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REVIEW & INTERPRETATION

Sustaining the Future of Plant Breeding: The Critical Role of the USDA-ARS National Plant Germplasm System

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ABSTRACT

Plant breeders require genetic diversity to develop cultivars that are productive, nutritious, tolerant of biotic and abiotic stresses, and make efficient use of water and fertilizer. The USDA-ARS National Plant Germplasm System (NPGS) is a major source for global plant genetic resources (PGR), with accessions representing improved cultivars, breeding lines, landraces, and crop wild relatives (CWR), coupled with passport and trait evaluation data. The goal of this article is to facilitate use of PGR in plant breeding programs. Our specific objectives are (i) to summarize the structure and operation of the NPGS and its consultative and support committees, (ii) to review current use of the system by plant breeders, (iii) to describe constraints to improving the utility of PGR, and (iv) to discuss ways in which the NPGS might evolve to better meet the challenges facing agriculture and society in coming decades. The NPGS will enhance its relevance to plant breeding provided there is (i) ongoing attention to filling the gaps in NPGS collections, especially for CWR; (ii) a major increase in efforts to phenotype and genotype accessions using standardized methods; (iii) enhanced information content of the Genetic Resources Information Network (GRIN)-Global system and improved interoperability with other databases; (iv) increased attention to prebreeding activities; (v) improved training opportunities in practices for incorporating PGR in breeding programs; and (vi) expanded outreach efforts to strengthen public support for the NPGS. We believe these steps will be implemented most effectively through coordinated efforts among USDA-ARS, universities, the private sector, and international partners.

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Abbreviations: CGC, Crop Germplasm Committee; CWR, crop wild relatives; GBIF, Global Biodiversity Information Facility; GEM, Germplasm Enhancement of Maize; GRIN, Genetic Resources Information Network; GWAS, genome-wide association study(ies); NGRAC, National Germplasm Resources Advisory Council; NGRP, National Genetic Resources Program; NIFA, National Institute for Food and Agriculture; NLGRP, National Laboratory for Genetic Resources Preservation; NPGCC, National Plant Germplasm Coordinating Committee; NPGS, National Plant Germplasm System; PBCC, Plant Breeding Coordinating Committee; PCR, polymerase chain reaction; PGR, plant genetic resources; RTAC, Regional Technical Advisory Committee; RWA, Russian wheat aphid; SAES, State Agricultural Experiment Stations; SNP, single-nucleotide polymorphism.

Agriculture faces daunting challenges in providing sufficient food, feed, fiber, and fuel for a growing global population with increasing dietary expectations (Khoury et al., 2014). A recent analysis found that global agricultural production must increase by 25 to 70% above 2014 levels to meet projected food demand in 2050 (Hunter et al., 2017). At the same time, the environmental impact of agriculture, including greenhouse gas emissions and nutrient runoff to waterways, must be reduced to

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help maintain and restore ecosystem functioning (Hunter et al., 2017). Emerging pest problems, as exemplified by the TTKSK race and its derivatives of stem rust of wheat (*Triticum aestivum* L.), caused by *Puccinia graminis* Pers.:Pers. f. sp. *tritici* Erikss. & E. Henning, in Africa and the Middle East (Singh et al., 2015) will continue to threaten crop harvests. Water availability for agriculture is predicted to become more limiting in many regions, including the western United States (Rosegrant et al., 2002; Walthall et al., 2012), and increasing temperatures will further constrain crop production (Jha et al., 2014).

All of these challenges can be partly addressed by plant breeding, in collaboration with the allied disciplines of agronomy, disease and pest management, horticulture, plant physiology, molecular biology, genomics, statistics, computer science, bioinformatics, engineering, and remote sensing, among others. Numerous studies have reported the relative contributions of plant breeding (genetic gain) and improved agronomic practices to increased crop production with resultant economic and environmental benefits (Laidig et al., 2014; Smith et al., 2014b). For example, the development of US maize (*Zea mays* L.) hybrids during the 1990s with increased biotic and abiotic resistances allowed continued gains in productivity, coupled with opportunities to realize environmental benefits from reduced soil and nutrient runoff, use of less fuel, and fewer carbon dioxide emissions that accrued from conservation tillage (Smith et al., 2014a).

Future crop production can be expected to rely increasingly on the more effective use of plant genetic resources (PGR), especially as economically viable means to achieve yield increases through other inputs are reduced. If appropriately characterized and deployed in an ongoing manner, genetic components of a crop production system can be used to replace at least some chemical inputs directed to weed, disease, and pest management, to develop cultivars that are more efficient users of water and fertilizer, and to improve nutritional and processing quality of harvested products. Achieving these goals, in our opinion, will require expanded, sustained, and mutually beneficial interactions between the germplasm and end-user communities, increased efforts in genetic and phenotypic evaluations, improved and integrated information systems, and creative approaches to exploiting the diverse resources in our global germplasm banks.

The USDA-ARS National Plant Germplasm System (NPGS) represents a major source of genetic resources of improved cultivars, breeding materials, landraces, and crop wild relatives (CWR), coupled with passport and evaluation data, that can be accessed by basic and applied plant scientists and educators. However, plant breeders do not always understand how the NPGS operates and how the user community may affect decisions on PGR conservation and use through participation on consultative and support committees. Although plant breeders are often well aware of the necessity of maintaining genetic diversity in their breeding populations, they may lack the information to determine which of the thousands of accessions of a given crop would be most beneficial for their breeding objectives. They may also be reluctant to introduce unadapted germplasm, with potentially negative impacts, into their elite breeding materials. In some cases, they may lack the technical expertise or facilities to make interspecific crosses, for example, between CWR and cultivars of different ploidy levels.

Given the urgency of improving the productivity and environmental sustainability of agriculture, the goal of this article is to motivate and facilitate the increased exploitation of PGR in plant breeding programs. Our specific objectives are (i) to summarize the structure and operation of the NPGS and the various consultative and support committees that provide input and guidance to the system, (ii) to review current use of the system by the plant breeding community, (iii) to describe challenges to improving the utility of PGR to plant breeders, and (iv) to discuss ways in which the NPGS might evolve so that public and private sector breeding can optimally overcome the challenges that agriculture and society will face in the coming decades. The intent of this review is to contribute not only to defining the needs of, but also to describing roles of the various stakeholders including plant genebank curators, researchers, breeders, and the public, who, as primary beneficiaries of improved agricultural production, can also help influence policymakers.

NPGS STRUCTURE AND OPERATION

Thomas Jefferson foresaw the importance of the NPGS in his oft-quoted statement, "The greatest service which can be rendered any country is to add an useful plant to it's culture…" (Jefferson, 1800). A comprehensive history of the evolution of the US government's efforts to expand agricultural productivity and provide for food security in the fledgling nation is included in the story of plant introduction by Griesbach (2013). The original plant introduction and breeding programs initiated in 1862 have evolved to become the current USDA-ARS-NPGS. The NPGS safeguards the genetic diversity of agriculturally important plants and their wild relatives by maintaining a vast collection of >575,000 accessions of PGR representing 15,116 species (GRIN-Global, 2017a). The NPGS supports agricultural production by acquiring, conserving, characterizing and evaluating, documenting, and distributing crop germplasm and associated information to national and international customers in the public, private, and nongovernmental organization sectors. As the largest distributor of PGR in the world, the NPGS distributes ~250,000 accessions annually to national and international researchers (Table 1). Germplasm is

Table 1. USDA-ARS National Plant Germplasm System (NPGS) holdings according to collection location: number of accessions, percentage of total NPGS accessions, and the number of distributions in 2015.

