Received: 22 January 2023 | Accepted: 15 April 2023

DOI: 10.1002/csc2.21003

Crop Science

ORIGINAL ARTICLE

Plant Genetic Resources

Safeguarding plant genetic resources in the United States during global climate change

Gayle M. Volk[1] | **Dan Carver**[1] | **Brian M. Irish**[2] | **Laura Marek**[3] | **Anne Frances**[4] | **Stephanie Greene**[1,5] | **Colin K. Khoury**[6,7] | **John Bamberg**[8] | **Alfonso del Rio**[9] | **Marilyn L. Warburton**[2] | **Peter K. Bretting**[10]

[1]USDA-ARS National Laboratory for Genetic Resources Preservation, Fort Collins, Colorado, USA

[2]USDA-ARS Plant Germplasm Introduction and Testing Research Unit, Pullman, Washington, USA

[3]Agronomy Department, Iowa State University, North Central Regional Plant Introduction Station, Ames, Iowa, USA

[4]USDA-ARS National Germplasm Resources Laboratory, Beltsville, Maryland, USA

[5]Retired

[6]San Diego Botanic Garden, Encinitas, California, USA

[7]International Center for Tropical Agriculture (CIAT), Cali, Colombia

[8]USDA-ARS, U.S. Potato Genebank, Sturgeon Bay, Wisconsin, USA

[9]Department of Horticulture, University of Wisconsin, Madison, Wisconsin, USA

[10]USDA-ARS Office of National Programs, Beltsville, Maryland, USA

Correspondence
USDA-ARS Office of National Programs, Beltsville, MD 20705–5139, USA.
Email: Peter.Bretting@usda.gov

Assigned to Associate Editor Irwin L. Goldman.

Abstract

Plant genetic resources (PGR) underpin the security of global agriculture. Rapid global climate change presents formidable challenges for ex situ and in situ PGR management programs that operate over extended timeframes. The U.S. Department of Agriculture National Plant Germplasm System (NPGS) maintains more than 605,000 PGR accessions representing over 16,300 plant species in 20 genebank locations. These PGR are maintained in cold storage as seeds and vegetative tissues that must be periodically regenerated; or as actively growing plants in fields, greenhouses, screenhouses, and in vitro; or in some cases within in situ reserves. The complicated relationships between crops and their growth environments present unique challenges regarding PGR maintenance under a changing climate. Here we present potential effects of climate change on ex situ PGR maintenance and reproductive success, pollinators and beneficial insects, pathogens and pests, infrastructure considerations, and wild populations within NPGS in situ reserves. We provide a novel tool that summarizes past US temperature and precipitation data alongside future climate projections to guide ongoing planning for the effects of climate change for NPGS genebanks throughout the United States. A series of case studies exemplify instances where climate change has already impacted NPGS PGR management. Ongoing improvements to NPGS PGR management in response to climate change require continued observations of the current effects, careful and innovative planning, and creative approaches to ensure that PGR are successfully conserved for future generations.

Abbreviations: CWR, crop wild relatives; NLGRP, National Laboratory for Genetic Resources Preservation; NPGS, National Plant Germplasm System; PGR, plant genetic resources; SOS, Seeds of Success; USFS, U.S. Forest Service; USPG, U.S. Potato Genebank; WCBA, Wild Chile Botanical Area.

1 | INTRODUCTION

Core Ideas

- Plant genetic resources (PGR) are crucial for continued crop improvement that underpins global food security.
- Climate change can threaten PGR safeguarded by the USDA-ARS National Plant Germplasm System (NPGS).
- Approaches developed by the NPGS to adapt its PGR management operations to climate change are reviewed.
- The new NPGS Climate Futures Application delivers key estimates for future climatic conditions at NPGS locations.
- The NPGS's PGR management operations can adjust to climate change using current experience and those estimates.

Plant genetic resources (PGR; synonymous with plant germplasm) comprise the organs and tissues (seeds, fruits, cuttings, pollen, tissue cultures, etc.) by which plants can be propagated. PGR provide the raw genetic materials instrumental for continued genetic gain through crop breeding that is crucial to food security. PGR underpin "the green line that stands between humanity and calamity" (Bretting, 2018). Without ready access to PGR, progress in crop research and breeding can be severely hampered. Furthermore, if PGR that constitute critical components of traditional cultures and agricultural economies were lost, the survival of key elements of traditional and indigenous cultures and knowledge might be threatened (Nabhan, 1989).

Climate change, the commonly used term for rapid global warming, threatens the persistence of crop agriculture (Pörtner et al., 2022). The consequences of climate change include rising temperatures, severe wildfires, increasingly damaging storms, flooding, drought, sea level rise, and threats to biodiversity (Pörtner et al., 2022). Climate change endangers the survival of plant communities (Thuiller et al., 2005) that include crop wild relatives (CWR; Dempewolf et al., 2014), PGR that are vital to the survival of some elements of traditional cultures, and that contain genes and traits valuable for crop production and protection (Castañeda-Alvarez et al., 2016; Dempewolf et al., 2017; Jarvis et al., 2008). Ex situ conservation in genebanks currently constitutes the most widely adopted strategy for safeguarding CWR and PGR from threats such as loss of natural and agricultural habitats, cultural and societal changes, and other factors (Byrne et al., 2018). Nevertheless, ex situ conservation is not fail proof: Fu (2017) and Khoury et al. (2021) comprehensively cataloged the factors, including climate change, contributing to the vulnerability of PGR protected ex situ in genebanks. Those factors can cause not only complete loss of PGR, but also genetic drift, genetic erosion, and overall reduction of diversity.

This essay describes some of the dangers from climate change faced by PGR protected in the United States. It focuses particularly on the actual or potential effects of climate change on PGR management in the U.S. National Plant Germplasm System (NPGS; Byrne et al., 2018) and covers the complementary approaches of in situ, dynamic PGR conservation and ex situ, static PGR conservation (Bretting & Duvick, 1997). This essay examines specific case studies from the NPGS's ex situ PGR management programs. The experiences and results from several in situ conservation projects, conducted by the NPGS in partnership with land management agencies, are also recounted. Methods to prepare the NPGS genebanks for climate change are provided, including a novel software application for rapidly delivering temperature and precipitation forecasts and climatic trends for NPGS genebank locations. Finally, the insights gained from this review are summarized as a means for identifying priorities for subsequent analyses and research, and future prospects are assessed for successfully safeguarding PGR from the effects of climate change.

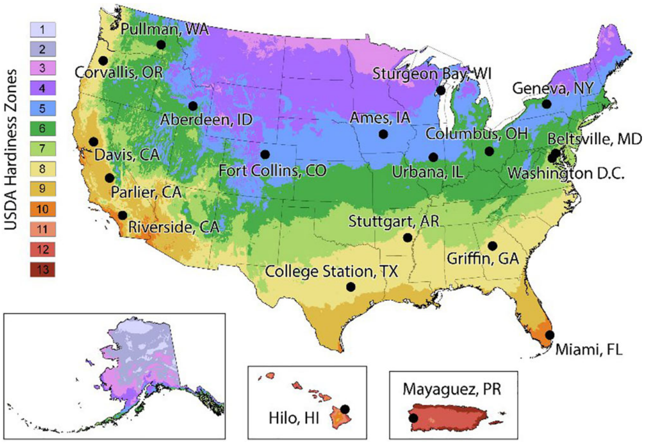

FIGURE 1 The 20 locations for National Plant Germplasm System genebanks (indicated by black dots) projected on the 2012 USDA Plant Hardiness Zone Map. Collectively, these genebanks are located in most of the different growing areas for US crops.

2 | PGR MANAGEMENT IN THE NPGS

The U.S. NPGS comprises genebank and support units at 20 geographical locations (Figure 1). Each NPGS genebank unit is operated by the USDA-Agricultural Research Service (ARS), often in partnership with land-grant universities. At this writing, the NPGS manages PGR ex situ in the form of 605,000+ accessions (plant samples) of 16,300+

species (USDA-ARS GRIN-Global, 2022a). These accessions encompass highly bred contemporary cultivars; traditional and heirloom cultivars developed historically and even prehistorically; genetic stocks that serve as research tools; wild species for ecological land restoration and research; and CWR for major and specialty crops. The NPGS acquires, maintains, characterizes, evaluates, documents, and distributes those PGR and associated information. The NPGS also conducts applied research to devise more efficient and effective management procedures for PGR and to add value to accessions through characterization and evaluation. In some cases, NPGS scientists work to improve PGR via genetic enhancement (Byrne et al., 2018).

PGR can contain novel alleles and allelic combinations that control plant responses to pests and pathogens, daylength, and extreme temperature and moisture levels (Byrne, 2023; Cortés & López-Hernández, 2021). In particular, CWR can encompass allelic diversity that was not captured or maintained during the domestication bottleneck, and thus could be valuable sources of new traits for crop improvement. Assessments of the status of CWR both in situ and ex situ will guide future acquisition and preservation efforts on a national and global scale (Castañeda-Álvarez et al., 2016; Dempewolf et al., 2014; Eastwood et al., 2022; Khoury, Carver, Greene et al., 2013, 2020; Ramirez-Villegas et al., 2022; Vincent et al., 2019).

By virtue of its mandate, the NPGS has emphasized PGR management ex situ, rather than in situ through protected land reserves. The USDA-ARS is not a land management agency but partners with other agencies and institutions (USFS & USDA-ARS, 2014) that manage lands where several in situ conservation projects for the PGR of US CWR are located, such as for chile peppers (Khoury, Carver, Barchenger et al., 2020) and cranberries (Khoury, Greene et al., 2020). Linking in situ and ex situ conservation in a complementary (or integrated) approach can efficiently increase the overall amount of genetic diversity conserved. In situ conservation preserves the intraspecific diversity in the entire plant population rather than just a sample of the population held in ex situ collections (USFS & USDA-ARS, 2014). As such, the NPGS's participation in such in situ conservation projects will likely expand in the future and efforts to do so are described in this review.

2.1 | Ex situ PGR management

Diverse PGR collections in NPGS genebanks are maintained as seeds in storage or as actively growing plants. Plant collections maintained ex situ have the advantage of being readily available for evaluation and distribution. Seed collections are often maintained in refrigerated (+4°C) or freezer (−18°C) conditions at low relative humidity levels that have been optimized for long-term storage (FAO, 2014). Seed lots are replenished through grow-outs (regenerations) when their quantities decline due to insufficient inventory or low viability. Most seed regeneration activities take place in the field, which expose the PGR to prevailing climatic conditions. Drought can affect plant establishment and growth throughout the season, as can other extreme weather. Many factors determine successful seed production including temperature and humidity effects on flower and seed development, pollen viability, and pollinator activity. Increasing night temperatures are also a serious confounding factor for seed production and overall yield (Desai et al., 2021; Hatfield & Pruger, 2015; Sadok & Jagadish, 2020), in part because plants cannot recover from high daytime temperatures affecting the circadian clock, pollen viability, and many other physiological and biochemical processes. Field regenerations also involve exposure to pests and pathogens, whose presence is often determined by specific weather conditions and changing climatic factors (Taylor et al., 2014).

