, other
- Researcher, other
- Education
- Farming
- Other

The remaining questions were almost identical to the questions asked on the 2000 census instrument.

NPGS germplasm accessions are categorized by improvement level of germplasm (or germplasm "type"). The census instrument used six improvement status categories for the material distributed in 2011–2015:

1. Cultivars
2. Advanced materials

[8] The National Genetic Resources Laboratory (NGRL) classification of international users of NPGS germplasm does not distinguish between international universities and other non-profit organizations in the same way it does for U.S. users.

3. Genetic stocks
4. Landraces
5. Wild relatives of domesticated crops
6. Improvement status unknown

NPGS collections generally use the term "cultivar" to mean a variety that is the product of post-Mendelian breeding. "Advanced materials" are also the result of these breeding efforts. Genetic stocks include mutants, genetic markers, and certain lines used in basic genetic research (Crop Science Society of America 2021). A landrace is a variety developed by farmers' seed selection over many generations. Wild relatives of domesticated crops are uncultivated species, often found near areas where crops were first domesticated.

To better understand what motivates the users of NPGS materials, users were asked how they intended to use the samples they received. Four answers were possible:

- Breeding or pre-breeding
- Evaluation for specific traits
- Basic research
- Add to collection

We included this question because the respondent's profession did not necessarily capture the intended purpose for a sample. For example, while acquisition/curatorial professionals often are associated with genebanks, many breeders maintain their own collections of materials used regularly and add to them. On the other hand, a geneticist or molecular biologist may request an accession searching for a particular trait for use in basic research.

Respondents were asked if the materials they received had been useful. Often, many years are necessary to incorporate traits into a commercial crop breeding program, even when using advanced technologies (Dempewolf et al. 2014; Swarup et al. 2021). We hypothesized that sufficient time had not passed for PGR to be incorporated into a breeding program in many cases. Therefore, the question was not structured as a binomial choice asking whether the material had been useful or not. Rather, respondents could report that samples had been useful in a breeding program, useful in other ways, still being evaluated, or not useful.

Given past findings on the role of accompanying data, we asked what percent of the material received already had (1) useful data for the trait(s) of interest, and (2) other useful data. A mix of answers was possible, i.e., a sample with useful data on the trait of interest could also have other useful data.

Finally, for each crop requested, respondents were asked, "Over the next ten years, do you expect your use of NPGS [crop x] accessions to change?" The possible answers were (1) increase, (2) decrease, or (3) stay the same.

Results

Our analyses of results varied somewhat depending on the question. For some questions, it made sense to concentrate on individual users. For others, it was more informative to base the analysis on a user-crop combination (e.g., a user who got both barley and wheat would be counted twice when analyzing questions of future use). For many questions, the most interesting analysis was the numbers of samples represented by particular responses because these numbers were most relevant to assessing current and future demand for NPGS germplasm.

Of the 5347 email invitations sent, 536 were not delivered because the email address was either terminated or incorrect. A total of 99 users opted out of the census. Both groups are included in the population (See Additional file 2: requestors by development status of country). Of the total population of 5347, 1483, or 28%, of individual users responded to the questionnaire. The response rate rose to 34% when weighted by all samples sent to individuals in the population represented by respondents (230,354 samples). In other words, respondents represented about one-third of all the samples sent to the population of users; respondents tended, on average, to have been sent slightly more samples than nonrespondents. The overall response rate was lower than that of the 2000 census (35%), but this most recent census did capture more developing country respondents (Table 1).

Users of the NPGS system

For the ten crops in the study, administrative data from the NGRL indicated the NPGS distributed a total of 682,973 samples. Roughly two-thirds of the samples were distributed to users located within the jurisdiction of the U.S. and one-third to international users. (See Additional file 3: distribution of NPGS samples by crop). International users in developed countries accounted for 17% of the samples; users in developing countries made up 15% of the samples. More samples went to international users in 2011–15 (217,563 total) than did in 1995–1999, when about 25% of the samples (63,555 total) were distributed to international users.