Site	Collection name	Location	No. of accessions†	% of NPGS total	NPGS distributions (2015)
BRW	National Germplasm Repository–Brownwood	Brownwood, TX	4,066	0.7	0
COR	National. Germplasm Repository–Corvallis	Corvallis, OR	12,241	2.1	6,483
COT	Cotton Collection	College Station, TX	9,521	1.7	
DAV	National Germplasm Repository–Davis	Davis, CA	8,719	1.5	9,441
DLEG	Desert Legume Program	Vail, AZ	2,611	0.5	
GEN	National Germplasm Repository–Geneva	Geneva, NY	7,468	1.3	6,795
GSOR	Rice Genetic Stock Center	Stuttgart, AR	36,678	6.4	16,553
GSPI	Pea Genetic Stock Collection	Pullman, WA	712	0.1	12
GSZE	Maize Genetic Stock Center	Urbana, IL	8,127	1.4	
HILO	National Germplasm Repository–Hilo	Hilo, HI	783	0.1	480
MAY	National Germplasm Repository–Mayaguez	Mayaguez, PR	1,153	0.2	614
MIA	National Germplasm Repository–Miami	Miami, FL	3,273	0.6	141
NA	National Arboretum	Washington, DC	4,517	0.8	189
NC7	North Central Regional PI Station	Ames, IA	54,067	9.4	34,152
NE9	Northeast Regional PI Station	Geneva, NY	12,624	2.2	7,349
NR6	Potato Germplasm Introduction Station	Sturgeon Bay, WI	5,931	1.0	6,904
NSGC	National Small Grains Collection	Aberdeen, ID	143,287	24.9	57,081
NSSL	National Laboratory for Genetic Resources Preservation	Fort Collins, CO	12,660	2.2	737
NTSL	Forest Service National Seed Laboratory	Dry Branch, GA	7,600	1.3	300
OPGC	Ornamental Plant Germplasm Center	Columbus, OH	5,050	0.9	378
PARL	National Arid Land Plant Genetic Resources Unit	Parlier, CA	1,494	0.3	678
PGQO	Plant Germplasm Quarantine Program	Beltsville, MD	951	0.2	
PVPO	Plant Variety Protection Voucher Collection	Fort Collins, CO	7,502	1.3	
RIV	National Germplasm Repository–Riverside	Riverside, CA	1,789	0.3	
S9	Plant Genetic Resources Conservation Unit	Griffin, GA	99,151	17.2	35,440
SOY	Soybean Collection	Urbana, IL	22,143	3.8	26,178
TGRC	C.M. Rick Tomato Genetics Resource Center	Davis, CA	3,716	0.6	
TOB	US Nicotiana Germplasm Collection	Oxford, NC	2,229	0.4	10
W6	Western Regional PI Station	Pullman, WA	96,262	16.7	29,203
	Total		576,325		239,118

† As of November 2016.

distributed in the forms of seeds, cuttings, dormant scionwood, other vegetative propagules, DNA, leaves, fruit, pollen, and in vitro cultures. The NPGS is funded by US federal appropriations to the ARS and by regional Capacity Funded (formerly known as Hatch funded) projects. Germplasm is freely available on request without restrictions anywhere globally for use in plant breeding (assuming required import permits are provided). Accessions distributed internationally will be accompanied by the Standard Material Transfer Agreement of the International Treaty on Plant Genetic Resources for Food and Agriculture, which specifies certain conditions of use (FAO, 2017).

The NPGS is a genebank system whereby PGR collections are maintained at 19 locations throughout the United States (Fig. 1). Two additional sites serve as resources to the entire NPGS, including the National Germplasm Resources Laboratory (NGRL; Beltsville, MD), where the Genetic Resources Information Network (GRIN)-Global information system is maintained and the Plant Exchange Office and GRIN-Taxonomy programs are colocated, and the National Laboratory for Genetic Resources Preservation (NLGRP; Fort Collins, CO). The GRIN-Global system is a suite of software programs for managing germplasm-associated information, facilitating genebank workflows, and providing a public interface for users to access germplasm and information. Users can search for accession information via its public website (GRIN-Global, 2017b).

Collections conserved primarily as seeds, such as those maintained in Aberdeen, ID, Ames, IA, College Station, TX, Geneva, NY, Griffin, GA, Pullman, WA, and Urbana, IL, primarily focus on the maintenance, regeneration, and documentation of high-quality collections of seed-propagated plants for characterization, evaluation, and distribution. These seed collections are maintained in 4 or −18°C storage facilities under optimal conditions to ensure that seeds remain viable for extended lengths of time. In contrast, the vegetatively propagated, or "clonal," plant collections are primarily maintained as actively growing plants in field, greenhouse, or as in vitro cultures (Postman et al., 2006). In these collections, accessions

Fig. 1. Map of USDA-ARS National Plant Germplasm System collection genebanks.

valued as specific cultivars or genotypes must be propagated and distributed as cuttings, scionwood for grafting, in vitro cultures, whole plants, roots, bulbs, rhizomes, or corms. Some accessions within "clonal" collections, particularly those of wild origin, may be maintained and distributed as seeds because they are valued for the genes they possess, rather than for their specific genotypes.

The NLGRP maintains the system backup of >445,000 accessions, representing 86% of the seed collection and 15% of the clonal collection. Collections of orthodox seed (which will survive drying and freezer temperatures) are maintained at either −18°C or cryopreserved in liquid nitrogen vapor. Vegetative propagules are conserved as either dormant buds or shoot tips under liquid nitrogen conditions. Plant Variety Protection and Crop Science Registration voucher specimens, as well as backups of international seed collections, are also secured. The NLGRP hosts an extensive genebanking research program devoted to developing strategies and technologies to increase the efficiency and effectiveness of plant genebanks.

SUPPORT AND CONSULTATIVE COMMITTEES

National Genetic Resources Advisory Council

The US National Genetic Resources Program (NGRP) includes multiple collections of genetic resources, including those for animals, aquatics, forestry, insects, microbes, and plants (Fig. 2). The National Germplasm Resources Advisory Council (NGRAC) (USDA, 2017b) works in this larger context to advise and make recommendations to the Director of the NGRP and ultimately to the Secretary of Agriculture. The NGRAC is composed of up to nine members appointed by the Secretary of Agriculture and seven or more *ex-officio* members. Recent projects include a report that addressed the commercial availability of nongenetically engineered and organic seed varieties and a plan to ensure that the needs of all farmers are met through a diverse commercial seed supply (NAREEE Advisory Board, 2016).

The NGRAC is preparing a report on conservation needs and opportunities that will provide guidance to US and global agriculture during the next several decades, as germplasm characterization, high-throughput phenotyping, and genomics-assisted breeding methods continue to evolve rapidly. The NGRAC is also focused on increasing the awareness among policymakers and the public of the crucial role of genetic resources and agriculture in food, health, and environmental security. The NGRAC strongly supported US ratification of the International Treaty on Plant Genetic Resources for Food and Agriculture, which occurred in 2016 (Smith, 2016; FAO, 2017).

National Plant Germplasm Coordinating Committee

The National Plant Germplasm Coordinating Committee (NPGCC) is a committee jointly established by the USDA and State Agricultural Experiment Stations (SAES) whose mission is to promote "a stronger, more efficient, more widely-recognized and better utilized NPGS" (ESCOP, 2017). Among its goals are to facilitate coordination of ARS, National Institute for Food and Agriculture (NIFA), and SAES policy and activities regarding the NPGS; to promote understanding and awareness of the NPGS; and to improve communication and discussion of issues affecting the NPGS. The committee is composed of three members each from the ARS, NIFA, and SAES, in addition to liaisons (e.g., from the National Association of Plant Breeders and the American Seed Trade Association).