Successful regeneration involves surmounting many challenges even in the absence of climate change. Diverse accessions of a crop likely cannot all be regenerated successfully under similar environmental conditions. For example, wild sunflower (*Helianthus* L.) species from southern latitudes do not flower if they are grown in the Northern United States. These accessions are regenerated by the NPGS at Parlier, CA where the Central Valley provides a long and dry growing season for successful seed production. In some climate change scenarios, wild species might have a greater resilience and capacity to adapt to climate change. In contrast, domesticated cultivars might have narrower parameters (i.e., temperature, moisture) for phenological processes such as flowering. In addition, accessions of inbred or introgressed cultivars can yield poorly due to reduced fertility resulting from the breeding process. To mitigate the effects of climate change on the sometimes inherently poor yielding PGR, increased irrigation applications or protective infrastructure can be necessary.

Many fruit, nut, and some vegetable PGR are maintained as plants in the field, greenhouse, screenhouse, or as in vitro cultures because seeds do not represent the desired genotype; the plants do not produce seeds; the regeneration cycle is long; or because seed storage methods have not yet been established (Panis et al., 2020; Volk & Walters, 2003). These plants require pruning, pest and disease control, irrigation, and field maintenance throughout the year (Postman et al., 2006). They also undergo weather-dependent physiological processes that include winter dormancy, spring bud break, flowering, pollination, and fruit set. In addition, they are susceptible to natural disasters (e.g., fires, hurricanes, and windstorms) that might damage protective structures or the plants themselves. Field, greenhouse, and screenhouse plants must be repropagated when plants reach the end of their life cycles or when they are lost due to abiotic or biotic (pests and pathogens) stresses. Maintaining PGR in vitro is labor intensive, and their survival depends on skilled staff who perform routine transfers to fresh medium. They are also susceptible to growth room arthropod infestations (e.g., spider mites [*Tetranychus urticae* Donnadieu, 1875] and thrips [*Thrips physapus* Linnaeus, 1758]), endophytic contamination, a loss in culture vigor, and potentially by somaclonal variation (Panis et al., 2020). Plants actively growing in vitro must be repropagated frequently, and those in cold storage will not survive beyond a year or two without repropagation.

The anticipated impact of climate change on PGR maintenance and regeneration makes safety duplication of PGR collections even more urgent. Secure storage at two separate geographic locations can guard against loss if PGR in the field are damaged by extreme weather and natural disasters exacerbated by climate change. Genebank best practices (FAO, 2014) recommend a long-term off-site secure back-up for PGR.

The National Laboratory for Genetic Resource Preservation (NLGRP) in Fort Collins, CO was built and is managed to withstand catastrophes and to serve as the NPGS long-term PGR back-up facility by providing −18˚C and liquid nitrogen PGR storage capacities. Depending on the type of PGR, plant materials can be backed-up at the NLGRP as seeds, embryos, dormant buds, shoot tips, pollen, or other plant propagule types. Approximately 82% of the NPGS seed accessions are currently stored at the NLGRP, where orthodox seeds, typified by those of many temperate annual crops, are secured according to standard methods (FAO, 2014; Pathirana & Carimi, 2022). Orthodox seeds can be dried and stored at cold temperatures without decreasing seed viability; however, seeds with recalcitrant or intermediate storage characteristics, including those of many tropical, perennial, or large-seeded species, might need to be cryopreserved as seeds or embryos. Crops that are clonally propagated can be backed-up by duplicate plantings, in vitro or as cryopreserved shoot tips or dormant buds. Cryopreservation is costly, but not as costly as maintaining duplicate collections of field-grown plants in different geographic locations, especially as climate change contributes to unpredictable field conditions (Dulloo et al., 2009; Keller et al., 2013). Cryopreservation is also not as costly in the long term as is in vitro storage, with its requirements for ongoing subculturing and whole plant regeneration. Cryopreservation will become increasingly important for backing up clonally propagated species and those with recalcitrant and intermediate seed because it avoids the risks associated with maintaining PGR in field cultivation.

2.2 | In situ reserves for PGR

The conservation of PGR in situ ensures that dynamic evolutionary forces can continue to influence plant adaptation and survival (Bretting & Duvick, 1997; Riordan & Nabhan, 2019). When land is designated as an in situ conservation area, the associated ecosystem is also conserved, ensuring that plant populations survive and coevolve with native ecosystems. Wild plant species occurring naturally in ecological communities throughout the world include CWR—the progenitors of domesticated crop varieties and species with close genetic relationships to crops—and wild plants used directly by people (Greene et al., 2018). More than 600 plant species native to the United States are CWR of 37 different crops (Warschefsky & Rieseberg, 2021) and have tremendous potential to contribute to the productivity, sustainability, and quality of agronomic and horticultural crops. Documenting and protecting CWR have advanced significantly in recent years (Castañeda-Álvarez et al., 2016). In the United States, many of these advances have been led by the NPGS (Greene et al., 2018; Greene, Williams et al., 2019; Khoury, Carver, Greene et al., 2020). Nonetheless, more than half of the CWR native to the United States are still insufficiently protected either in situ or ex situ (Khoury, Carver, Greene et al., 2020, Khoury, Greene, 2020). In view of their importance, additional in situ reserves will be considered in the future whenever inter-agency cooperation enables their establishment.

Many native CWR can be conserved in situ in the United States on lands managed by federal or state agencies that likely already confer some protection to wild plant populations (Williams & Greene, 2018). The NPGS developed a process to select in situ conservation sites for CWR and a policy to guide the establishment of agreements between the NPGS and landholding agencies for in situ conservation (Pavek et al., 2003; USFS & USDA-ARS, 2014; Williams & Greene, 2018). In particular, the NPGS and the U.S. Forest Service (USFS) developed a Joint Strategic Framework on the Conservation and Use of Native CWR in the United States (USFS & USDA-ARS, 2014). This framework outlines two approaches to establishing In Situ Genetic Resource Reserves (IGRRs) for complementary in situ and ex situ conservation. The crop-specific approach establishes IGRRs for populations of CWR for specific crops based on several factors, including the population size, genetic profile, sustainability, and ease of access for monitoring and collecting samples for ex situ conservation. The protected area approach focuses on land encompassing multiple important taxa of CWR for several crops. Criteria for designating these protected areas as IGRRs include the number and significance of CWR present and some of the same factors included in the crop-specific approach.

In the United States, two sites have been officially designated to protect CWR in situ: the Cranberry Glades Botanical Area in the Monongahela National Forest in West Virginia, and the Wild Chile Botanical Area (WCBA) in the Coronado National Forest. Originally designated to conserve the wild chile, or chiltepin (*Capsicum annuum* var. *glabriusculum* (Dunal) Heiser & Pickersgill), the WCBA provides habitat for many other CWR, serving as an example of both the crop-specific approach and the protected area approach (Khoury et al., 2020; Riordan & Nabhan, 2019). In addition to conserving the wild chile, the NPGS has selected in situ conservation sites for three of the most imperiled wild grape species (*Vitis* L. spp., Pavek et al., 2003). The crop-specific approach was also applied to select in situ reserves for a pilot project focused on two wild cranberry species (Rodriguez-Bonilla et al., 2020). The NPGS continues to collaborate with the USFS and other landowners to officially designate as IGRRs the selected in situ conservation sites for wild grapes and cranberries.

3 | ESTIMATING CLIMATE CHANGE EFFECTS AT NPGS GENEBANK SITES

PGR management will be affected by climate change in many ways. Warmer temperatures, altered precipitation patterns, and more frequent extreme weather will have an impact on PGR maintenance, including plant physiology and reproductive processes, as well as biotic interactions. Estimating quantitatively the scale of climate change effects at NPGS sites informs preparations for safeguarding NPGS PGR.

The atmospheric concentration of CO_2 has increased from 280 ppm at the start of the Industrial Age, to 420 ppm now (NOAA, 2022). Increased atmospheric CO_2 affects many climatic components, but one of the strongest effects is higher atmospheric temperatures (annually and seasonally), with more days of extreme temperatures, particularly in temperate locations. The current pattern of warmer night temperatures and fewer days of extreme cold is predicted to continue into the future (Dox et al., 2020). Future temperature and precipitation levels have been predicted based on regional models (Vano et al., 2015). The site specificity of these models makes it difficult to formulate generalized approaches, although it can assist with planning at specific locations.

Future precipitation levels are difficult to predict and cannot be forecast reliably across a geographic area as large as the United States (Vano et al., 2015). Some locations will experience more frequent heavy precipitation events and flooding. Others will have reduced precipitation and drier soils, with increased vulnerabilities to wildfire. Lower snowpack and shorter winters will reduce the availability of water for agriculture. Higher sea levels could result in saltwater contamination of irrigation water sources and flooded agricultural fields, resulting in salt deposition (Gibson et al., 2021). Although models can help to predict future climate conditions, the decreased accuracy of predictions over longer timeframes represent a major challenge, particularly for precipitation (Vano et al., 2015).

Optimal PGR management practices are determined by the nature of the crop and the environmental conditions at the genebank. Planning ex situ and in situ PGR management in the United States to account for the changing climate requires integrating information from numerous sources such as the Intergovernmental Panel on Climate Change (IPCC, 2022), USDA Climate Hubs (2022), the USDA Forest Service (2022), and others. The NPGS needs climatic predictions specific to each NPGS site to prepare for climate change. Consequently, an application titled “NPGS Climate Futures,” has been developed and made publicly available at https://geocentroid.shinyapps.io/npgsclimatefutures

The NPGS Climate Futures Application provides visual displays and downloadable datasets for climate predictions for 31 ex situ and 6 in situ locations associated with the NPGS. Data for the climate prediction are generated for four scenarios of shared socioeconomic pathways (SSP): Low greenhouse gas emissions (SSP1–2.6), intermediate greenhouse gas emissions (SSP2–4.5), high greenhouse gas emissions (SSP3–7.0), and very high greenhouse gas emissions (SSP5–8.5) (Pörtner et al., 2022). All climatic prediction data were generated from an ensemble model consisting of 10 individual climate models with the lowest average weighted normalized relative error for the continental United States (Ashfaq et al., 2022; Fick & Hijmans, 2017; Vano et al., 2015). Historic temperature and precipitation data were gathered from WorldClim, based on observed measurements available from 1970 to 2000 (see Supporting Information).

For NPGS locations, the application presents data for six temperature bioclimatic indicators: BIO5 (Average Maximum Temperature of Warmest Month), BIO6 (Average Minimum Temperature of Coldest Month), BIO8 (Mean Temperature of Wettest Quarter), BIO9 (Mean Temperature of Driest Quarter), BIO10 (Mean Temperature of Warmest Quarter), and BIO11 (Mean Temperature of Coldest Quarter); and six precipitation bioclimatic indicators: BIO13 (Precipitation of Wettest Month), BIO14 (Precipitation of Driest Month), BIO16 (Precipitation of Wettest Quarter), BIO17 (Precipitation of Driest Quarter), BIO18 (Precipitation of Warmest Quarter), and BIO19 (Precipitation of Coldest Quarter) (O’Donnell & Ignizio, 2012). In the examples provided in this essay, graphical visualizations of data are provided for historic data (1970–2000), as well as predicted data for the following timeframes: 2021–2040, 2041–2060, 2061–2080, and 2081–2100. Tabulated information for bioclimatic indicators and mean monthly maximum temperature, mean monthly minimum temperature, and total monthly precipitation data can be downloaded from the NPGS Climate Futures Application.