The census results provided detail about those users who responded to the information collection. The NPGS supplies samples for research, breeding, conservation, regulation, and scientific education. Further classification indicated that most respondents selecting "other" were scientists, such as plant pathologists, entomologists, plant physiologists, and medical researchers. We

Table 1 Response rates by development status of user' country

	Population	Respondents	% of total
By user			
U.S	4010	1004	25
Non-U.S. developed	920	331	36
Developing	417	148	35
Total	5347	1483	28
By samples distributed			
U.S	465,410	153,547	33
Non-U.S. developed	117,029	31,544	27
Developing	100,534	45,263	45
Total	682,973	230,354	34

Source: The Census of Users of the National Plant Germplasm System, 2018

defined scientists as respondents working in acquisition/curatorial activities, breeding, prebreeding/evaluation activities, genetics/molecular biology, and other scientists. Scientists accounted for 72% of respondents from the U.S (728). Among international respondents, 87% of developing country respondents were scientists (289), and 90% of respondents in non-U.S. developed countries were scientists (133). However, because the NPGS now reviews requests more stringently to ensure recipients are qualified to receive materials, these results should be viewed with caution, particularly when estimating the make-up of future recipients (Table 2).

Another method to assess who used germplasm from the NPGS was to analyze the number of samples received by the respondent's profession. Measured this way, almost all of the samples were distributed to respondents who were scientists in research and breeding. For non-U.S. respondents, 98 percent of samples were received by scientists (approximately 75,200). Samples received by scientists made up 97% of total U.S. samples (148,900). Scientists, as a group, requested more samples from the NPGS than non-scientists.[9]

Material requested

The aforementioned NGRL distribution information indicated that, between 2011 and 2015, the NPGS distributed 682,973 samples of the ten crops in our case study. This was an increase compared with the distributions made between 1995 and 1999 (300,317). The most frequently distributed crops were wheat, soybeans, sorghum, and maize, followed by rice, barley, beans, squash, cotton, and potato (Fig. 2).

Developing countries accounted for 15% of the total distribution for these ten crops, in total slightly more

Table 2 Respondents' professions by country development status, 2011–2015

	U.S	Non-U.S. developed countries	Developing countries
	No. of respondents (% of total)		
Acquisition/curatorial activities	13 (1%)	4 (3%)	10 (3%)
Breeding	194 (19%)	36 (24%)	134 (41%)
Pre-breeding/evaluation activities	111 (11%)	23 (16%)	51 (16%)
Genetics/molecular biology	314 (31%)	60 (41%)	85 (26%)
Science, other	96 (10%)	10 (7%)	9 (3%)
Research, other	7 (1%)	23 (< 1%)	4 (1%)
Education	128 (13%)	6 (4%)	34 (10%)
Farming	99 (10%)	5 (4%)	2 (< 1%)
Other	42 (4%)	2 (1%)	2 (< 1%)
Total respondents	1004	148	331

Source: The Census of Users of the National Plant Germplasm System of 2018

[9] Respondents whose primary professions were farming or education did not request as many samples, likely because the issues they were addressing were not as complex as those of scientists.

Table 3 Germplasm types requested by NPGS census respondents 2011–2015

Germplasm type	Requests by all respondents	Requests by respondents in developing countries	NPGS holdings, all crops, 2009
	% of total		
Cultivars	31	29	9
Advanced material	10	10	18
Genetic stocks	11	10	
Landraces	33	23	36
Wild relatives	11	22	15
Unknown/other	4	6	22

Source: The Census of Users of the National Plant Germplasm System of 2018

than 100,000 samples.More than 50% of samples sent to developing countries were wheat (54,771 samples). Rice (12,687), maize (9101), sorghum (6385), and soybean (5918) were the next most frequently distributed crops. Beans, barley, cotton, and squash accounted for less than 5% of distributions. A small number of potato samples (336) were distributed. Including or excluding wheat samples—samples of the crop with accounting for over half the total–from the developing country data did not change our overall conclusions but did change some of the specific estimates related to developing country responses. (Some of these differences are reviewed in Additional file 4: A comparison of wheat with other crops for NPGS users in developing countries.) (Fig. 3).

In terms of improvement level (or germplasm type), landraces were the most frequently-distributed type. Cultivars accounted for 31% of total distributions. When we combine the products of post-Mendelian breeding (cultivars, advanced material, and genetic stocks), they made up 52% of samples requested by all respondents and 49% requested by respondents in developing countries (Table 3).

Census respondents requested proportionately more cultivars than the percentage in the NPGS collections, even though the FAO (2010) reported only three of our study crops had cultivars representing more than 10% of the NPGS collection: beans (21%), barley (15%), and wheat (13%). This phenomenon was particularly pronounced for sorghum, maize, and soybean.