Regional Technical Advisory Committees

A series of Regional Technical Advisory Committees (RTACs) focuses on issues relevant to PGR in their respective regions. Each is associated with one of the regional Plant Introduction Stations of the NPGS. These committees include NC7 for the North Central region (Ames, IA), NE9 for the Northeast region (Geneva, NY), S9 for the Southern region (Griffin, GA), and W6 for the Western region (Pullman, WA). In addition to their ARS funding, each of the four Plant Introduction Stations receives crucial support from USDA/SAES Capacity Funded Multi-State projects. Similarly, the NPGS Potato Genebank (Sturgeon Bay, WI) receives funding from both the ARS and SAES through the National Research Support Project-6 (NRSP-6).

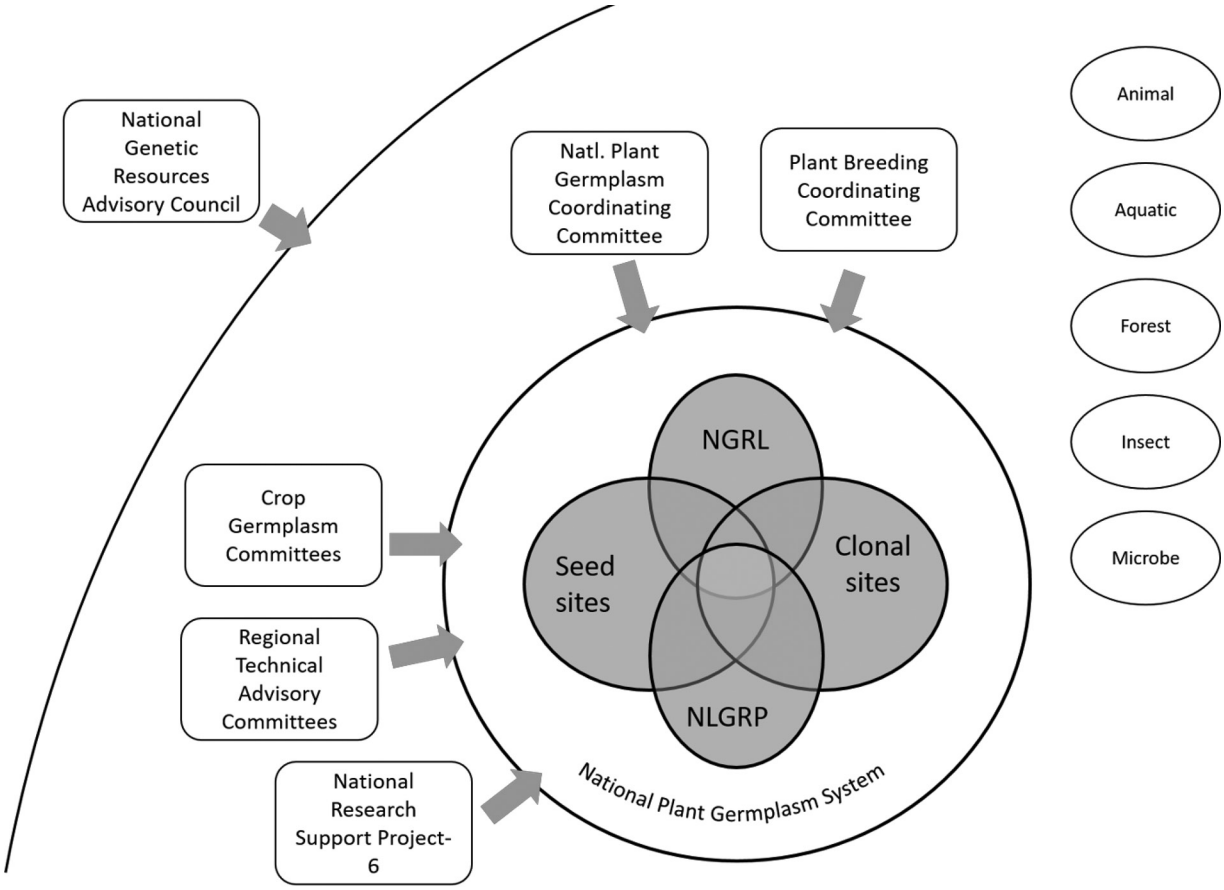

Fig. 2. Relationship of National Plant Germplasm System units and advisory committees. NGRL, National Germplasm Resources Laboratory; NLGRP, National Laboratory for Genetic Resources Preservation.

All states use germplasm provided by the NPGS and have a complex array of collaborative research efforts between their institutions and PGR curators at the NPGS sites. The RTACs and NRSP-6 Technical Advisory Committee provide useful insights for the ARS and administrators with respect to programmatic decision making and operational guidance; this key function has direct impact on the public interest, as well as on the specific research interests of more directly involved stakeholders.

Crop Germplasm Committees

A total of 42 crop-specific Crop Germplasm Committees (CGCs) have been established to provide subject matter technical expertise to NPGS genebanks and collections (USDA, 2017a). Plant breeders from university, industry, nongovernmental organizations, and the USDA are key stakeholders who serve on these committees to provide input and expertise to crop curators with regard to acquisition needs, best practices, and collection management strategies. Members review Plant Exploration and Plant Evaluation funding proposals for scientific rigor and to assist in prioritization. Key issues addressed vary by crop and by CGC, and may include (i) identifying and filling gaps in collections, (ii) identifying key collections and/or materials in danger of being lost, (iii) assisting curators in identifying duplication in collections, (iv) prioritizing traits for evaluation, (v) assisting in data acquisition and documentation, (vi) assisting in identifying additional germplasm regeneration resources, (vii) working with quarantine officials regarding pathogen identification and eradication, (viii) developing and updating Crop Vulnerability Statements (see paragraph below), and (ix) evaluating the development and use of core subsets (USDA, 2017a). Plant breeders who would like to become more involved in setting germplasm-related priorities for their crops are encouraged to contact the relevant CGC (USDA, 2017a; Supplemental Table S1).

Crop Vulnerability Statements provide comprehensive assessments of the NPGS crop collections. They summarize key aspects of crops that include (i) crop introduction (biological features, distribution, breeding, products and value), (ii) urgency and extent of crop vulnerabilities (genetic uniformity, threats of genetic erosion in situ, current and emerging biotic, abiotic, production, dietary, and accessibility threats and needs), (iii) status of the NPGS collection (holdings and in situ reserves, associated information, research, fiscal and maintenance capacities), and (iv) prospects and future developments. The Crop Vulnerability Statements are posted online (Supplemental Table S1; USDA, 2017a).

Plant Breeding Coordinating Committee

Established in 2006, the Plant Breeding Coordinating Committee (PBCC), also known as SCC80, is a USDA/SAES multistate committee "to raise awareness of plant breeding's contributions to the US economy and to strengthen plant breeding infrastructure and education capacity" (SAAESD, 2017a). The core membership of the PBCC includes representatives of SAES that have plant breeding programs. Therefore, one of the PBCC's primary emphases has been on issues facing public plant breeding at land-grant universities. In 2015, the PBCC was renewed for 5 yr with the new title "Sustaining the Future of Plant Breeding" (SAAESD, 2017b), though it is still commonly referred to as the PBCC. Among the objectives of the renewed project is to "promote the conservation, characterization, and utilization of plant genetic resources and access to those resources for plant breeding." To help achieve that objective, the PBCC has been granted liaison status with the above described NPGCC. This publication is a product of the PBCC task force on genetic resources.

CURRENT USE OF NPGS ACCESSIONS BY PLANT BREEDERS

The NPGS is a major contributor to global germplasm exchange, with an average of 250,000 accessions distributed annually (Table 1). A comprehensive compilation of cultivars and breeding materials developed with NPGS accessions was published in the early 1990s (Shands and Wiesner, 1991, 1992). It is beyond the scope of this review to provide a similar report for the past 25 yr. Instead, we offer a few examples of how NPGS accessions continue to be a major source of useful genetic variation for breeding programs.