4 | PROJECTED IMPACTS OF CLIMATE CHANGE ON NPGS PGR MANAGEMENT

4.1 | Climate change effects on ex situ PGR management

The effects of climate change currently relevant to NPGS PGR management are projected to intensify in the future. Changes in temperature and precipitation can alter the growth and reproduction of plants, reduce the abundance of beneficial wildlife that act as pollinators and seed dispersers, and increase the threats from pests and pathogens. Ex situ PGR management entails assessing these effects and adapting to changing field conditions. Many challenges described below constitute more severe cases of current operational difficulties. Others will be new but can be foreseen and planned for; but some will be too complicated to predict or project and must be addressed as they occur. Regardless of the challenge, the effects of climate change on PGR must be minimized before genetic diversity is lost and NPGS infrastructure is damaged.

4.1.1 | Plant reproductive success

Plant growth and reproduction are affected by intricate interactions of CO_2 levels, temperature, and precipitation. Growth and reproduction requirements of some crops have been extensively studied, while others have not. Regardless, it is still unknown how each species will adapt to the changing conditions at each site where they are grown; however, analyzing existing data, we review scenarios of how the growth and reproduction of PGR will be affected.

The effect of increased CO_2 on plant growth has been extensively studied. Some crops such as wheat, rice, and soybeans yield more in response to increased CO_2 (up to a saturation point) but maize, sugar cane, sorghum, and millet are much less responsive (Ainsworth & Long, 2020; Cho, 2022; Hatfield et al., 2011). Nitrogen or phosphorus, and not carbon, are often the nutrients limiting biomass production (Du et al., 2020; Terrer et al., 2019); but, when nitrogen is well supplied by fertilizer, a positive growth effect can be observed from increased CO_2. Seed regeneration of PGR in the NPGS usually takes place under optimal nutrient conditions, so for some species, increases in seed yield can be expected in response to increased atmospheric CO_2 with climate change.

On the other hand, increasing temperatures caused by increased atmospheric CO_2 can offset any photosynthetic gain from increased CO_2 concentrations. Although optimal growth temperatures have not been determined for many plant species, increased temperature can impede growth and reproduction for many species studied to date (Moore et al., 2017). Exposure of plants to temperature extremes at the onset of reproduction decreases fruit and grain production (Hatfield & Pruegar, 2015; Lohani et al., 2021; Pravallika et al., 2020). An especially critical variable is maximum night temperature, which has been increasing faster than the daytime temperature maxima (Hatfield & Pruegar, 2015). Cooler nighttime temperatures enable plants to recover physiologically. High temperatures also can reduce pollen viability, especially for species with determinant flowering that coincides with hottest months of the year. High temperatures during embryo and seed development can result in embryo abortion or in low-quality seed. In addition to the direct effect of higher temperature on seed production, higher and fluctuating temperatures can cause erratic rainfall in areas that had been ideal for crop production in the past. Irregular amounts of moisture can affect the development of fruit and consequently seed, especially of tree fruits that mature over a long period. Some CWR species might be affected less by extremes in temperature and rainfall, especially those that can flower throughout the growing season and mature seeds during cooler periods.

For all these reasons, higher temperatures can reduce the amount and quality of viable seed produced by each PGR regeneration. To mitigate these effects, curators could plant regeneration plots earlier in the season. If these early plantings do not experience damaging late frosts, higher-quality seeds could mature before the hottest months of the year. But species with flowering times regulated by daylength might not be amenable to earlier planting. Multiple plantings and harvests could capture optimal seed maturation times under these more variable conditions, and larger plots with more plants might produce sufficient seeds.

4.1.2 | Pollinators and other beneficial insects

For regenerating PGR, naturally occurring and managed insect pollinators are often key to successful production of needed quantities and qualities of seed during regeneration activities. Climate change effects have been documented for plant phenology when synchrony of flowering and pollinator activity shift due to warming, with predicted trends leading to increased asynchrony (Freimuth et al., 2022). Populations of honeybee (*Apis mellifera* L.), the best-known and essential crop pollinator, have declined because of agricultural pesticides, increases in pathogens, and increasing temperatures (Zhao et al., 2021). Honeybees maintain hive humidity and temperature within critical limits for bee survival and brood rearing. Honeybee pollinator activity decreases at high temperatures because bees focus on collecting more water than nectar to help maintain hive temperatures and humidity

(Kunholz & Seeley, 1997; Oliver, 2022; Seeley, 2009, 2019). Extreme temperatures can even melt the wax in the hive.

Integrated pest management often incorporates predatory arthropods for managing insect pests. Supplies of predatory arthropods might be affected by adverse climatic conditions. Biological control of pests (e.g., aphids, scale, and mites) is often an important tool for managing PGR, as insecticide application does not promote insect pollinator populations. For example, cold-adapted ladybird species might decline or retreat to higher latitudes or altitudes under warming temperatures (Sloggett, 2021). Not all climate change effects are negative because some research shows that many insect pollinators and biological control agents are resilient to such changes (Sloggett, 2021). The effects of climate change on these pollinators and beneficial insects are not entirely understood, but should be considered in future plans for PGR management practices.

4.1.3 | Pathogens and pests

Complicated by climate change, disease management is an increasingly challenging goal for both crop production and PGR management. Plant pathogen survival, infection timing, and virulence are influenced by temperature, precipitation/moisture, and concentrations of atmospheric gasses. Velásquez et al. (2018) and Kybartaite et al. (2020) suggest that rising temperatures are a leading factor for higher incidence and severity of crop diseases. Unpredictable and changing precipitation patterns have increased in the United States and globally (Environmental Protection Agency, 2022). Increased atmospheric moisture often leads to increases in fungal and bacterial diseases that can be especially problematic for spring established, seed-propagated annuals or clonally propagated perennial PGR maintained in the field. Soil-borne diseases, especially root-rot complexes, can be particularly severe and easily disseminated during floods or prolonged waterlogging (Reeksting et al., 2014).

Like plant diseases, the survival of many plant pests are favored by warming trends, erratic precipitation, and increased levels of CO_2 brought on by climate change. The expanded local, regional, and global distribution of pests; earlier outbreaks due to overwinter survival and warmer springs; expanded multiplication rates and generation numbers; and the possibility of more frequent disease outbreaks vectored by insect pests are all predicted to complicate crop production and PGR management (Skendžić et al., 2021). Under scenarios of only moderate warming, earlier infestations coupled with migration and expanded distribution into higher latitudes has been forecast for several insect pest species (Porter et al., 1991; Zeng et al., 2020). Increasing temperatures can lead to larger insect pest populations. Consequently, plant pathogens vectored by insects and mites would also increase. Huanglongbing disease of citrus (Ajene et al., 2020) and zebra chip of potato (Zelinger et al., 2017) are both examples of psyllid-vectored bacterial diseases with expanded global ranges attributed to globalization, but also to larger insect pest populations favored by global warming trends. The same insects and mites that endanger agricultural production will impede PGR regeneration and maintenance in the field and greenhouses or screenhouses.

4.1.4 | Genebank infrastructure considerations

As mentioned earlier, increased temperatures in some cases could improve the success of PGR regenerations. Warmer (non-freezing) temperatures earlier or later in the season can extend plant growth, which could enhance seed production for some species that need longer growing seasons. Nonetheless, increased temperatures and extreme weather can also make field work more challenging for both personnel and plants. Higher summer temperatures can make greenhouses and screenhouses without cooling systems unusable for plant growth, necessitating costly infrastructural investment in cooling systems or new greenhouses. Decreased rainfall as part of changing weather patterns could necessitate expanding costly irrigation capacities (Rosa et al., 2020) which could be especially challenging at NPGS locations currently without that infrastructure. If higher summer temperatures limit plant growth in some areas beyond what new infrastructure can economically allay, regenerations and seed production for some PGR might need to be transferred to more favorable locations. If PGR management were moved to locations farther north, the shorter nights during the growing season might interfere with flowering; consequently, higher elevation sites at lower latitudes might serve as an alternative. As a more extreme resort, establishment and maintenance of PGR by in vitro cultures, much more expensive than growing plants in the field or greenhouse, might be warranted.

Extreme and erratic weather can impede field work. For example, if soil is too wet to cultivate in the spring, then plant establishment can be delayed, preventing seed maturity before the end of the growing season. Warmer early-spring weather could enable earlier planting dates. Although earlier planting can help plants escape injuriously high temperatures later in the summer, it could result in poor stand establishment because of cold soil temperatures in the spring. Extreme weather that occurs randomly across the growing season, such as hail, heavy rains and high winds, can destroy established plots so that regenerations must be repeated. In addition, cages and other field structures that enable pollination control for seed production (Figure 2) can be damaged or destroyed.

Clonally propagated PGR maintained in the field are particularly susceptible to the effects of climate change. Perennial

FIGURE 2 Insect-proof cages for seed regenerations of National Plant Germplasm System plant genetic resources. (a) Intact cages in Prosser, WA (photo credit B. Irish); (b) Cages with sunflower seed regenerations destroyed by a windstorm in Ames, IA (photo credit L. Marek).

plants might not experience the chilling hours required to break winter dormancy, thus impeding subsequent flowering and vegetative growth. Specialized growth chambers/rooms could be needed for vernalization to occur in controlled environments. Perennials that do experience the required winter dormancy could experience budbreak during early warm springs, and then be damaged by late spring frosts that kill flower buds and young fruit (Atkinson et al., 2013; Pagter & Arora, 2013). More frequent hurricanes in warmer southern NPGS locations might imperil subtropical and tropical clonal PGR. The expense and logistics of relocating established, large perennial PGR will be significant, but might need to be considered to avoid the loss of diversity in these PGR.

4.2 | Climate change effects on PGR management at in situ reserves

CWR and other PGR face the same threats in nature as other wild plant species, although the frequency of specific threats might differ for certain CWR (Frances et al., 2018). The survival of wild plant species can be reduced by several interacting threats, including many that occur in protected areas, such as invasive species, grazing, and energy development (Frances et al., 2018; Hernández-Yáñez et al., 2016). For example, a natural area with a high diversity of potato (*Solanum* L. spp.) CWR is now dominated by cheatgrass (*Bromus tectorum* L.), a non-native invasive grass found throughout much of the Western United States (J. Bamberg, personal communication, 2022). Cheatgrass not only competes with native species, but also increases the risk of severe wildfire with climate change through increased fuel loads. Highly diverse native populations of potato CWR are currently difficult to find due to fluctuating environmental conditions, and it is expected that potential in situ conservation sites will become harder to locate because of the effects of climate change (J. Bamberg, personal communication, 2023). Consequently, IGRRs must be managed to mitigate current and future threats.

Climate change introduces additional challenges to ensuring CWR persistence when selecting, designating, and managing IGRRs. Wild plants and their associated ecological communities are impacted by climate change much as are cultivated plants (Aguirre-Liguori et al., 2022; Cho, 2022; Hatfield & Pruger, 2015; Jarvis et al., 2008) including altered growth and reproduction, changes in pollinators and dispersers, and increased threats from pests and pathogens. Moreover, it can take years or even decades for ecosystems, habitats, and plant populations to recover (if possible) from the increased frequency of catastrophic wildfire, floods, and storms.

Changing climatic conditions interact with and intensify existing threats and plant populations will likely shift their geographic ranges in response. With changing environmental conditions, plant populations of interest should be monitored more frequently and intensively. Physical boundaries for designated IGRRs might need to be modified to encompass the shifting locations of plant populations. Creating, expanding, or relocating in situ reserves for PGR might be aided by other federal initiatives to safeguard biodiversity in the face of climate change. The "30 × 30" federal initiative (National Climate Task Force, 2021) aims to actively conserve 30% of US land and water by 2030. Incorporating the in situ conservation of CWR into this initiative and others (USDA, 2021; USDA Forest Service, 2022) could help safeguard the nation's PGR in situ.