NPGS distributions of landraces were also notable (33%), roughly equivalent in percentage to the percentage of landraces over all NPGS crop collections (36%), though respondents in developing countries requested somewhat fewer landraces (23%). Wheat, barley, and soybean accounted for many of the landraces received by respondents. Other features of note in the NPGS distributions included genetic stocks, which accounted for 62% of all the rice requests, 23% of all the maize requests, but relatively small percentages for many of the other crops. Maize and rice are not only globally important crops but also are important "model systems" for genetic research. Wild relatives accounted for 43% of the NPGS potato distributions, 18% of soybean, and 17% of wheat. Respondents in developing countries requested slightly more wild relatives than the percentage found in NPGS collections for these ten crops.

The purpose of requests

Respondents intended to evaluate 38% of samples for specific traits and to use an almost equal amount (37%) for basic research. Breeding or prebreeding accounted for 13% of samples, whereas respondents intended to add 12% of samples to their collections. Adding NPGS accessions to a collection was cited more commonly by respondents outside the U.S., particularly in developing countries (Table 4).

The purposes of respondents' requests have changed markedly since the 2000 census, (Smale and Day-Rubenstein 2002; Rubenstein et al. 2006). From 1995 to 1999, evaluation for specific traits was the most common purpose for requests, accounting for 62% of samples. Samples intended for breeding/prebreeding and basic research were 13% and 14%, respectively. (Samples to be added to collections were almost unchanged: 12% in 1995–1999 and 11% in 2011–2015.) Both developed and developing countries increased the proportion of their requests to be directed to basic research between the two study periods. Respondents in developing countries increased their use of samples for basic research from 15 to 40%. This result is consistent with the finding that scientists working in genetic/molecular biology received a substantial portion of samples (Table 5).

Utility of materials received

Respondents were asked if the materials they received had been useful in a breeding program, useful in other ways, still being evaluated, or not useful. Overall, respondents found 41% of the materials they received

Table 4 Purpose of requests by development status of the respondents' country, 2011–2015

	Breeding or pre-breeding	Evaluation for specific traits	Basic research	Add to collection	No. of respondents	Samples requested
	Percentages normalized to add to 100%					
U.S	12%	46%	36%	6%	839	214,928
Non-U.S. developed	20%	23%	40%	17%	283	31,363
Developing	13%	18%	40%	29%	119	49,970
All countries	13%	38%	37%	12%	1241	296,261

Source: The Census of Users of the National Plant Germplasm System of 2018

Table 5 Purpose of requests by development status of respondents' country, 1995–1999

	Breeding or pre-breeding	Evaluation for specific traits	Basic research	Add to collection
U.S	12%	68%	12%	8%
Non-U.S. developed	17%	32%	35%	16%
Developing	15%	45%	15%	25%
Transitional[a]	14%	39%	26%	22%
All countries	13%	62%	14%	11%

Source: Rubenstein et al. (2006)

[a] The term "transitional countries" was used in the 2000 Census to refer to the former countries of the Soviet Union and Eastern Europe. Generally, results for transitional countries and developing countries did not differ greatly; we note cases when that was not the case. See Additional file 1 for more information on countries formerly designated as having transitional economies

Table 6 Usefulness of samples requested by development status of the respondents' country, 2011–2015

	Useful in a breeding program	Useful in other ways	Still being evaluated	Not useful	No. of respondents	Total samples received*
	Percentages normalized to add to 100%					
U.S	12%	30%	33%	25%	809	208,913
Non-U.S. developed	16%	19%	36%	29%	285	30,234
Developing	11%	27%	38%	24%	119	48,259
All countries	12%	29%	34%	25%	1213	287,406

[*] as estimated by respondents

Source: The Census of Users of the National Plant Germplasm System of 2018

of 2018

useful either in a breeding program or some other way. Across country classifications, "still being evaluated" was the largest category (34%) (Table 6).

In the 2000 census of NPGS users, respondents stated 23% of the materials received from the NPGS had already been used in a breeding program or had been useful in other ways. An additional 27% was still being evaluated. (Smale and Day-Rubenstein 2002; Rubenstein et al. 2006). Respondents found 50% of materials not useful. Therefore, the percentage of materials found to be not useful declined considerably between 1995–1999 and 2011–2015 (from one-half to one-quarter of all samples). Comparison between respondents in developing countries in 2011–2015 and 1995–1999 were somewhat complicated because respondents in transitional countries (many of which are now classified as developing) found 53% of samples not useful (Table 7).