For any crop in the United States, there is usually at least some breeding effort that includes the characterization of less-adapted or wild germplasm as part of a programmatic focus to introgress greater diversity into the crop. The recognition that greater diversity in cultivated germplasm is critical for sustained crop improvement drives the characterization and consequently the utilization of PGR. To encourage germplasm evaluation, funds to evaluate horticultural germplasm have been made available annually through the respective CGCs, explicitly for that purpose. In recent years, several NIFA-funded Coordinated Agricultural Projects have supported germplasm characterization, along with development of genomic tools that are shared by related crops (e.g., for Triticeae, Solanaceae, and Cucurbitaceae). Smaller projects have been developed with a similar focus on individual crops (e.g., bean [*Phaseolus vulgaris* L.], carrot [*Daucus carota* L.], lettuce [*Lactuca sativa* L.], and walnut [*Juglans* L. spp.]). For example, apple (*Malus* Mill. spp.) researchers are evaluating much of the *Malus* germplasm collection for resistance to several diseases and for variation in fruit pigmentation. The combination of phenotypic characterization of these important traits, combined with development of an extensive genomic database, sets the stage to undertake more advanced levels of germplasm characterization, such as gene discovery, genomic selection, and assessment of crop vulnerability (Kumar et al., 2012; Volk et al., 2015; Sandefur et al., 2017).

Among the most frequent uses of the germplasm collections is the identification of sources of disease and insect resistance. The marketability of leafy greens is especially sensitive to presence of leaf disease lesions, and spinach (*Spinacia oleracea* L.), which has become an increasingly important vegetable crop globally, is an illustrative example. First reported in the early 1800s, downy mildew (blue mold), caused by *Peronospora farinosa* f. sp. *spinaciae* Byford, has significant impact, and the pathogen rapidly evolves new pathogenic variants (Correll et al., 2011). Spinach accessions and their wild relatives are routinely requested for downy mildew and other disease resistance screening (Jones et al., 1956; Zink and Smith, 1958; Jones, 1982; Correll et al., 1990; Brandenberger et al., 1991, 1992). A study comparing accessions of spinach and its wild relatives for resistance to an isolate of race 4 of *P. farinosa* f. sp. *spinacieae* identified *S. oleracea* and *S. turkestanica* Iljin accessions from the NPGS, and from genebanks in the Netherlands and Germany, as useful for breeding programs (Brandenberger et al., 1992).

Resistance to late blight of tomato (*Solanum lycopersicum* L.), a devastating disease caused by *Phytophthora infestans* (Mont.) de Bary, was identified in PI 365957, an accession of the wild tomato relative *Solanum pimpinellifolium* Jusl. collected in Peru in 1971 (Panthee et al., 2015). The resistance gene *Ph-3* from that accession was mapped with molecular markers and has been used in marker-assisted selection by several US public tomato breeding programs (Robbins et al., 2010; Panthee et al., 2015).

The Russian wheat aphid (*Diuraphis noxia* Kurdjumov, RWA), was first detected in the United States in 1986 and soon became a major pest of wheat crops in the Western Great Plains. Large-scale screening of NPGS accessions identified PI 372129 ('Turcikum 57'), an introduction from the former Soviet Union, as showing a high level of resistance to US RWA populations (Quick et al., 1991). PI 372129 was the source of resistance in 'Halt', the first RWA-resistant wheat cultivar released in the United States (Quick et al., 1996), and several other cultivars were later released based on the same resistance source. After a new, more virulent RWA biotype appeared (Haley et al., 2004), another screening was conducted of NPGS materials previously observed to be resistant to the original US biotype of RWA. This screening identified 10 wheat accessions, mostly from Central Asia, that were highly resistant to the new biotype (Collins et al., 2005). One of those accessions, CItr 2401 from Tajikistan, has been

incorporated into advanced lines in the Colorado State University breeding program.

Crop wild relatives of sunflower (*Helianthus annuus* L.) have contributed high-value traits such as cytoplasmic male sterility and resistance genes for rust (*Puccinia helianthi* Schwein.), downy mildew [*Plasmopara halstedii* (Farl.) Berl. & De Toni in Sacc.], Verticillium wilt fungus (*Verticillium dahlia* Kleb.), Alternaria leaf spot [*Alternaria helianthi* (Hansf.) Tubaki & Nishihara], and powdery mildew [*Golovinomyces cichoracearum* (DC) V. P. Heluta] (Seiler et al., 2017). In addition, NPGS genebank materials were used to better understand plant architecture and its influences on aspects of plant growth and development, including the genetic basis of variation of branching and its role in crop domestication (Nambeesan et al., 2015). As a result of the study, an association mapping population of 288 lines is now available for research, together with rich genomic data resources (Mandel et al., 2011, 2013).

In common bean (*P. vulgaris*), slow darkening of the seed coat's cream-colored background is a favorable quality trait in pinto bean cultivars (Felicetti et al., 2012). Slow-darkening lines retain a bright, attractive appearance after storage and canning compared with regular darkening types. The breeding line SDIP-1 was released by Singh et al. (2006) and has become an important parent for introgression of the slow darkening trait (M. Brick, Colorado State University, personal communication, 2017). The source of the trait in SDIP-1 was the Michigan State University cultivar 'Matterhorn', deposited in the NPGS system as PI 604228 (Kelly et al., 1999; S. Singh, University of Idaho, personal communication, 2017).

The Florida citrus industry has experienced a 50% decline in crop production in the past decade, as a result of the citrus greening disease (USDA National Agricultural Statistics Service, 2015), and 80% of the Florida citrus trees are infected with the causative bacteria *Candidatus* Liberibacter spp. (Singerman and Useche, 2016). Seedling trees of *Citrus* L. and *Citrus* relatives grown from seeds provided by the NPGS were screened for resistance to citrus greening. Distant citrus relatives, as well as *C. medica* L., *C. limetta* Risso, *C. limettioides* Tanaka, *C. limonia* Osbeck, *C. volkameriana* V. Ten. & Pasq., and some *C. limon* (L.) Burm. accessions exhibited few or no symptoms of citrus greening and may be useful for breeding tolerant cultivars (Ramadugu et al., 2016; Miles et al., 2017).

CHALLENGES TO INCREASED USE OF PGR BY PLANT BREEDERS

Availability of Information on Accessions

The usefulness of materials in genebanks is directly correlated with the amount and especially the quality of information associated with those accessions (Rubenstein et al., 2006). As genebank materials are often used as type specimens, it is crucial to have taxonomically correct identification of accessions (GRIN Global, 2017c). Passport data that include georeferenced locality and sampling information for wild materials, as well as pedigrees for cultivated materials, allow users to identify materials of interest. In addition, desirable genebank materials can be more easily selected when standardized phenotypic data collected in replicate in one or more environments are documented and publicly available in a searchable database (such as GRIN-Global). Although GRIN-Global does not have the capacity to maintain vast genomic data types, interoperability with genomic databases would allow users to leverage the use of multiple datatypes in their collection assessments (USDA-ARS, 2017).

Challenges of Unadapted Germplasm

Plant breeders must balance potential risks and rewards when they select germplasm to be introduced into breeding programs. Breeders have traditionally relied mostly on already well-adapted germplasm for the further development of improved varieties (Duvick, 1984; Goodman, 1999; Goodman et al., 2000; Cowling et al., 2017), so long as this germplasm provides useful sources of diversity. This could include the choice of unrelated yet adapted germplasm used in other countries having similar maturity and other agronomic traits. Where improvements need to be made for specific traits that are simply inherited, breeders then minimize the introduction of additional donor germplasm that may have negative effects on other desirable traits by backcrossing, often through the use of marker-assisted selection. It is important to weigh potential disruption of agriculturally productive, adapted gene networks from the introduction of maladapted and less thoroughly characterized germplasm with the potential opportunities that can come from the deployment of new and useful germplasm derived from unadapted material, because breeding within a closed system inevitably reduces genetic diversity within that breeding pool.