5 | CASE STUDIES FOR THE EFFECTS OF CLIMATE CHANGE ON PGR MANAGEMENT AT NPGS LOCATIONS

5.1 | Cool-season legumes in Pullman and Central Ferry, Washington

At the end of June 2021, the US Pacific Northwest experienced a “heat dome” in which extremely high temperatures were recorded for 5 days (Cotlier et al., 2022; Emerton et al., 2022; USDA Climate Hubs, 2022). In Eastern Washington, where the NPGS genebank in Pullman manages cool-season pulse PGR, summer rainfall is negligible, and irrigation is usually unavailable for crop production. The heat dome caused record high temperatures as high as 46.3˚C during the day and 23.5˚C at night in Eastern Washington (Cotlier et al., 2022). This novel weather phenomenon occurred during peak flowering of pea (*Pisum* L.), lentil (*Lens* Mill.), wild and cultivated chickpea (*Cicer* L.), lupin (*Lupinus* L.), and faba bean (*Vicia faba* L.) (Figure 3a,b). Pollen quality and availability, flower abortion, and seed development were likely all impacted leading to drastically reduced yields for plantings both at Pullman and Central Ferry, WA (Gogoi et al., 2018; Jiang et al., 2019; Walters et al., 2022). Numerous regenerations and evaluations failed completely or failed to replace the number of seed sown, even with access to irrigation at the Central Ferry farm. The reduction in seed yield can be determined by comparing seed yields in 2021 to either 2020 or 2022, when temperatures were normal and within the optimal range for pulse crops (Gogoi et al., 2018). Yield reductions due to the heat in a replicated phenotypic characterization plot for lentils averaged 87% (121.9 g/plot in 2022 vs. 15.6 g/plot in 2021). Yield data were not available for other pulse species, but 100 seed weight, which is a yield component and important measure of seed quality, was reduced due to the heat by 54% in field-grown chickpeas (USDA-ARS GRIN-Global, 2022b).

In the future, expanding the capacity for irrigation is planned for the Pullman farm to reduce drought stresses. Nonetheless, because the main threat during the 2021 summer growing season was heat and not lack of water, irrigation might be of limited help in remedying the low seed set in the pulse PGR. Strategies to overcome high summer temperatures (Figure 3c) for cultivating pulses and cold tolerant grass species in the future might require fall planting and field overwintering; earlier spring sowing might be possible for non-cold tolerant species. This would enable these PGR to flower and set seed earlier before summer temperatures become prohibitively high. An additional, cooler field location might be needed for spring-planted regeneration of some PGR managed at the Pullman genebank.

5.2 | Maize (*Zea* L.) PGR in Ames, Iowa

The NPGS maize PGR collection maintained at Ames, IA contains 20,157 accessions. Maize is grown during the summer in rows in the field and hand pollinated from early July (occasionally late June) into September depending on when each accession flowers. Increasing temperature, a hallmark of climate change, has a clear, negative effect on pollination success in maize (Herrero & Johnson, 1980; Figure 4a). For the daily maximum temperature range of 23 to 31˚C, the median number of ears harvested per pollination exceeds 75%. In contrast, above 31˚C, the median number of ears harvested decreases sharply and by 38˚C, median success of the pollinations is only 12%. It is likely that any successful pollinations on these hottest days represent the earliest pollinations of the day, rather than heat resistant genotypes, but time of pollination is not generally recorded to confirm that. Maximum temperatures during the maize pollination season (summer quarter) are expected to increase in Ames during the coming decades (Figure 4b, maximum temperature for July). These increasing temperatures are expected to decrease the success of pollinations. By 2100, the worst-case scenario (emission SSP5–8.5 and predicted maximum temperature of 41˚C; Figure 4b), maize pollination during the current usual growing season would have limited success in Ames.

5.3 | *Prunus* L. PGR in Davis, California

The NPGS *Prunus* PGR collection is maintained in orchards at Davis, CA and Geneva, NY. The Davis orchards, including plum (*Prunus domestica* L. and others), sweet cherry (*Prunus avium* (L.) L.), peach (*Prunus persica* (L.) Batsch), apricot (*Prunus armeniaca* L.), and almond (*Prunus dulcis* (Mill.) D. A. Webb), have experienced warmer, shorter winters with cold periods interrupted by unseasonably warm temperatures (Figure 5). *Prunus* trees (depending on crop and cultivar) require between 200 and 1800 h below a threshold temperature of 7˚C before shoots will sprout in the spring (Baldocchi & Wong, 2008). Currently, some accessions in the NPGS sweet cherry collection are not achieving their full winter dormancy. The inadequate chilling hours can delay pollination and foliation, and reduce plant performance, fruit yield, and quality (C. DeBuse, personal communication, 2022; Pathak et al., 2018). In addition, plum are reacting with later leafing and flowering that extend over a longer period in the spring (C. DeBuse, personal communication, 2022). These trends are expected to continue with warmer winter temperatures predicted for the future (Figure 6a). Cryopreservation of dormant buds for the *Prunus* PGR in the Davis, CA location has been challenging, likely because the trees do not experience sufficient cold temperatures for winter dormancy required for

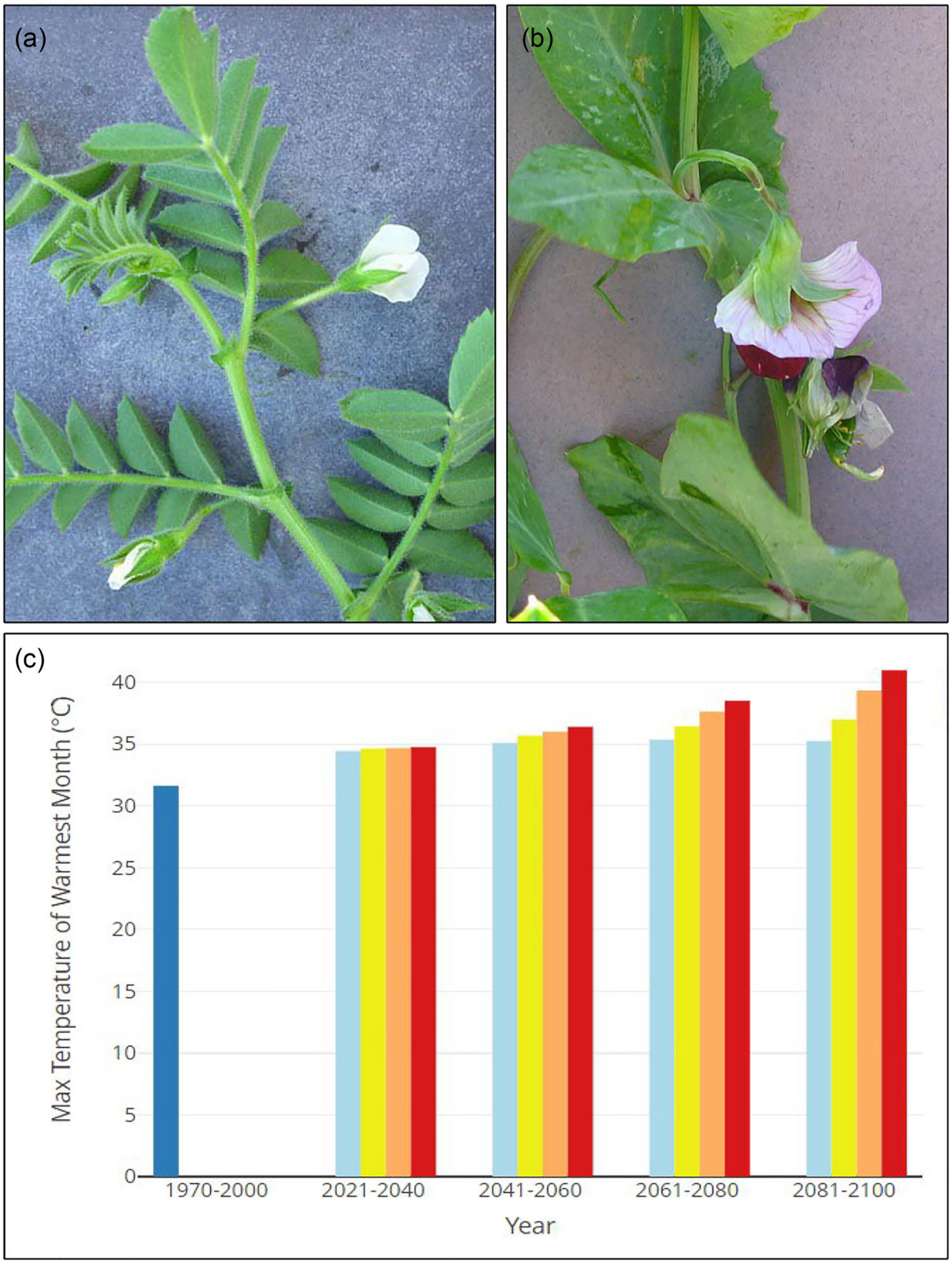

FIGURE 3 Cool-season legume plant genetic resources (PGR) maintained at the National Plant Germplasm System (NPGS) Pullman, WA genebank and regenerated at that genebank's Central Ferry, WA field site. (a) Flowering chickpea (*Cicer*) PGR and (b) Flowering pea (*Pisum*) PGR. (c) Modeled climate conditions expressed as average maximum temperature (˚C, *Y*-axis) of the warmest month (BIO5) in Central Ferry, WA for SSP1–2.6 (light blue column), SSP2–4.5 (yellow), SSP3–7.0 (orange), and SSP5–8.5 (red) emission scenarios for historic (dark blue) and four different future time intervals (*X*-axis). Data are available from the National Plant Germplasm System Climate Futures Application (https://geocentroid.shinyapps.io/npgsclimatefutures).

successful dormant bud cryopreservation. Sour cherry, maintained in Geneva, NY, and sweet cherry from Prosser, WA can be successfully cryopreserved as dormant budwood (Jenderek et al., 2022; Towill, 1999). In the coming years, *Prunus* PGR from Davis will be grown in experimental plantings at Geneva, NY for dormant bud cryopreservation as well as phenotypic evaluations.