Data associated with NPGS accessions

The usefulness of samples is partially dependent on the data accompanying the given accessions (Rubenstein et al. 2006, Halewood et al. 2020). In the 2018 census, respondents said that 39% of the samples had useful data

Table 7 Usefulness of samples requested by development status of the respondents' country, 1995–1999

	Useful in breeding program	Useful in other ways	Still being evaluated	Not useful
U.S	8	14	22	56
Non-U.S. developed	6	29	39	26
Developing	17	8	53	22
Transitional	7	17	23	53
All countries	9	14	27	50

Source: Rubenstein et al. (2006)

Table 9 NPGS accessions with useful data by development status of the respondents' countries, 1995–1999

	Samples with useful data for trait of interest	Samples with useful data for other purposes
U.S	16%	24%
Non-U.S. developed	26%	25%
Developing	30%	13%
Transitional	21%	14%
All countries	18%	23%

Source: Rubenstein et al. (2006)

for the trait of interest. Thirty-eight percent of the samples had data useful for other purposes (Table 8).

These percentages rose considerably from the 2000 census, in which 18 percent of the samples had useful data for the trait of interest, and 23 percent of the samples had data useful for other purposes. The percentages of samples with useful trait data increased in both developing and developed countries between the two study periods. For respondents in the U.S. and developing countries, the percentage of samples found to have other useful data also increased (Table 9).

Expected future use of the NPGS

Users of NPGS accessions were asked, "Over the next ten years, do you expect your use of NPGS samples of [crop X] to change?" To make our analysis strictly comparable to the results of the 2000 Census, we present results here in terms of respondent-crop combinations. For example, a respondent who answered this question for barley and wheat was counted twice, once for each crop. Across all country groups and crops, 46% of respondents expected their use of NPGS resources to stay the same. Of those expecting to change their use of the NPGS, more respondents expected to increase their use (34%) than decrease it (20%). Among non-U.S. developed countries, more than 70% of respondents expected their use of the system to increase or stay the same. The highest level of increasing expectations of future use was found among developing country respondents: 64% expected their use to increase. Only 8% of respondents expected their use to decrease (Table 10).

The results from the 2000 census of users also suggested that demand for NPGS resources was likely to increase (Smale and Day-Rubenstein 2002; Rubenstein et al. 2006). A nearly identical percentage (47%) of the respondents expected their demand for NPGS germplasm to stay the same. Of those expecting changes to their demand for NPGS resources in 2000, 39% of respondents expected their demand to increase, while only 14% expected it would decrease. Of respondents in developing countries, 70% expected their use to increase over the next ten years.

We can also analyze future use in terms of the number of samples represented by a given response. For example, a respondent answering the question who requested 100 samples of barley would contribute more to the aggregate comparison than a respondent answering the question who only requested ten samples. In such a weighted analysis, the number of overall samples represented by the "stay the same" answer was 45% of all samples, very similar to the percentage of respondent-crop combinations that stated NPGS germplasm use would remain constant. In the aggregate, the number of samples representing

Table 8 NPGS accessions with useful data by development status of the respondents' countries, 2011–2015

	Samples with useful data for trait of interest	Samples with useful data for other purposes	No. of respondents	Total samples received*
U.S	35%	42%	699	191,640
Non-U.S. developed	54%	18%	250	26,919
Developing	46%	30%	110	40,721
All countries	39%	38%	1059	259,280

* as estimated by respondents

Source: The Census of Users of the National Plant Germplasm System of 2018

Table 10 Census respondents' expectations for future use of NPGS materials, 2011–2015

	Total	U.S	Non-U.S. developed	Developing
	% of all respondent-crop combinations*			
Decrease	20%	23%	17%	8%
Stay the same	46%	48%	47%	28%
Increase	34%	29%	36%	64%
Number of respondent-crop combinations*	1680	1172	356	152

*Observations are on respondent-crop combinations; i.e., respondents who estimated future use for more than one crop are counted for their response on each crop individually

Source: The Census of Users of the National Plant Germplasm System of 2018

Table 11 Respondent's expectations for future use weighted by samples received, 1995–1999

	All	U.S	Non-U.S. developed	Developing
Decrease	26%	31%	26%	4%
Stay the same	45%	48%	31%	41%
Increase	29%	21%	44%	55%
Total samples received = 298,171				

Source: Rubenstein et al. (2006)

expected increased use was only slightly greater than the number of samples representing expected decreased use, suggesting overall demand for NPGS germplasm was expected to remain relatively stable. This result was driven particularly by U.S. respondents. When weighed by samples received, 55% of respondents in developing countries expected their future use to increase; only 4% expected their future use to decrease (Table 11).