Introduction of novel germplasm is the least challenging for annual crops and for traits that are simply inherited and thus more amenable to rapid evaluation and introgression with minimal negative linkage drag. Alternatively, introduction of new germplasm is the most challenging for crops with long generation times and for traits that are under polygenic control, especially when associated with undesirable expression of other traits. Some traits may even be precluded from evaluation unless preceded by generations of adaptation or prebreeding using other well-adapted germplasm. Nonetheless, studies of genetic gain demonstrate that it is the improved performance of traits that are under polygenic control that determines the genetic potential of yield, in contrast with the contributions of single-gene traits, which are useful for protecting, but not increasing, that potential (Smith et al., 2014a).

Technical Obstacles to Greater Use of PGR

In addition to fears of disrupting productive gene combinations in elite germplasm, there are other technical obstacles to greater use of PGR. There may be limited fertility in interspecies crosses between a domesticated crop and a wild form, due to differences in ploidy level or other reproductive barriers. Common wheat, for example, is a hexaploid species, whereas most of its relatives are diploids or tetraploids, necessitating an embryo rescue and chromosome doubling step in most cases to obtain fertile progeny from a cross. Furthermore, recombination between chromosomes of wild and domesticated species is sometimes suppressed (Chetelat et al., 2000), resulting in large blocks of unadapted chromatin being transmitted to progeny along with the desired gene(s), an accentuated form of linkage drag. Techniques to increase recombination between chromosomes of different species would help alleviate this concern. Another constraint is that useful alleles may be linked to incompatibility alleles or hidden within an otherwise unadapted background, resulting in delayed maturity, unsuitable plant architecture, disease susceptibility, or unacceptable fruit or seed characteristics. This can make the trait of interest difficult or impossible to evaluate in the target growing environment without generations of selection for adaptation or crossing to adapted materials. In addition, the genes affecting important quantitative traits like yield or drought tolerance may be difficult to identify due to their small effect size. Favorable alleles at several or even many of these small-effect loci may be needed to have sufficient impact on trait expression.

Recent Perspectives by US Maize Breeders

Current opinions of breeders on the utility of PGR in breeding programs are informative for improving the relevance of the NPGS. Perspectives on this topic were gleaned from responses by 10 US public and private sector maize breeders to a recent informal questionnaire from one of the authors (Stephen Smith). There was overall concern that the availability of a relatively limited array of diversity in well-adapted US maize germplasm could limit further progress, especially with increasing biotic and abiotic challenges requiring additional useful diversity. Maize landrace accessions collected from outside the United States were seen as potentially useful sources of new germplasm, with CWR teosinte (*Zea* L. spp.) and sister genus *Tripsacum* L. being potential, but last resort, sources of new specific diversity, possibly informing the application of genome-editing methods. It was understood that the ability to find marker-trait associations facilitates access to exotic germplasm, yet this ability is dependent on the genetic complexity of the trait and requires large investments in research that may be beyond the scope of resources available to genebanks.

MAKING THE NPGS EVEN MORE RELEVANT TO PLANT BREEDING

Among the factors considered critical for increased use of PGR in plant breeding are the size and scope of collections, information about the accessions, and access to the materials (Brown, 1989). In addition to these considerations, there is a need for creative thinking on strategies for identifying beneficial alleles and incorporating them in applied breeding programs (USDA Plant Breeding Working Group, 2015).

Strengthening the linkage between PGR conservation and plant breeding is not a new concept. In their influential article in *Science*, Tanksley and McCouch (1997) promoted the identification of useful exotic alleles from germplasm collections through strategic evaluation and quantitative trait locus mapping of exotic × adapted populations. Kresovich et al. (2006) felt that the integration of evolutionary principles with molecular and population genetics would improve the ability to discover useful variation and traits in PGR collections. As examples, they offered research conducted in maize and sorghum [*Sorghum bicolor* (L.) Moench] to identify genic regions selected during domestication. McCouch et al. (2013) proposed an ambitious three-step program for mining genetic diversity in the world's germplasm banks, consisting of (i) obtaining a sample of DNA sequence data from all nonredundant, internationally accessible accessions; (ii) phenotyping a subset of accessions per se or offspring of crosses between accessions and adapted varieties; and (iii) developing an informatics infrastructure capable of integrating passport, genotypic, and phenotypic data. Undoubtedly there are many datasets which, if linked to germplasm resources, would facilitate discovery and utilization of useful trait variation. Unfortunately, there are few sources of support to pursue this task.

Optimizing Collections

Collection Coverage

Individual crop collections are complex because the many plant forms are unique in their maintenance, regeneration, and management needs. Ideally, collections are comprehensive, yet realistic and "right sized" with respect to coverage or representation of genetic variation and geographic adaptation.

Acquisition priorities must be balanced with multiple resource demands and maintenance and regeneration needs to ensure that the viability and availability of the collections prevail. Priorities are driven by recommendations to add specific germplasm with useful traits and genes, materials that may be threatened or endangered,

or germplasm provided by collectors or breeders whose programs are being discontinued. Filling these gaps may be constrained by political (access to species native to other countries), logistical (war, civil strife, distance from roads, quarantine restrictions), and economic (cost to collect and maintain) factors. Input from stakeholders, including input from CGC members, helps guide collection managers to ensure that germplasm additions to collections are relevant to current and future customers (USDA Plant Breeding Working Group, 2015). Collection gaps can be identified through consultations with stakeholders who have identified critical cultivars, unusually adapted landrace materials, or desirable phenotypes through assessments of documents to identify historically important cultivars, use of herbaria and geographic occurrence information, and by using genomic tools to identify materials with novel alleles that offer relevance to breeding programs. In addition, taxonomic, geospatial, and climatic models can be used to identify and prioritize wild species and ecogeographical collection gaps (Berger et al., 2013; Khazaei et al., 2013; Gourdji et al., 2015; Kantar et al., 2015; Khoury et al., 2015a, 2015b).

Crop Wild Relatives

The importance of CWR for the future of plant breeding cannot be overstated. It is likely that these resources will be the source of new alleles to provide plants with resistance and tolerance to biotic and abiotic threats and pressures (Maxted et al., 2016). International efforts have been initiated to identify the holdings of CWR in national and international genebanks and then prioritize materials for future collection efforts (Castañeda-Álvarez et al., 2016). Within the United States, a concerted effort has been made to use ecogeographic modeling methods to identify gaps in collections of native species (Khoury et al., 2013). Priority rankings for collections were determined based on their potential and current contributions to global agricultural production and food security, and the value of the gene pool to breeding programs (Khoury et al., 2013).

The challenges of using CWR in breeding programs such as crossing barriers and linkage drag are a significant disincentive for plant breeders. To stimulate more research on CWR, the Crop Trust (formerly called the Global Crop Diversity Trust) is establishing ~20 prebreeding projects to characterize CWR variation for traits of key relevance for plant breeding, including abiotic stress tolerance (Crop Trust, 2017c).

Plant Explorations and Exchanges

To facilitate filling gaps in germplasm collections identified by curators and CGCs, the USDA-ARS funds foreign and domestic plant explorations and exchanges to acquire plant germplasm for inclusion in the NPGS. Participants on foreign ARS-supported explorations are required to follow the NPGS Code of Conduct for Foreign Plant Explorations. Explorations must be made in compliance with the host country's laws governing access to germplasm, and permission for access to germplasm must be obtained from the host country authority designated by the national government (Williams, 2005). A portion of all germplasm collected in explorations is shared with the host country, with the remainder entering the United States through the quarantine program. Disease-free materials are incorporated into the NPGS, where they are conserved, characterized, evaluated, and made available for distribution. Domestic ARS-supported explorations must also abide by all US federal, state, and local regulations governing legally protected species and access to property.