5.4 | Pecan (*Carya* Nutt.) PGR in College Station, Texas

The NPGS pecan PGR collection is maintained in College Station and Brownwood, TX. High temperatures and drought have affected both PGR maintenance and associated pecan breeding programs. High temperatures combined

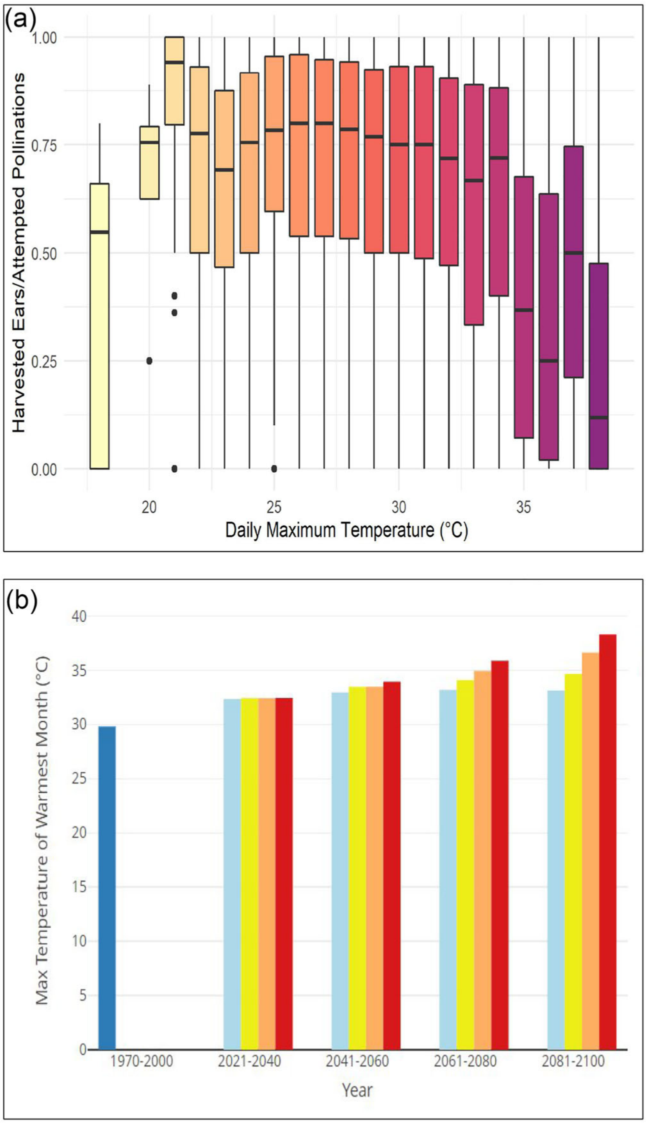

FIGURE 4 Impact of warmer temperatures on maize pollination in Ames, Iowa. (a) The effect of daily maximum temperatures (*X*-axis) on pollination success in maize (measured as harvested ears per pollinations made, *Y*-axis) at the NCRPIS, Ames, IA July to September, 2021. The 279,650 plants of 1602 different accessions were pollinated to generate these data. The colored boxes capture the ranges of 50% of the pollination success data at each temperature. The number of pollinations ranges from 719 (37˚C) to more than 52,000 (28˚C). Harvest success ranged from zero to 100% except at 18˚C (to about 80%) and at 21˚C (from about 80 to 100%, with 0% an infrequent outlier). The horizontal black bars within each of the boxes represent the data median and the black dots are outlier values. (b) The maximum temperature of the warmest month historically and what is predicted for the coming decades through 2100 under four different emission scenarios for Ames, Iowa. Modeled climate conditions expressed as average maximum temperature (˚C, *Y*-axis) of the warmest month (BIO5) at Ames, IA. Data for SSP1–2.6 (light blue column), SSP2–4.5 (yellow), SSP3–7.0 (orange), and SSP5–8.5 (red) emission scenarios for historic (dark blue) and four different future time intervals (*X*-axis) are presented. Data are available from the National Plant Germplasm System Climate Futures Application (https://geocentroid.shinyapps.io/npgsclimatefutures).

with drought have led to increased prevalence of shuck decline disease that results in poorly filled nuts and premature shuck split (W. Chatwin, personal communication, 2022). The split shucks create openings for opportunistic fungal pathogens that cause further damage (Sparks et al., 1995). In 2022, approximately 70% of the breeding crosses were lost due to high temperatures (~32˚C) at the time of hand pollination. The temperature inside the pollination bags were as much as 8˚C higher than ambient and desiccated many flowers/nutlets and leaves within a couple of weeks after pollination (Conner, 2002). The high temperature might also have impacted pollen viability. The NPGS pecan PGR collection includes both cultivars and US native CWR, which offer valuable resilience to fungal diseases that can be incorporated into breeding programs (Lovell et al., 2021). These PGR will face even warmer temperatures in the coming decades (Figure 6b). Consequently, mitigation measures such as irrigation or relocation of the collection to a cooler location might one day become necessary.

5.5 | Coffee (*Coffea* L.) PGR in Hilo, Hawaii

Although temperate regions of the world—where most of the NPGS PGR collections are located—are predicted to be affected most by higher temperatures resulting from climate change, NPGS genebanks located in US tropical and subtropical regions are also affected. Warmer temperatures and increased precipitation in the tropics have led to disease expansion to higher elevations where conditions were previously not as favorable for disease development (Tadesse et al., 2021). A new NPGS PGR collection for coffee (*Coffea arabica* L.) is under development by the NPGS to add genetic diversity needed for broadening the currently narrow genetic base of the cultivated crop (Figure 7a). Coffee leaf rust (CLR), caused by *Hemelia vastatrix* Berk. and Broome, currently the most important disease of coffee, continues to spread due to globalization, global warming, and projected trends for more rainfall (Figure 7b). The disease has recently been reported on the Hawaiian Islands, affecting most of the susceptible cultivars grown (Aristizábal et al., 2022; Keith et al., 2022). Belachew et al. (2020) found that the severity of CLR disease decreased at higher elevations where conditions were less favorable but cautioned that predicted higher temperatures and cultivation of susceptible cultivars could become problematic even at higher elevations. Future coffee PGR management must address CLR and the other predicted effects of climate changes through access to different sites in Hawaii and Puerto Rico at higher elevations and isolated from commercial coffee production.

FIGURE 5 The National Plant Germplasm System *Prunus* plant genetic resources collection at the Davis, CA genebank. (a) *Prunus* trees in field orchards; (b) Immature peach fruit from a typical tree (photo credit: G. Volk).

5.6 | Apple (*Malus* Mill.) PGR in Geneva, New York

The NPGS apple collection, maintained primarily as a field collection in Geneva, NY, is threatened by fire blight (*Erwinia amylovora*), a bacterial disease that infects flowers, fruits, shoots, and rootstocks of many Rosaceae crops. The extent of fire blight infections is determined by the presence of the pathogen under certain environmental conditions, combined with cultivar susceptibility (Kostick et al., 2019). Rain followed by warm cloudy weather, especially during bloom and young shoot growth, promotes fire blight infections. It is particularly difficult to control fire blight outbreaks in diverse PGR with a wide range of flowering times, such as the NPGS apple PGR collection (Figure 8). Higher temperatures increase bacterial pathogen levels, with an optimum around 28˚C, and moisture enhances pathogen dissemination and infection (Farkas et al., 2012; Shtienberg et al., 2015). Temperatures also affect flowering duration, with higher temperatures reducing the period when flowers are susceptible to bacterial infections (Pusey & Curry, 2004). In 2020, the NPGS apple PGR collection experienced a significant fire blight outbreak, which revealed disease resistance levels in species and cultivars (Dougherty et al., 2021). Predictions of future climates suggest warmer, wetter springs at Geneva, NY in the future could lead to additional devastating fire blight infections. Horticultural practices that can limit the severity of these outbreaks must be adopted for the apple PGR maintained at Geneva to counter the potential effects of fire blight in the future.

5.7 | Cranberry PGR maintained in situ and at the NPGS Corvallis, Oregon genebank

Cranberry CWR (large-fruited *Vaccinium macrocarpon* Aiton and small-fruited *Vaccinium oxycoccos* L.) are native to North America (Hummer et al., 2019). Both species are found in temperate forest wetlands that are particularly sensitive to environmental changes. The USDA-ARS and the University of Wisconsin recommend several high priority sites in National Forests to protect cranberry CWR populations with rich genetic diversity (Rodriguez-Bonilla et al., 2020; Figure 9). The NPGS genebank in Corvallis, OR maintains ex situ PGR from these sites, as well as many additional *Vaccinium* species and cultivars, as seeds and plants cultivated in protected structures.

Climate change will affect both in situ and ex situ cranberry conservation efforts. Throughout cranberry species' ranges, including three selected IGGRs and at the NPGS Corvallis genebank, minimum temperatures of the coldest month are predicted to increase by 1 to 8˚C (Figure 10d). This may result in earlier flowering and fruit maturation dates and lower levels of fruit production. The geographical distributions of wild cranberry populations are generally shifting north (Ellwood et al., 2014; Hirabayashi et al., 2022) and future plant collecting at those in situ sites will be complicated by the earlier fruiting times and lower yields. Wild and cultivated cranberries require a minimum number of chilling hours to complete a dormancy period and to flower. Cranberries are maintained in the Corvallis genebank's greenhouses, which need improved temperature regulation for successful cranberry

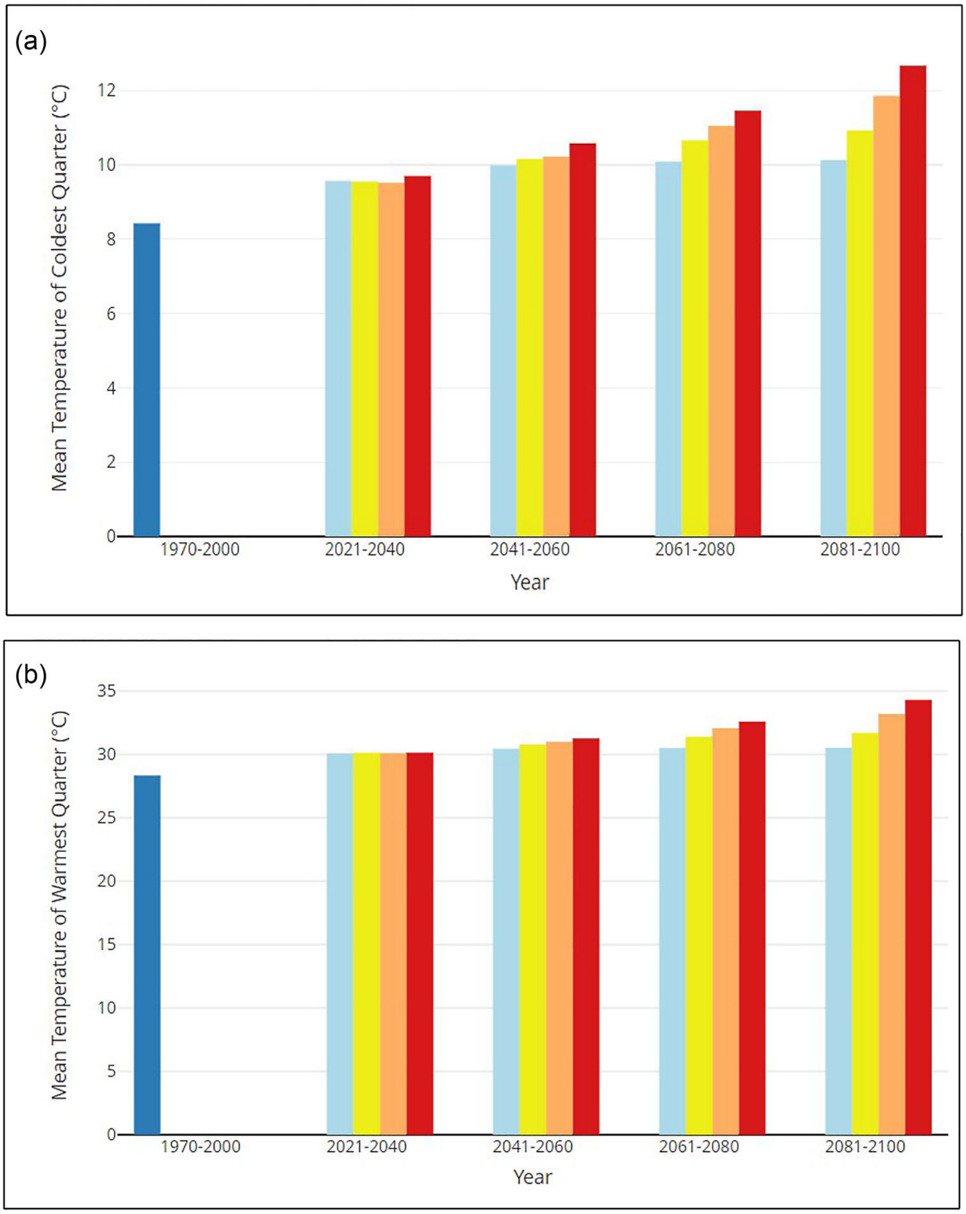

FIGURE 6 Modeled climate conditions for SSP1–2.6 (light blue column), SSP2–4.5 (yellow), SSP3–7.0 (orange), and SSP5–8.5 (red) emission scenarios for historic (dark blue) and four different future time intervals (Years, in *X*-axis). Mean temperatures (˚C) are shown on the *Y*-axis. (a) Mean temperature of the coldest quarter of the year (BIO11) in Davis, CA; and (b) Mean temperature of the warmest quarter of the year (BIO10) in College Station, TX. All figures were obtained from the National Plant Germplasm System Climate Futures Application (https://geocentroid.shinyapps.io/npgsclimatefutures).

collection maintenance, particularly with estimated future climatic conditions (J. Oliphant, personal communication, 2022).