Discussion

Often, genebanks are described in terms of the crops and germplasm types they contain. However, distribution data indicate how genebanks are used. In the case of these ten crops, landraces are the most common type of accession, followed by unknown or other types of material. For 2011–2015, landraces requested were roughly proportional to their presence in the collections. A substantial number of landraces from the NPGS were distributed to users (especially wheat and barley landraces). However, unknown materials, which made up 22% of the collections, accounted for only 4% of materials requested by respondents. When we combined the materials that were the product of post-Mendelian breeding—cultivars, advanced materials, and genetic stocks—these made up roughly half of the materials requested by respondents in developing countries (and all respondents). For example, with soybeans, sorghum, and maize, the combined percentages of cultivars, advanced materials, and genetic stocks requested were more than 90%, and for rice, this combination was 74%.

For added perspective, we can compare the NPGS to the CGIAR genebanks. As previously noted, many CGIAR institutions have breeding programs that also distribute germplasm. Distributed PGR are usually cultivars

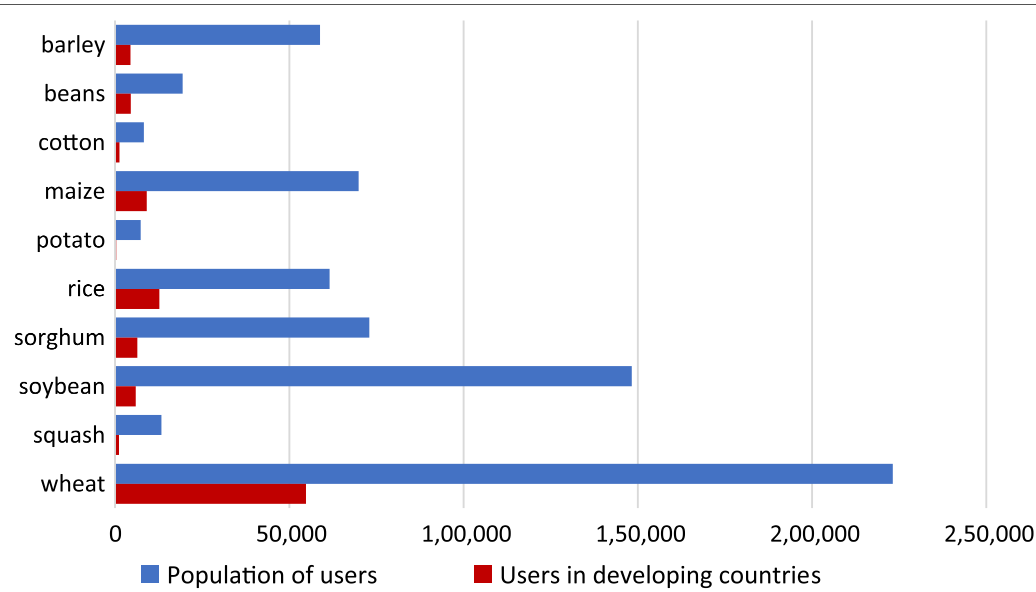

Fig. 2 NPGS samples distributed to users. Source: USDA National Genetic Resources Laboratory