In 2016, 12 explorations and exchanges yielded new small fruit, carrot, onion (*Allium cepa* L.), ornamentals, wild sunflower (*Helianthus* L. spp.), ash (*Fraxinus* L.), Kentucky coffeetree [*Gymnocladus dioicus* (L.) K. Koch], wild apple [*Malus angustifolia* (Aiton) Michx.], hardy kiwifruit [*Actinidia arguta* (Siebold & Zucc.) Planch. ex Miq.], wild bean (*Phaseolus* L. spp.), and wild potato (*Solanum* L. spp.) accessions from Vietnam, Spain, the Republic of Georgia, and the United States to fill gaps in NPGS collections. Globally, as landraces of unique germplasm are replaced by modern cultivars and development and/or changing climatic conditions threaten CWR, the opportunities to fill gaps are likely to diminish.

Core Collections

One barrier to more extensive use of PGR by breeders is the sheer number of germplasm bank accessions for a given crop (Table 1), most of which have not been adequately evaluated for traits of interest. To address this constraint, Brown (1989) proposed the concept of core collections, groups of accessions representing ~10% of the total collection of a crop with minimal redundancy, but including the majority of allelic diversity. This idea has been extended to development of mini-cores, representing ~1% of the entire collection (Sharma et al., 2013). The main objective of core and mini-core collections is to improve access to the entire collection. After an initial evaluation of core accessions, a researcher may be guided to accessions in the broader collection with stronger expression of a trait or in a more adapted genetic background (Brown, 1989). Core collections may also facilitate management of PGR by genebank curators by identifying sets of predefined accessions to have ready for distribution and evaluation of new traits (Marshall, 1990). Core collections have been formed based on geographical, morphological, and molecular data (Berger et al., 2013).

The identification and use of core collections in the NPGS varies by crop. According to GRIN-Global, 45 crops currently have core collections identified. In some

cases, such as apple and other fruit crops that are maintained as large perennial trees in orchard settings, core collections have been distributed and planted at multiple sites around the United States. These multilocation field trials have allowed researchers to have access to a diverse set of locally grown field trees for evaluation and breeding (Hokanson et al., 1998; Potts et al., 2012). In apple, one core set was defined to capture the diversity of the collection as a whole, and four additional core sets were designated to capture diversity from specific species or even within populations collected from a single wild species (Volk et al., 2005, 2009; Richards et al., 2009). The defined apple core sets were successfully used in physiological studies to identify materials with novel forms of diversity (Stushnoff et al., 2003; Glenn and Bassett, 2011).

Alternative to Core Collections

Another approach favors goal-focused customized subsets of accessions rather than predetermined core subsets. Although it becomes more economically tractable for the full suite of genomic and phenomic technologies to be brought to bear on the reduced sample size of core collections, there are limitations to the biological questions that can be asked and the supported conclusions. Most core collections are constructed on the basis of maximizing the number of sampled unique alleles, which are typically derived from a modest number of single-nucleotide polymorphism (SNP) marker loci having moderately high to very high minor allele frequencies (common alleles). However, given that most alleles are rare in plant species, along with increasing evidence that rare causative variants are important to explaining the genetic basis of phenotypic variation and in weak linkage disequilibrium with common alleles (Yang et al., 2010), large sample sizes are ultimately needed to identify rare alleles and provide the requisite statistical power if the intent is to identify an association between a phenotype and rare causative alleles. Even if not considering rare alleles, when conducting genome-wide association studies (GWAS), the typical size of core collections (no more than 300 accessions) is underpowered to dissect the genetic architecture of complex traits controlled by numerous genes with small allelic effects (Long and Langley, 1999). Furthermore, if the intent is to find an extreme phenotype that is biologically rare, screening the entire collection will inevitably be needed, especially if the common variants predominantly genotyped by molecular marker technologies are not predictive of the targeted extreme phenotype.

Through the eventual confluence of high-dimensional phenotypic and genomic datasets generated for the entire collection, the best future outcome would be for researchers to have the necessary information to design custom core collections for any goal, be it maximal sampling of alleles at a gene or genome-wide level, or capturing the extremes of a phenotypic distribution while achieving a desired degree of statistical power. This would allow fluid construction of core collections, tailored to the needs of individual plant geneticists and breeders.

An example of an alternative to genetic diversity-based core collections is the Focused Identification of Germplasm Subsets (FIGS) strategy (Berger et al., 2013; Khazaei et al., 2013). This strategy relies heavily on climatic and other habitat characterization data from collection sites to identify accessions that are hypothesized to possess a trait of interest. Berger et al. (2013) provided examples of selection for accessions with terminal drought tolerance and chilling tolerance according to collection site data. The major limitation of this method is that it depends on data from well-characterized sites, which may not be available for all accessions.

Improving Phenotypic Information

Phenotypic Evaluation

The NPGS has expended tremendous effort to collect, assemble, and maintain accessions. Arguably the most important challenge now in terms of time, cost, and complexity is to phenotype the collections. Without a research budget of massive size, screening collections over multiple locations and years in replicated field trials for numerous agronomic phenotypes is impossible for any germplasm repository. Therefore, a strategic design is necessary to glean the most phenotypic information from grow-outs of the collection when regenerating seed stocks. Arraying the accessions for seed increase into augmented designs (Piepho and Williams, 2016) provides an analytical framework for downstream data analysis. Furthermore, these types of designs with different sets of seed-increased accessions can be used for a series of several years to progressively collect phenotypic data from the entire collection of a species while spreading the phenotyping workload across years and allowing for a unified phenotypic dataset. Such piggybacking of phenotyping projects could be further magnified when collaborators also evaluate sets of accessions with comparable experimental designs at different field locations. For the NPGS collections, this might be done as part of a Multi-State USDA Capacity Funded project. The CGCs, described above, will fill an invaluable role by prioritizing traits for evaluation in their respective crop collections.

The continued development and implementation of phenotyping technologies is at the center of enabling phenomics on a large scale for the numerous collections that exist in the NPGS (White et al., 2012; Pauli et al., 2016). This will necessitate a conscious effort to employ low-cost phenotyping platforms that can be accurately replicated and dispersed across all NPGS stations, along with sharing to external collaborators. Leveraging the advancements in imaging, spectroscopy, deep learning

algorithms, and robotics will be critical for field-based phenotyping as the discipline of plant breeding strives to construct a platform with such specifications.

The first wave of tools might be focused on rapidly and cheaply scoring traditional agronomic phenotypes at single time points around flowering and harvest, followed by a second generation of more sophisticated tools working in concert to simultaneously measure numerous phenotypes at multiple plant developmental stages. Standardization of the phenotyping platform and data collection protocols, including the growing of standard reference genotypes, will be paramount to allow for the comparison of datasets across years and locations. To complement the field efforts, a single dedicated controlled-environment facility could be used for year-round evaluation of germplasm collections, at the very least from the seedling to juvenile phases and to maturity for the smaller stature crops. The collection of these field and controlled environment datasets and their processing in high-performance computing analytical pipelines would truly begin to enable understanding of the extent of phenotypic variability that remains untapped within the protected walls of seed banks, but which can be fully exploited only when connected to a wealth of genomics data.