5.8 | Acquisition and conservation of US native PGR through the Seeds of Success program

The Department of Interior, Bureau of Land Management Seeds of Success (SOS) program, in collaboration with the NPGS, collects and conserves the most comprehensive collection of native plant seeds in the United States and supports native plant restoration, management, and research. Targets for PGR collection for the SOS program include US native plant species collected for land restoration and other uses (Barga et al., 2020). The acquisition priorities for SOS thus emphasize US native species, including CWR that add important diversity to the NPGS PGR collections (Greene, Carver et al., 2019).

Climatic factors, including prolonged drought and increased temperatures, have affected collecting native plant

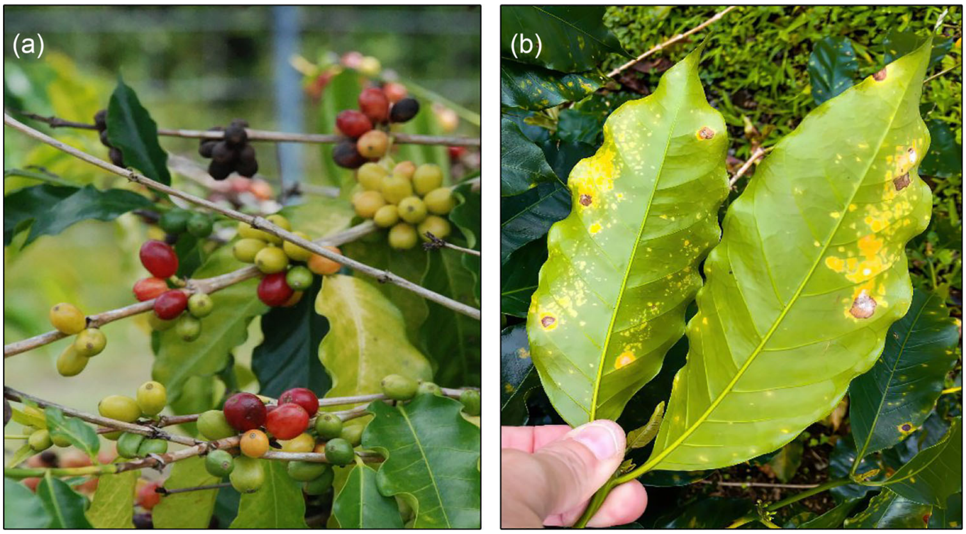

FIGURE 7 (a) Coffee plant in the National Plant Germplasm System plant genetic resources collection at the Hilo, HI genebank (photo credit G. Volk); (b) Coffee leaf rust on coffee plants in the Hawaiian Islands (photo credit L. Keith).

FIGURE 8 Removal of fire blight infected branches in the National Plant Germplasm System plant genetic resources apple collection at the Geneva, NY genebank (photo credit G. Peck).

FIGURE 9 In situ cranberry reserve at the Little Crater Meadow in Mount Hood National Forest, Oregon (photo credit K. Williams).

species because plant population sizes and seed quantities/qualities have declined, especially in the Western United States. The prolonged drought in western states and the extreme heat, especially during the summer of 2021 (Cotlier et al., 2022; Emerton et al., 2022; USDA Climate Hubs, 2021), resulted in unsuccessful field collecting due to seeds that dehisced prematurely in annual species, and reduced viabilities of seed collected of many forbs (A. Lindquist, personal communication, 2022). As noted previously in this essay, heat and drought stress also affect plant reproductive physiology of native wild species, affecting seed filing, quality, and viability. The increased number, sizes, and intensities of fires have also endangered plant populations targeted for collection. In addition, invasive species like cheatgrass often are favored by fire (Taylor et al., 2014) and frequently outcompete native grass and forbs (see the earlier discussion of potato CWR), limiting the number of populations available for field collecting.

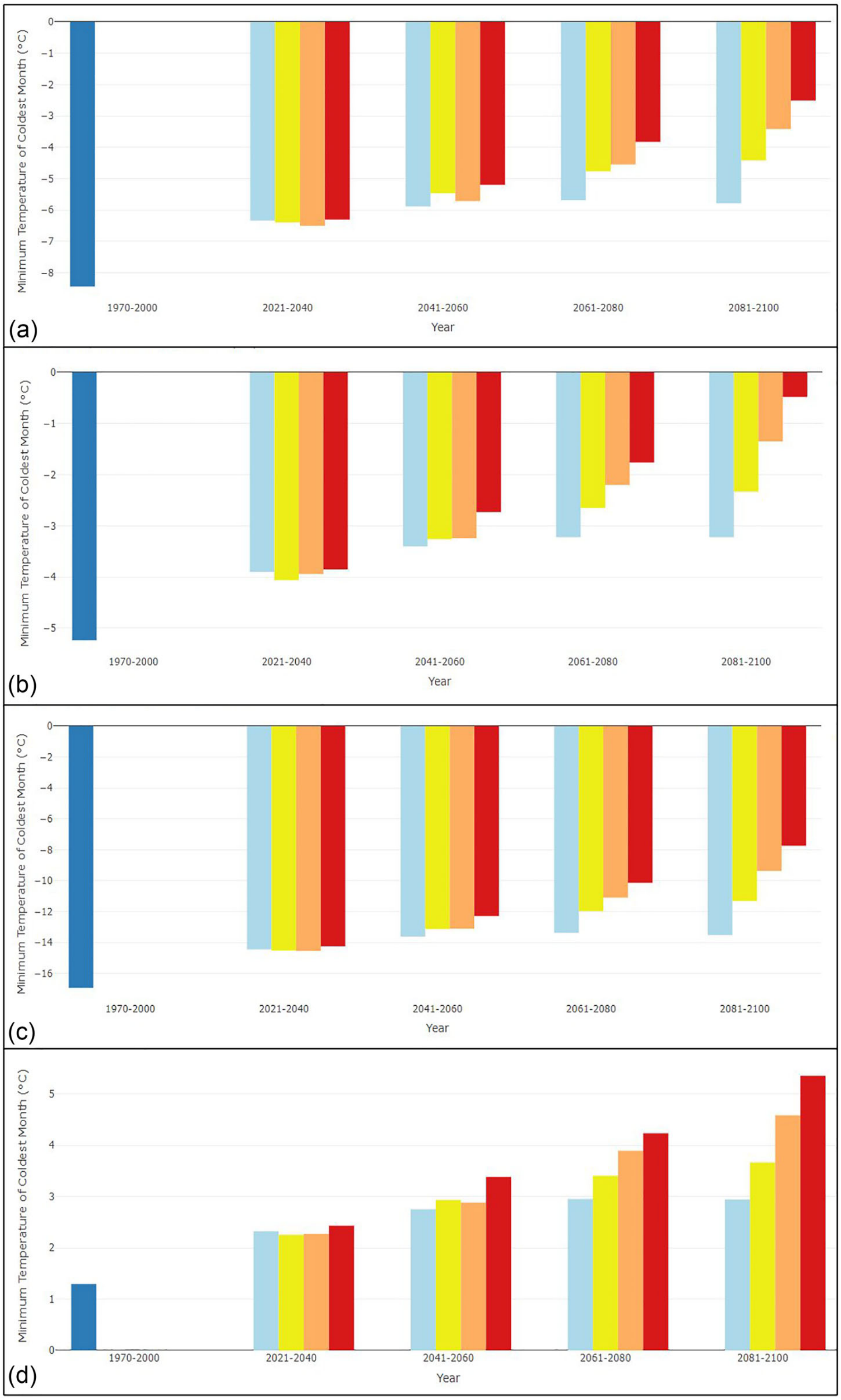

FIGURE 10 Modeled climate conditions for SSP1–2.6 (light blue column), SSP2–4.5 (yellow), SSP3–7.0 (orange), and SSP5–8.5 (red) emission scenarios for historic (dark blue) and four different future time intervals (Years, in *X*-axis). Mean temperatures (˚C) are shown on the *Y*-axis. Projected minimum temperature of the coldest month (BIO6) under the four emissions scenarios for four locations where cranberries grow in nature. The minimum temperatures at locations A–C were below 0˚C, consequently the temperature scale is inverted as compared to other histogram figures. (a) In situ reserve Cranberry Glades 1 in the Monongahela National Forest, WV, containing *Vaccinium macrocarpon* and *Vaccinium oxycoccos*; (b) In situ reserve Little Crater Meadow in the Mount Hood National Forest, OR, containing *V. oxycoccos*; (c) In situ reserve Upper Island Lake in the Chequamegon-Nicolet National Forest, WI, containing *V. macrocarpon*; (d) Ex situ cranberry plant genetic resources field planting at National Plant Germplasm System (NPGS) Corvallis, OR genebank. Data are available from the NPGS Climate Futures Application (https://geocentroid.shinyapps.io/npgsclimatefutures).

FIGURE 11 Potato CWR in nature in New Mexico. (a,c) Plants of *Solanum jamesii*; (b,d) Plants of *Solanum stoloniferum* (photo credit J. Bamberg).

5.9 | Augmenting ex situ potato PGR collections with the genetic diversity from in situ potato CWR populations

From 1992 to 2022, extensive annual expeditions throughout the Southwestern United States were performed by staff at the NPGS U.S. Potato Genebank (USPG) to collect two native US potato CWR species, the diploid outcrossing *Solanum jamesii* Torr. and the disomic tetraploid self-pollinated *Solanum stoloniferum* Schltdl. (historic name *Solanum fendleri* A. Gray) (Figure 11). These potato CWR represent two of the most common breeding systems of the nearly 100 tuber-bearing potato species (Bamberg et al., 2018). Only 46 accessions of the two native US species were included in the USPG PGR collection prior to 1992, but subsequent collecting increased that to 454 accessions. DNA marker studies suggest that the gain of diversity in the USPG collection has plateaued (Bamberg & del Rio, 2021), but after 31 annual expeditions, new collection sites with novel diversity continue to be identified.

Repeated visits to the same locations for these two potato CWR species revealed information important for PGR management. Most collections of those species capture only a snapshot of their genetic diversity from few places and times. Precise, georeferenced locality data and site-specific access information should be recorded so that the same site can be revisited in subsequent years. Populations that are readily apparent in 1 year might be difficult to identify in another because the visual appearance of some wild populations might vary with annual weather conditions and physiology. Seeds and tubers might remain in the soil for multiple seasons without germinating or producing above-ground growth (Bamberg, 2010; Bamberg et al., 2020). These conditions make it difficult to identify sparse populations, but repeated collections over three decades enable many more populations to be found compared to a single visit to each location.