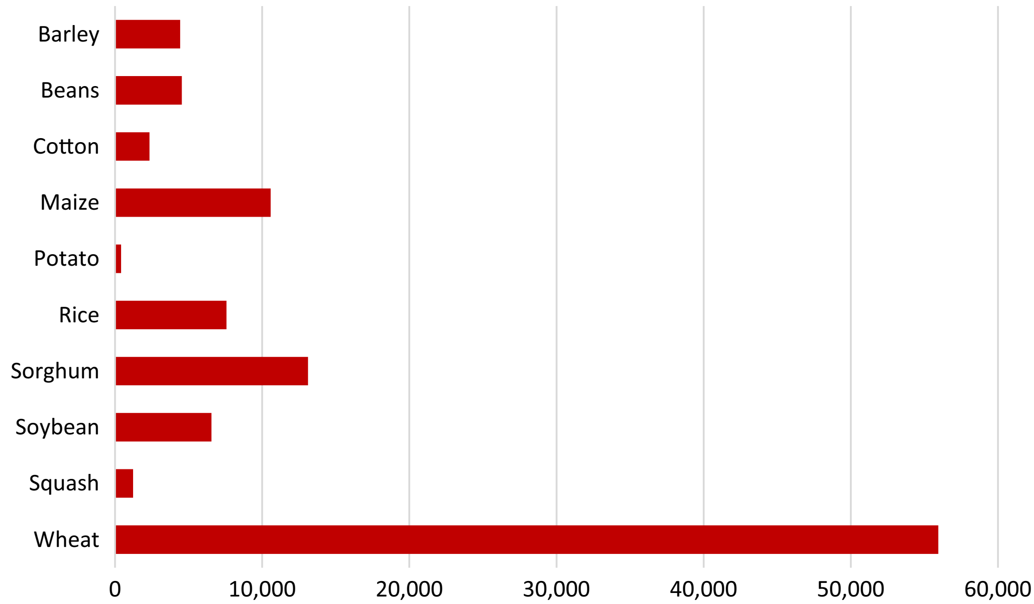

Fig. 3 NPGS samples distributed to users in developing countries. Source: USDA National Genetic Resources Laboratory

or advanced lines that can go immediately into testing or breeding programs in other countries. The NPGS is simply a system of genebanks, not a plant breeding program. While this is relevant when comparing the NPGS and the CGIAR genebanks, it is not determinative. Indeed, previous studies of the CGIAR genebanks (e.g., Galuzzi et al. 2016; Halewood et al. 2020) mention the CGIAR breeding programs but do not attempt to enumerate them completely or to evaluate them, and we follow this principle in our comparison.

Germplasm that is the product of post-Mendelian breeding makes up a relatively larger share of the NPGS collections than it does of the CGIAR genebanks (FAO 2010). This may be related to the fact that CGIAR genebanks are not focused on maintaining breeding populations; the breeding programs play that role in the CGIAR. In contrast, the NPGS gene banks play a relatively greater role in making available germplasm types such as cultivars or advanced lines, including material formerly protected by intellectual property that has passed the period of protection.

Unsurprisingly, the percentages of cultivars distributed by the NPGS to respondents were much higher than the percentage of cultivars in the CGIAR distributions (6%). We hypothesize that users requested cultivars and advanced materials from the NPGS more often because they sought the products of elite plant breeding efforts that would not be available through other means. The largest category of CGIAR genebank distributions was landraces, accounting for half the total in 2017 (CGIAR 2021). CGIAR coverage of landraces is particularly strong for rice, beans, wheat, and maize (Halewood et al. 2020). Respondents in developing countries requested fewer landraces from the NPGS than the proportion in NPGS collections, perhaps because they relied on the CGIAR for landraces. In addition, certain NPGS specializations might have been of value to users in developing countries. For example, the NPGS has a large collection of soybean accessions. It distributed 12,920 samples to external users from 2011–2015. The CGIAR classifies soybean with miscellaneous legumes; for the five years between 2012–2016, total external distributions for the entire collection were less than half that of the NPGS (CGIAR Genebank Platform 2022). In another example, the NPGS appeared to be a major source of crop wild relatives for wheat and barley. Strong demand for wheat samples may be why respondents in developing countries requested relatively more wild relatives than other respondents.

Lusty et al. (2021) stated that the usefulness of distribution data is limited because data are aggregated, and publicly available information is restricted to a basic set of parameters. They noted a dearth of information about user demand and future needs for PGR held in genebanks. By soliciting information from the population of users, this study explored the purposes for which PGR were sought, the usefulness of germplasm received, the presence of accompanying data, and future expectations of use of the NPGS.

Increasingly, diversity is sought not only to breed more productive varieties better adapted to changing growing conditions but also for highly complex research functions. Results from the census show that the NPGS was increasingly used for broader purposes than originally envisioned. Respondents in all countries said that the use of NPGS materials for basic research increased; respondents in developing countries intended to use 40% of materials for basic research, a substantially larger percentage than reported in1995–1999. So, not only did the volume of requests increase between 1995–1999 and 2011–2015, the NPGS had to meet the needs of a broader range of users. Yet funding did not increase in real terms.

In terms of usefulness, 34% of materials were "still being evaluated." That was not, in itself, surprising; it often takes more than a decade to develop and screen new crop varieties and get them to farmers. (Dempewolf et al. 2014; Swarup et al. 2021). What was less expected was that respondents already found 41% of materials from 2011 to 2015 useful in breeding or in another way. Roughly a quarter of materials were found not useful. This declined significantly from the 53% of samples not found useful in 1995–1999. We note two factors that could have affected the usefulness of the NPGS genebanks, namely: accession-level data and the technology available to the user.