Databases

Access to genebank information is essential for the enhanced use of genetic resources. The GRIN-Global system has now been implemented by eight major international and national genebanks and is being evaluated by many more. As the GRIN-Global system is developed collaboratively, there will be accelerated access to database tools developed by the user community. Ideally, use of shared, common schema and multicrop descriptor standards by genebanks, coupled with common standards used by other types of information providers, supports extraction and linking diverse information sources. Although GRIN-Global does hold a modest amount of genomic information, the crop model organism databases, the National Center for Biotechnology Information (NCBI), and specific international resources hold most of the world's publicly accessible crop genome information. Future linkages of geographic, ecological, and climate information resources, coupled with information held in genebank and genomic information systems, will support inquiries and analyses to address complex questions. Software development advances must deal with challenges in exchange of software code and applications, and maintaining multiple systems across independent entities that can be systematically updated.

Genesys and the Global Biodiversity Information Facility (GBIF) are additional key global database resources for the genebanking community. The Genesys system (Genesys, 2017) is a portal for worldwide plant genebanks for basic information on collection holdings and provides information on the state of global genetic resources and their accessibility. The GBIF provides open access to biodiversity occurrence and species data for all types of life on Earth in 35,241 datasets from 881 data publishers worldwide (GBIF, 2017). The GBIF facilitates access to standardized collection data on the basis of collections, species, and geography.

Prebreeding Activities

Prebreeding is often mentioned as a necessary prerequisite for the increased use of many types of PGR by plant breeders. "Prebreeding refers to all activities designed to identify desirable characteristics and/or genes from unadapted materials that cannot be used directly in breeding populations and to transfer these traits to an intermediate set of materials that breeders can use …" (Crop Genebank Knowledge Base, 2017b). Prebreeding often takes the form of initial hybridization between wild or unadapted germplasm and an adapted cultivar, followed by backcrosses to the adapted material, or recurrent selection within populations derived from the unadapted material (Falk, 2016).

An example of prebreeding activities is the dedicated USDA-ARS effort to identify and characterize high-value traits in the NPGS tuber-bearing *Solanum* collection and to incorporate those traits into germplasm that will benefit the US potato industry. Jansky et al. (2006, 2008, 2009) have evaluated the value of taxonomic predictivity for sources of disease and pest resistance and identified species crossable to potato germplasm that tolerate a range of biotic stresses. Intercrosses of wild species with diploid potato have been developed with new sources of tuber russetting resistance, chip color, and most recently, genetic self-compatibility that sets the stage for breeding potato as a diploid crop (Jansky et al., 2012, 2016).

Another example of a systematic prebreeding effort is the development of synthetic hexaploid wheats to facilitate the incorporation of genetic diversity from *Aegilops tauschii* Coss. into wheat breeding programs. *Aegilops tauschii* is the ancestral donor of the D genome of bread wheat, the least diverse of wheat's three genomes. Synthetic hexaploids are made by crossing diploid *Ae. tauschii* with tetraploid *Triticum turgidum* L., or *T. dicoccoides* Koern. Ex Schweinf., followed by embryo rescue and chromosome doubling (Ogbonnaya et al., 2013). The synthetic hexaploids can then be easily crossed to hexaploid bread wheats without the barrier of ploidy differences. Over 1500 synthetic hexaploids have been developed, notably by the CIMMYT in Mexico (Ogbonnaya et al., 2013). Synthetic hexaploids and lines derived from them have been shown to have high levels of disease and pest resistance, favorable root traits, and tolerance to abiotic stresses (Reynolds et al., 2007; Ogbonnaya et al., 2013; Becker et al., 2016).

A successful use of a synthetic hexaploid in the United States has been the incorporation of resistance to greenbug [*Schizaphis graminum* (Rondani)] into the widely planted hard red winter wheat cultivar 'TAM 112' (PI 643143) (Rudd et al., 2014).

Gorjanc et al. (2016) evaluated new breeding strategies to transfer useful variation for polygenic traits from maize landraces into well-adapted germplasm using genomic selection coupled with stochastic simulation. They concluded that initiating prebreeding directly in landrace germplasm was more effective than selection after testcrossing to elite material, because the latter method rapidly reconstructed the elite genome. Other examples of research with the goal to more efficiently utilize exotic germplasm include Prada (2009), Posadas et al. (2014), Cowling et al. (2017), and Wu et al. (2016).

As technologies have been applied in maize breeding to increase the precision of selection, one outcome has been fixation of large sections of the genome within a heterotic pattern, or increased genetic separation of breeding pools and decreased diversity in the ancestry of individual lines (van Heerwaarden et al., 2012). The Germplasm Enhancement of Maize (GEM) project was formed in response to recognition by the commercial sector that generation of useful, diverse maize germplasm needs to continue (Pollak and Salhuana, 2001). The project is a unique example of public-private sector collaboration and has focused on introgression of tropical germplasm, collaborative testing, and public release of breeding products. More than 300 conventionally derived prebreeding lines have been released from the GEM programs in Raleigh, NC (50% tropical), and Ames, IA (25% tropical). More than 200 doubled haploid exotic lines have been released jointly by USDA-ARS and Iowa State University. Designated as BGEM lines, the doubled haploids were not evaluated and selected for agronomic traits, unlike the GEM lines, and therefore are a resource for mining novel alleles (GEM, 2014, 2017).

Incorporating Genotypic Information

Targeted Sequencing of Accessions

The tremendous technological advances in DNA sequencing have opened up the potential to generate an extensive catalog of genomic resources for even the most orphan of crops (e.g., African Orphan Crops Consortium, 2017). With many of the world's most important crop species having or projected to have a draft reference genome sequence, efforts have turned to a number of whole-genome resequencing projects consisting of hundreds to thousands of accessions spanning the domesticated to wild continuum for a single species. Additionally, projects now exist to construct the "pangenome" (the full complement of genes) of a given species, allowing the extent of gene content to be sampled, characterized, and connected to phenotypic variation (e.g., Montenegro et al., 2017). Not only can this multitude of genome sequences be used to accelerate complex trait dissection and applied breeding endeavors, but they can also be used to design very low-cost polymerase chain reaction (PCR)-based genotyping assays. Targeting low-to-moderately repetitive sequences with a couple of primer pairs in rAmpSeq (Buckler et al., 2016), or a number of low-copy sequences with many primer pairs in AmpSeq (Yang et al., 2016), have notable advantages over the need for restriction enzymatic digestion, as is used for genotyping-by-sequencing (Elshire et al., 2011), although rAmpSeq and AmpSeq sequence fewer loci at higher coverage. Thus, these PCR-based approaches are ideal for genotyping a large number of NPGS accessions, as well as for surveying levels of heterogeneity and heterozygosity within accessions. As sequencing costs continue to plummet, entire core collections can be resequenced at lower coverage, followed by efficient imputation of missing marker genotypes (Swarts et al., 2014). Availability of improved sequence or molecular marker data will not only allow improved gene discovery through GWAS, it will also guide breeders to the geographic regions or taxa with greatest genetic diversity, as indicated in *Capsicum* L. spp. by Silvar and Garcia-Gonzalez (2016).

"Turbocharging" Genebanks

A creative approach for integrating genotypic and phenotypic information for genebank accessions was recently provided by Yu et al. (2016). They employed a genomic prediction strategy to identify promising sorghum accessions for biomass production. A set of 962 accessions was first characterized genetically with >300,000 SNPs via genotyping-by-sequencing. A subset of 299 accessions that represented the genetic diversity of the entire set was then selected as the training set and was evaluated for biomass yield and related characters in three environments. Genomic prediction models developed from the training set were then applied to the larger set to identify promising accessions, and the models were validated in several ways. The authors felt this strategy could be applied broadly to exploit (or "turbocharge") germplasm collection data more efficiently, and their work is being validated. Improvements in high-throughput phenotyping, bioinformatics infrastructure, optimization of the training and validation sets of accessions, and incorporation of genotype-by-environment interaction into prediction models will aid this effort.