The status and dynamics of genetic richness of potato CWR populations in the wild and in the genebank can contribute to predicting vulnerability to climate change. Many of the potato PGR accessions have been genotyped and provide valuable experimental material for extensive genomic studies to reveal both the structure of potato CWR populations and genomic regions that have undergone selection or local adaptation. This information can contribute to evaluating potato CWR for genotypes to incorporate into breeding programs for genomic-assisted selection (del Rio & Bamberg, 2020) for adaptation to climate change. Phenotypic and genotypic data can also help select PGR from in situ sites for long-term ex situ conservation. One outcome of this research has been identifying CWR with tuber freezing tolerance throughout the studied geographic range. This tuber freezing tolerance trait might help wild populations resist severe weather conditions that occur at those locations (Bamberg & Lombard, 2022).

6 | PREPARING NPGS PGR MANAGEMENT FOR THE EFFECTS OF CLIMATE CHANGE

The wide range of genetic diversity in NPGS PGR collections includes traits valuable for crop improvement in response to, or in anticipation of, changing climates. Nonetheless, as the preceding case studies illustrate, that diversity also complicates preparing NPGS PGR management—itself a complicated, multi-phase operation conducted over an extended timeframe (Byrne et al., 2018)—for the effects of climate change. Comprehensive planning for the NPGS's future development is already underway through the 2018 Farm Bill-directed National Strategic Germplasm and Cultivar Collection Assessment and Utilization Plan (115th Congress of the United States., 2017–2018. H. R. 2—Agriculture Improvement Act of 2018). The approaches outlined below draw on that Plan, the NPGS Climate Futures tool (Section 3) and other information included in the current essay. The approaches encompass diverse tools and strategies ranging from fairly simple, inexpensive, and short term to complicated, costly, and long term. Overall success will depend on strengthened cooperation with and support by the NPGS's diverse long term and new partners, customers, and stakeholders.

Where close cooperation with land-management agencies and organizations is feasible, the NPGS in situ PGR management program will expand to encompass additional tactics and IGRR, according to priorities described in Sections 2.2 and 4.2. The 30+ year US potato CWR field monitoring and collection program (Section 5.9) provides demographic and genetic analytical approaches that could be expanded judiciously to assist long-term, in situ conservation. For example, potato CWR sites with large "mega-populations" and substantial genetic diversity would be advantageous for repeated sampling, research, and for monitoring local weather trends, as well as conservation. In contrast, sites with few plants and reduced genetic diversity might merit ex situ conservation because of the stronger risk of local extinction. Close monitoring and analyses of PGR in situ might also identify key CWR traits—especially those recently evolved—such as tolerance to drought, higher temperatures, and resistance to pests and pathogens. Such information can guide field PGR collecting to fill gaps in ex situ PGR collections, subsequent extensive genotypic characterization, trait evaluations, and eventual incorporation of newly discovered traits into crop breeding programs. Furthermore, extensive datasets resulting from those analyses can help estimate the current and future impacts of climate change on specific species and on plant ecosystems as a whole.

Climate change has different effects on diverse crops and CWR (see preceding sections) at the dispersed geographical locations of the NPGS genebanks (Figure 1). Notably, climate change will also differentially affect the numerous components of NPGS's ex situ PGR management operations. As explained above, additional acquisitions of US CWR for ex situ conservation might be necessary, but also might become more difficult in the future because of the changing climatic conditions. Management of CWR PGR is often more complicated and costly than for cultivars, consequently additional NPGS genebank capacities and budgetary support will be needed.

NPGS genebanks and in situ reserves located in temperate zones will likely experience more pronounced temperature increases than those situated in the subtropics or tropics (Section 3). The higher temperatures might increase energy costs for maintaining PGR in cold storage. Higher temperatures might also increase substantially the energy and funds expended for cooling greenhouses to levels acceptable for maintaining PGR. Securing alternative sources of power for genebanks, including solar, wind, geothermal, or hydrological, should be investigated. Beyond the valuable climatic estimations provided by the NPGS Climate Futures Application (Section 3) adequate meteorological stations should be established at NPGS genebank locations that lack such instrumentation to both refine future predictions and document meteorological trends in growing areas before they affect PGR cold storage or field maintenance operations too greatly. Meteorological stations associated with genebank locations and evaluation sites also are needed to support priority research on plant adaptation to changing abiotic stresses.

Maintaining clonally propagated PGR in field plantings will not only require dealing with elevated temperatures but also with potentially more frequent and severe droughts, and extreme weather in the form of stronger and more frequent winds associated with hurricanes/cyclones at NPGS tropical/subtropical locations and tornadoes at NPGS continental genebank locations (Figure 1). More frequent and severe droughts will require greater and more reliable irrigation capacity at some NPGS genebanks. These elevated weather-related risks underscore the critical importance of backing up clonal germplasm at distant locales or as cryopreserved shoot tips and dormant buds at the NLGRP. More resources will be required to develop and implement additional clonal cryopreservation methods for the NPGS or to maintain duplicate plantings at multiple locations.

For PGR maintained as seeds, more frequent extreme or severe weather during regeneration represents the highest risks associated with climate change (see examples in Sections 2.1, 4, and 5). Both the costs and the risks associated with regeneration can be reduced by increasing the intervals between regenerations through improved seed storage conditions. Expanded capacity of −18˚C storage facilities and development of additional long-term preservation and seed quality monitoring methods will decrease regeneration frequency for many seed-propagated PGR endangered by failing viability due to inadequate storage temperature.

The NPGS genebank facilities and their constituent PGR collections were originally situated at particular locations because the growing conditions there met the needs of assigned crops; the sites were located in major production regions; or because of the availability of adequate PGR management capacity (Byrne et al., 2018). If environmental conditions at genebank sites shift to the extent that PGR can no longer be maintained in the field, greenhouse, or regenerated successfully, some PGR management operations, or even entire PGR collections, must be relocated to other NPGS sites where they can be grown and managed successfully. Upgrades and, when needed, relocations should start as soon as possible to avoid the worst predicted impacts of climate change on PGR collections.

Phenotypic evaluation of NPGS PGR will become more difficult but more important for generating information needed to mitigate and adapt to the effects of climate change. The PGR should be evaluated at multiple locations to assess plant performance under a wide range of current conditions and to understand better the potential future effects of climate change. Fortunately, large-scale PGR phenotyping is forecast to become more cost-effective once high-throughput technologies are more readily available and affordable (Volk et al., 2021). Phenotypic data, as well as genotypic characterizations, will reveal NPGS PGR potentially valuable for breeding programs (Byrne, 2023).

Importantly, the diverse, multi-location organization of the NPGS has bestowed the inherent resilience and flexibility so crucial for meeting the formidable challenge of climate change. In the future, the NPGS PGR operations must be even more closely coordinated across multiple locations to exploit more effectively the numerous NPGS system-wide assets. The coordination between the NPGS Davis and Geneva genebanks to generate *Prunus* buds that can be successfully cryopreserved at the NLGRP (Section 5.3) exemplifies how closely aligned cross-locational PGR management can solve NPGS operational challenges generated by climate change. The NPGS genebanks will continue to collaborate with university, private industry, and international and non-governmental partners, to ensure the safety and integrity NPGS PGR collections during the era of rapid climate change.

AUTHOR CONTRIBUTIONS

Gayle M. Volk: Conceptualization; software; writing—original draft; writing—review and editing. **Dan Carver**: Software; writing—original draft. **Brian M. Irish**: Conceptualization; software; writing—original draft; writing—review and editing. **Laura Marek**: Conceptualization; writing—original draft; writing—review and editing. **Anne Frances**: Conceptualization; writing—original draft. **Stephanie Greene**: Conceptualization; software; writing—original draft. **Colin K. Khoury**: Writing—review and editing. **John Bamberg**: Writing—original draft. **Alfonso del Rio**: Writing—original draft. **Marilyn L. Warburton**: Conceptualization; writing—original draft; writing—review and editing. **Peter K. Bretting**: Conceptualization; project administration; writing—original draft; writing—review and editing.

ACKNOWLEDGMENTS

The authors thank Profs. David Rupp and Christopher Daly at Oregon State University for their guidance on the selection of climate models, as well as NPGS crop curators and staff of the NPGS for their thoughtful input and suggestions. Maize curator Vivian Bernau provided data and graphs for the maize case study. The use of trade, firm, or corporation names in this publication is for the information and convenience of the reader. Such use does not constitute an official endorsement or approval by the United States Department of Agriculture or the Agricultural Research Service of any product or service to the exclusion of others that might be suitable. USDA is an equal opportunity employer and provider.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

ORCID

Gayle M. Volk https://orcid.org/0000-0002-8652-9348

REFERENCES

115th Congress of the United States. (2017–2018). *H. R. 2—Agriculture Improvement Act of 2018*. https://www.congress.gov/bill/115th-congress/house-bill/2/text

Aguirre-Liguori, J. A., Morales-Cruz, A., & Gaut, B. (2022). Evaluating the persistence and utility of five wild *Vitis* species in the context of climate change. *Molecular Ecology*, *31*, 6457–6472. https://doi.org/10.1111/mec.16715

Ainsworth, E. A., & Long, S. P. (2020). 30 years of free-air carbon dioxide enrichment (FACE): What have we learned about future crop productivity and its potential for adaptation. *Global Change Biology*, *27*(1), 27–49. https://doi.org/10.1111/gcb.15375

Ajene, I. J., Khamis, F., van Asch, B., Pietersen, G., Rasowo, B. A., Ekesi, S., & Mohamed, S. (2020). Habitat suitability and distribution potential of *Liberibacter* species ("*Candidatus Liberibacter asiaticus*" and "*Candidatus Liberibacter africanus*") associated with citrus greening disease. *Diversity and Distributions*, *26*, 575–588. https://doi.org/10.1111/ddi.13051

Aristizábal, L. F., & Johnson, M. A. (2022). Monitoring coffee leaf rust (*Hemileia vastatrix*) on commercial coffee farms in Hawaii: Early insights from the first year of disease incursion. *Agronomy*, *12*(5), 1134. https://doi.org/10.1029/2022JD036659

Ashfaq, M., Rastogi, D., Kitson, J., Abid, M. A., & Kao, S. C. (2022). Evaluation of CMIP6 GCMs over the CONUS for downscaling studies. *Journal of Geophysical Research: Atmospheres*, *127*, e2022JD036659. https://doi.org/10.1029/2022JD036659

Atkinson, C. J., Brennan, R. M., & Jones, H. G. (2013). Declining chilling and its impact on temperate perennial crops. *Environmental and Experimental Botany*, *91*, 48–62. https://doi.org/10.1016/j.envexpbot.2013.02.004

Baldocchi, D., & Wong, S. (2008). Accumulated winter chill is decreasing in the fruit growing regions of California. *Climatic Change*, *87*, S153–S166. https://doi.org/10.1007/s10584-007-9367-8

Bamberg, J. B. (2010). Tuber dormancy lasting eight years in the wild potato *Solanum jamesii*. *American Journal of Potato Research*, *87*(2), 226–228. https://doi.org/10.1007/s12230-009-9124-9