It's difficult to overstate the influence of accession-level data on the usefulness of genebank materials (Khoury et al. 2010). Targeting requests from the system increases efficiencies for both the scientists and the genebank providing samples. (Halewood et al. (2020) noted that accession-level data helps curators make suitable recommendations to users.) This case study found that between 1995–1999 and 2011–15, NPGS samples sent to developing country respondents were accompanied by increasing levels of useful trait-related data (an increase from 30 to 46%) and increasing levels of other useful data (an increase from 13 to 30%). Similar increases in the presence of useful data occurred across all respondents, not just respondents in developing countries. While the usefulness of NPGS samples increased simultaneously with the increase in useful data accompanying samples, we cannot establish intertemporal causation from the previous study to this one using only data from this census.[10]

Galluzzi et al. (2020) and Khoury et al. (2010) noted the importance of internationally-agreed upon formats for accession-level data, as did Bretting (2018). To facilitate the use of NPGS data, the NPGS cooperates with other plant genetic resource information systems (GRIN-Global Project 2021). These include the Crop Trust's Genesys, which as of January 2021, now contains passport data from the NPGS (Genesys 2021). The DivSeek Initiative aims to harmonize genome databases (Bretting, 2018). GRIN is also compatible with the Global Information System associated with the International Treaty on Plant Genetic Resources for Food and Agriculture, another data management system (FAO, n.d., Genesys 2021). Assessing the presence of useful data is somewhat confounded by the type of material requested. Galluzzi et al. (2020) stated that one reason breeders prefer working with advanced materials is that they are accompanied by better information on their traits. While we cannot establish causation, we note the association between the increase in usefulness and the increase in useful data over time.

We hypothesize that other related technological developments played a role in the increasing usefulness of NPGS samples, though our data do not allow us to determine an association between them. Since the 2000 census, the technology used by users has advanced enormously (Swarup et al. 2021; Gollin 2020). Genomics has increased the usefulness of germplasm for both breeders and basic researchers. We believe these advances were reflected in (1) the increased usefulness of samples in 2011–2015; (2) the rise in basic research as a purpose for requests (particularly for developing countries); and (3) the prominence of users working in genetics/molecular biology. Respondents working in genetics/molecular biology accounted for 54% of samples distributed to developing countries. However, the ability to adopt advanced technologies is determined by available resources. Halewood et al. (2020) said that while the costs of sophisticated assessments declined, the need for expertise and computing power did not. A broad range of countries are defined as developing countries by the World Bank. Some, such as India, routinely use the same technologies as developed countries, while the poorest regions may have few resources to develop new crop varieties. Therefore, the benefits of new technologies may not be as accessible to low-income developing countries as they are to medium-income developing countries (Galluzzi et al. 2020; Bohra et al. 2021).

Respondents' answers about the future use of NPGS materials provided some insight into demand in the next decade. In the next ten years, 28% of developing country respondents expected to be using the same amount of NPGS materials. An even larger percentage (64%) expected their use to increase in the future. Likewise, when weighted by samples received, 90% of the respondents in developing countries expected their use of NPGS germplasm to either stay the same or increase. Expected increases in future use were much more likely among developing country respondents than among other individuals in the study population. Because many centers

[10] Rubenstein and Smale (2006), in a regression analysis within that study period, found statistically significant relationships between the presence of useful data and the perceived usefulness of germplasm samples.

of origin are in cooler climates, the pool of suitable landrace/wild germplasm is already small. Therefore, continued access to diverse genetic resources will be especially critical for developing countries in the hottest regions (Dempewolf et al. 2014). Galluzzi et al. (2020) surveyed breeders in developing countries and noted that breeders who explored broader sources of diversity reported more success with climate-related breeding efforts. Khoury et al. (2020) noted that breeders on the cutting edge of climate adaptation work require more diverse materials. Therefore, one factor that may lead to unanticipated increases in future demand is the acceleration of climate change.

A constraint that may limit future use is the transaction costs international users of the NPGS may face when importing NPGS material, particularly for countries where national laws related to PGR are not clearly defined (Halewood et al. 2020; Galluzzi et al. 2020). Time spent in quarantine can reduce or eliminate the number of samples received (Halewood et al. 2020). Countries with strict phytosanitary rules have lower acceptance rates of international PGR. On the other hand, breeders in developing countries who use landraces may be eager to access sources of variation outside their institutions, but they may not have the resources to cover the shipping costs of samples from external sources (Galluzzi et al. 2020). NPGS materials are provided free of charge, and the NPGS generally covers standard shipping costs, particularly for users in developing countries. It was not clear from this study the degree to which this may outweigh transaction costs, though our findings of increased demand suggested that it may.