Genome Editing

The development of new biotechnologies for precise site-specific DNA modification (collectively known as genome editing) has created new opportunities for plant breeding and genetics (Cardi, 2016; Liu et al., 2016).

These modifications include gene knockouts, substitution of a single nucleotide with another, and replacement of an entire gene; applications of the technology have included disease resistance, herbicide resistance, and quality trait improvement (Cardi, 2016). There are several ways in which these technologies might be applied with respect to PGR: (i) identifying beneficial alleles through association or functional genomic studies of PGR collections, followed by site-specific editing of elite cultivars; (ii) correcting a deficiency in a landrace or heirloom variety (such as those related to maladaptation) while leaving the genetic background intact; and (iii) transfer of entire genes from a related genotype into a crop cultivar (so-called cisgenesis) (Cardi, 2016). Despite these developments, the maintenance of germplasm collections, not just their DNA sequences, will remain of utmost importance. Genome editing relies on detailed information on phenotype-genotype associations, and the phenotypes of importance in the future (e.g., resistance to a new disease biotype or a novel quality factor) cannot be known in advance. Therefore, access to seeds or other propagules to allow evaluation of whole plants in appropriate agricultural settings will be required into the foreseeable future.

Enhancing Collaborative Activities

International Collaborations

Collaborations are crucial to the success of future networked international genebanking systems. By fully understanding the extent and coverage of >1700 national and international genebanks around the world, one can identify gaps in the global system. With its vast holdings, public database, worldwide distribution policy, and innovative research programs, the NPGS plays a key role in the international genebanking community.

To meet worldwide genebank management needs, the Crop Trust was established in response to a need for long-term funding to support the conservation "in-perpetuity" of PGR through the use of an endowment fund (Crop Trust, 2017b). The Crop Trust has oversight and financial responsibility for 11 global genebanks that are part of the CGIAR Consortium of International Agricultural Research Centers. In 2006, the Crop Trust, which is an international nonprofit organization, entered into a relationship agreement with the governing body of the International Treaty on Plant Genetic Resources for Food and Agriculture, which recognizes the Trust as an "essential element" of the Treaty's funding strategy in regards to the ex situ conservation and availability of PGR for food and agriculture (FAO, 2017).

The NPGS works closely with the Crop Trust, particularly with regard to the development of GRIN-Global plant genebank management software, the DivSeek project (DivSeek, 2017; see below), the conservation of CWR, contribution of materials to the Svalbard Global Seed Vault (for which the NPGS is the largest contributor), contribution of data to the Genesys online portal (Genesys, 2017), development of optimized cold-storage and cryopreservation technologies, and the development of Global Crop Conservation Strategies (Crop Trust, 2017a).

The DivSeek initiative arose from the recognition that the value of genebank PGR cannot be fully realized unless the materials are characterized and evaluated and the information is made publicly available. DivSeek partner organizations have a mission to "enable breeders and researchers to mobilize a vast range of plant genetic variation to accelerate the rate of crop improvement and furnish food and agricultural products to the growing human population" (DivSeek, 2017). A number of working groups have been established to organize this immense effort. As key players in the international genebank community, the NPGS and other US institutions play prominent roles in both leadership and active participation in these working groups.

Training and Outreach Needs for PGR

For the value of germplasm bank accessions to be fully realized, additional research and training opportunities are needed for the incorporation of unadapted germplasm into breeding programs (USDA Plant Breeding Working Group, 2015). The use of PGR is sometimes included as a topic in university plant breeding courses, and practical research and training occurs through student and postdoctoral research projects. For example, the NPGS genebank locations frequently host visiting students, scientists, policymakers, etc., with shared interests in germplasm use and conservation. Still, a more systematic effort is needed. The best ways to incorporate PGR into breeding populations are not always obvious and may differ depending on the species, type of germplasm, and breeding objective. Some relevant questions for which both research and training are needed include the following: are there gaps in the collection that might be filled? Is evaluation of accessions per se a valuable practice, or should accessions first be crossed into adapted material? How many backcrosses to adapted material are advisable prior to evaluation to make the most efficient use of time and resources? How should new sources of genetic diversity be brought into populations undergoing genomic selection, which may rapidly deplete diversity? The CGIAR maintains an extensive set of learning resources as part of the Crop Genebank Knowledge Base (Crop Genebank Knowledge Base, 2017a), including a self-paced training module on prebreeding and several other modules on genebank management. Other potential opportunities for training include workshops at annual meetings of the Crop Science Society of America, American Society for Horticultural Science, or National Association of Plant Breeders and 1- or 2-wk dedicated courses at relevant land-grant universities or CGIAR centers.

Ultimately, the ability to achieve the vision of a fully functioning and coordinated germplasm system, as outlined above, will depend on public support for the NPGS and the resulting funding resources needed to accomplish the interconnected objectives. Therefore, all parties that benefit, directly or indirectly, from the use of PGR have an interest and responsibility in raising awareness among public audiences about the current (and even greater potential) value of NPGS collections. Outreach programs might take the form of attractive and engaging websites, popular press articles, show-and-tell visits to K-12 schools, and tours and field days at NPGS sites. It is also important that breeders and their employers give due recognition when NPGS germplasm is incorporated into a germplasm or cultivar release. There is a great deal of latent support among the public for NPGS activities, but those involved in PGR conservation and use need to increase their outreach efforts so the public recognizes their long-term contributions to society.

Sharing Responsibility

The numerous activities outlined here are well beyond the ability of the NPGS to implement on its own. The core responsibilities of genebanks should remain the preservation of healthy, viable germplasm, timely regeneration of accessions, distribution of plant materials to the user community, and increasingly, development and enhancement of databases to store and provide access to organized, searchable data in a form useful to plant breeders. Other activities, such as large-scale genotypic and phenotypic evaluation of accessions, prebreeding, and training, will require coordinated input from other units of USDA-ARS, universities, the private sector, and nongovernmental organizations. The CGCs provide opportunities to develop partnerships among federal, state, and industry members. The USDA-NIFA can continue to play a constructive role through grant funding that encompasses germplasm enhancement, prebreeding, allele mining, and other research that exploits NPGS holdings. Public-private collaborations have made major contributions in researching and utilizing PGR through prebreeding projects including the GEM project for maize (GEM, 2017) and the Wheat Genetic Resources Center (WGRC, 2017) for wheat. Similar collaborations for other crops are underway and encouraged, given the likely continued trend toward declining resources for agricultural research in the public sector. Everyone involved in the conservation and use of PGR has a role to play in strengthening public awareness of and support for the NPGS.

CONCLUSIONS

With the multitude of challenges facing agriculture now and in the future, the genetic diversity conserved in the world's germplasm banks needs to become more available and useful to plant breeders. The NPGS will enhance its relevance to plant breeding programs, provided there is (i) ongoing attention to closing the gaps in NPGS collections, especially for CWR; (ii) a major increase in efforts to phenotype and genotype accessions using standardized methods; (iii) public availability of the resulting data through enhanced information content of the GRIN-Global system and improved interoperability with other databases; (iv) increased attention to prebreeding activities; (v) improved training opportunities for students and practicing plant breeders in best practices for incorporating PGR in breeding programs; and (vi) expanded outreach efforts to strengthen public support for the NPGS. Given the resource constraints of individual entities, we believe these steps will be implemented most effectively through shared responsibility and coordination among USDA, land-grant universities, the private sector, and international partners.

Conflict of Interest

There may be a perceived conflict of interest in that coauthors Volk and Gardner work for the USDA National Plant Germplasm System, which is the subject of the article.

Supplemental Material Available

Supplemental material for this article is available online.

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