One limitation of this case study was that only a little over one-third of users in developing countries returned the census instrument. (This response rate was slightly higher than the response rate for the entire population of users.) Administrative data on NGRL distributions did not show major differences in the crop requests of respondents and non-respondents. Respondents, on average, requested slightly greater amounts of germplasm than non-respondents, suggesting information received from respondents covered more germplasm samples than would be implied by raw response rates alone. Given the relatively small size of the developing country sub-population of users, the results of this case study should be treated with caution.

For this set of data, some promising areas are left to explore. More information on the interaction between variables such as crop, germplasm type, and intended purpose for materials would be helpful. The traits sought were an area of analysis outside the scope of this paper. Further analysis could lead to findings on subjects such as the use of maize landraces for abiotic tolerance or how often advanced materials were evaluated for resistance to pests and diseases. Information about how crop wild relatives were utilized could provide guidance to genebank managers and users. It could help determine whether certain crop/germplasm type/trait combinations have useful accession-level data. Such information would be valuable not only for the NPGS but also for managers of other genebanks serving developing countries, such as those of CGIAR.

Conclusions

Although not solely established or maintained for this purpose, the U.S. National Germplasm System has become an important supplier of crop germplasm to users in developing countries. In this case study, we focused on empirical estimates of the use of the NPGS by developing countries for ten significant crops. For the ten crops in this study, the NPGS distributed more than 100,000 samples to developing countries for 2011–2015. An earlier study of NPGS users in the late 1990s recorded relatively high use of NPGS germplasm by developing country recipients; nonetheless, this distribution increased in more recent years.

A questionnaire was sent to users of these crops. For developing countries, roughly a third of users responded to the census; they accounted for 45% of samples distributed to those areas. Most of the respondents were scientists. Respondents in developing countries found 38% of the materials they received useful in some way, and another 38% was still being evaluated.

Respondents requested materials that are the products of post-Mendelian science (such as cultivars and advanced germplasm), farmer-developed varieties, and the wild relatives of crops. Advanced materials are easier to incorporate into breeding programs than landraces or wild relatives. The large percentages of cultivars and other advanced materials requested by developing country recipients suggest that these users were interested in NPGS germplasm that had been subjected to greater degrees of genetic improvement. The NPGS represents a valuable source of advanced germplasm developed in a country with a long history of crop improvement research.

As with users elsewhere, respondents in developing countries increased the proportion of genetic resources from the NPGS used in basic research. During 1995–1999, 15% of samples requested were for basic research. This percentage increased dramatically in 2011–2015: developing country respondents intended to use 40% of materials requested for basic research. This is likely explained by advances in the technology available to researchers and the rise in upstream research efforts.

Prior research established that accompanying data can enhance the value of germplasm from genebanks. Enormous strides have been made in providing germplasm-related data that are more comprehensive and accessible internationally. This case study indicates that NPGS samples distributed in 2011–15 were considerably more likely to be accompanied by useful data than samples in 1995–1999. Nonetheless, the fact that estimates of the presence of useful data were still relatively low suggests the need continues for even more improvements in passport, characterization, and evaluation data.

Respondents in developing countries were more likely than other users to expect constant or increasing use of NPGS resources (28% and 64%, respectively). This underscored the importance of its collections to developing countries. Accelerations in climate change may lead to future demand increases not captured by these results. As the NPGS is called upon to provide more diverse services, further research that pinpoints more specific relationships between variables such as germplasm type, purposes, and traits sought might be a relatively low-cost means of making these collections even more useful to developing countries.

Abbreviations
CGIAR: Consultative Group on International Agricultural Research; FAO: United Nations Food and Agricultural Organization; GRIN: Germplasm Resources Information Network; IPGRI: International Plant Genetic Resources Institute; IRRI: International Rice Research Institute; IT: International Treaty for Plant Genetic Resources for Food and Agriculture; NGRL: National Germplasm Resources Laboratory; NPGS: U.S. National Plant Germplasm System; PGR: Plant genetic resources; USDA: U.S. Department of Agriculture.

Supplementary Information
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Additional file 1. International users of NPGS germplasm for 10 crops, 2011-15, by income category.

Additional file 2. Users by development status of country.

Additional file 3. Distribution of NPGS samples by crop.

Additional file 4. A comparison of wheat with other crops for NPGS users in developing countries.

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Declarations

Ethics approval and consent to participate
The Census of Users of the National Plant Germplasm System was approved by the U.S. Office of Management and Budget.

Consent for publication
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Competing interests
The authors declare that they have no competing interests.

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