Bamberg, J., & del Rio, A. (2021). A metric for species representation in the US potato genebank. *American Journal of Potato Research*, *98*(3), 263–265. https://doi.org/10.1007/s12230-021-09833-4

Bamberg, J., del Rio, A., Fernandez, C. J., & Bamberg, I. (2020). A "mega population" of the wild potato species *Solanum fendleri*. *American Journal of Potato Research*, *97*(5), 531–533. https://doi.org/10.1007/s12230-020-09790-4

Bamberg, J. B., del Rio, A., Jansky, J., & Ellis, D. (2018). Ensuring the genetic diversity of potatoes. In G. Wang-Pruski (Ed.), *Achieving sustainable cultivation of potatoes* (pp. 57–80). Burleigh Dodds. https://doi.org/10.19103/AS.2017.0016.02

Bamberg, J., & Lombard, K. (2022). Cold hardiness variation in *Solanum jamesii* and *Solanum kurtzianum* tubers. *American Journal of Potato Research*, *99*(1), 69–72. https://doi.org/10.1007/s12230-022-09862-7

Barga, S. C., Olwell, P., Edwards, F., Prescott, L., & Leger, E. A. (2020). Seeds of Success: A conservation and restoration investment in the future of U.S. lands. *Conservation Science and Practice*, *2*, e209. https://doi.org/10.1111/csp2.209

Belachew, K., Senbeta, G. A., Garedew, W., Barreto, R. W., & Del Ponte, E. M. (2020). Altitude is the main driver of coffee leaf rust epidemics: A large-scale survey in Ethiopia. *Tropical Plant Pathology*, *45*(5), 511–521. https://doi.org/10.1007/s40858-020-00383-4

Bretting, P. K. (2018). 2017 Frank Meyer medal for plant genetic resources lecture: Stewards of our agricultural future. *Crop Science*, *58*(6), 1–8. https://doi.org/10.2135/cropsci2018.05.0334

Bretting, P. K., & Duvick, D. N. (1997). Dynamic conservation of plant genetic resources. *Advances in Agronomy*, *61*, 1–51. https://doi.org/10.1016/S0065-2113(08)60661-6

Byrne, P. (2023). Plant breeding for climate change: Opportunities for adaptation and mitigation. In G. Volk, T. Moreau, & P. Byrne (Eds.), *Climate ready plant collections: Conserving, using, and building capacity*. Colorado State University. https://colostate.pressbooks.pub/climatereadyplantcollections/chapter/plant-breeding-for-climate-change/

Byrne, P. E., Volk, G. M., Gardner, C., Gore, M. A., Simon, P. W., & Smith, S. (2018). Sustaining the future of plant breeding: The critical role of the USDA-ARS National Plant Germplasm System. *Crop Science*, *58*, 451–468. https://doi.org10.2135/cropsci2017.05.0303

Castañeda-Álvarez, N. P., Khoury, C. K., Achicanoy, H. A., Bernau, V., Dempewolf, H., Eastwood, R. J., Guarina, L., Harker, R. H., Jarvis, A., Maxted, N., Müller, J. V., Ramirez-Villegas, J., Sosa, C. C., Struik, P. C., Vincent, H., & Toll, J. (2016). Global conservation priorities for crop wild relatives. *Nature Plants*, *2*(4), 1–6. https://doi.org/10.1038/nplants.2016.22

Cho, R. (2022). How climate change will affect plants. *Columbia Climate School, State of the Planet*. https://news.climate.columbia.edu/2022/01/27/how-climate-change-will-affect-plants/

Conner, P. (2002). The effect of pollination bag type on fruit set and quality in pecan hybridization. *Journal of the American Pomological Society*, *56*, 189–192.

Cortés, A. J., & López-Hernández, F. (2021). Harnessing crop wild diversity for climate change adaptation. *Genes*, *12*(5), 783. https://doi.org/10.3390/genes12050783

Cotlier, G. I., & Jimenez, J. C. (2022). The extreme heat wave over western North America in 2021: An assessment by means of land surface temperature. *Remote Sensing*, *14*(3), 561. https://doi.org/10.3390/rs14030561

Del Rio, A. H., & Bamberg, J. B. (2020). Detection of adaptive genetic diversity in wild potato populations and its implications in conservation of potato germplasm. *American Journal of Plant Sciences*, *11*(10), 1562–1578. https://doi.org/10.4236/ajps.2020.1110113

Dempewolf, H., Baute, G., Anderson, J., Kilian, B., Smith, C., & Guarino, L. (2017). Past and future use of wild relatives in crop breeding. *Crop Science*, *57*, 1070–1082. https://doi.org/10.2135/cropsci2016.10.0885

Dempewolf, H., Eastwood, R. J., Guarino, L., Khoury, C. K., Müller, J. V., & Toll, J. (2014). Adapting agriculture to climate change: A global initiative to collect, conserve, and use crop wild relatives. *Agroecology and Sustainable Food Systems*, *38*, 369–377. https://doi.org/10.1080/21683565.2013.870629

Desai, J. S., Lawas, L. M. F., Valente, A. M., Leman, A. R., Grinevich, D. O., Jagadish, S. K., & Doherty, C. J. (2021). Warm nights disrupt transcriptome rhythms in field-grown rice panicles. *Proceedings of the National Academy of Sciences*, *118*(25), e2025899118. https://doi.org/10.1073/pnas.2025899118

Dougherty, L., Wallis, A., Cox, K., Zhong, G.-Y., & Gutierrez, B. (2021). Phenotypic evaluation of fire blight outbreak in the USDA Malus collection. *Agronomy*, *11*, 144. https://doi.org/10.3390/agronomy11010144

Dox, D. T. C., Maclean, I. M. D., Gardner, A. S., & Gaston, K. J. (2020). Global variation in diurnal asymmetry in temperature, cloud cover, specific humidity and precipitation and its association with leaf area index. *Global Change Biology*, *26*, 7099–7111. https://doi.org/10.1111/gcb.15336

Du, E., Terrer, C., Pellegrini, A. F. A., Ahlström, A., van Lissa, C. J., Zhao, X., Xia, N., Wu, X., & Jackson, R. B. (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, *13*, 221–226. https://doi.org/10.1038/s41561-019-0530-4

Dulloo, M. E., Ebert, A. W., Dussert, S., Gotor, E., Astorga, C., Vasquez, N., Rakotomalala, J. J., Rabemiafara, A., Eira, M., Bellachew, B., Omondi, C., Engelmann, F., Anthony, F., Watts, J., Qamar, Z., & Snook, L. (2009). Cost efficiency of cryopreservation as a long-term conservation method for coffee genetic resources. *Crop Science*, *49*, 2123–2138. https://doi.org/10.2135/cropsci2008.12.0736

Eastwood, R. J., Tambam, B. B., Aboagye, L. M., Akparov, Z. I., Aladele, S. E., Allen, R., Amri, A., Anglin, N. L., Araya, R., Arrieta-Espinoza, G., Asgerov, A., Awang, K., Awas, T., Barata, A. M., Boateng, S. K., Brehm, J. M., Breidy, J., Breman, E., Angulo, A. B., … & Kilian, B. (2022). Adapting agriculture to climate change: A synopsis of coordinated National Crop Wild Relative Seed Collecting Programs across five continents. *Plants*, *11*(14), 1840. https://doi.org/10.3390/plants11141840

Ellwood, E. R., Playfair, S. R., Polgar, C. A., & Primack, R. B. (2014). Cranberry flowering times and climate change in southern Massachusetts. *International Journal of Biometeorology*, *58*(7), 1693–1697. https://doi.org/10.1007/s00484-013-0719-y

Emerton, R., Brimicombe, C., Magnusson, L., Roberts, C., Di Napoli, C., Cloke, H. L., & Pappenberger, F. (2022). Predicting the unprecedented: Forecasting the June 2021 Pacific Northwest heatwave. *Weather*, *77*(8), 272–279. https://doi.org/10.1002/wea.4257

Environmental Protection Agency. (2022). *Climate change indicators: U.S. and global precipitation*. https://www.epa.gov/climate-indicators/climate-change-indicators-us-and-global-precipitation

FAO, Food and Agriculture Organization. (2014). *Genebank standards for plant genetic resources for food and agriculture*. http://www.fao.org/3/a-i3704e.pdf

Farkas, Á., Mihalik, E., Dorgai, L., & Bubán, T. (2012). Floral traits affecting fire blight infection and management. *Trees*, *26*, 47–66. https://doi.org/10.1007/s00468-011-0627-x

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, *37*(12), 4302–4315. https://doi.org/10.1002/joc.5086

Frances, A. L., Smith, A. B., & Khoury, C. K. (2018). Conservation status and threat assessments for North American crop wild relatives. In S. L. Greene, K. A. Williams, C. K. Khoury, M. B. Kantar, & L. F. Marek (Eds.), *North American crop wild relatives. Vol. 1: Conservation strategies*. (pp. 189–208). Springer. https://doi.org/10.1007/978-3-319-95101-0_7

Freimuth, J., Bossdorf, O., Scheepens, J. F., & Willems, F. M. (2022). Climate warming changes synchrony of plants and pollinators. *Proceedings of the Royal Society B*, *289*(1971), 20212142. https://doi.org/10.1098/rspb.2021.2142

Fu, Y. B. (2017). The vulnerability of plant genetic resources conserved ex situ. *Crop Science*, *57*, 2314–2328. https://doi.org/10.2135/cropsci2017.01.0014

Gibson, N., McNulty, S., Miller, C., Gavazzi, M., Worley, E., Keesee, D., & Hollinger, D. (2021). Identification, mitigation, and adaptation to salinization on working lands in the US Southeast. *General Technical Report SRS-259. Asheville, NC: US Department of Agriculture Forest Service, Southern Research Station*, *259*, 1–69. https://doi.org/10.2737/SRS-GTR-259

Gogoi, N., Farooq, M., Barthakur, S., Baroowa, B., Paul, S., Bharadwaj, N., & Ramanjulu, S. (2018). Thermal stress impacts on reproductive development and grain yield in grain legumes. *Journal of Plant Biology*, *61*(5), 265–291. https://doi.org/10.1007/s12374-018-0130-7

Greene, S. L., Carver, D., Khoury, C. K., Irish, B. M., Olwell, P., & Prescott, L. (2019). Seeds of success: Collateral benefits to agricultural crop improvement, research, and education. *Crop Science*, *59*, 2429–2442. https://doi.org/10.2135/cropsci2019.06.0372

Greene, S. L., Williams, K. A., Khoury, C. K., Kantar, M. B., & Marek, L. F. (Eds). (2018). *North American crop wild relatives, Volume 1: Conservation strategies*. Springer.

Greene, S. L., Williams, K. A., Khoury, C. K., Kantar, M. B., & Marek, L. F. (Eds). (2019). *North American crop wild relatives, Volume 2. Important species*. Springer.

Hatfield, J. L., Boone, K. J., Kimball, B. A., Ziska, L. H., Izaurralde, R. C., Ort, D., Thomson, A. M., & Wolfe, D. (2011). Climate impacts on agriculture: Implications for crop production. *Agronomy Journal*, *103*(2), 351–370. https://doi.org/10.2134/agronj2010.0303

Hatfield, J. L., & Prueger, J. H. (2015). Temperature extremes: Effect on plant growth and development. *Weather and Climate Extremes*, *10*, 4–10. https://doi.org/10.1016/j.wace.2015.08.001

Hernández-Yáñez, H., Kos, J. T., Bast, M. D., Griggs, J. L., Hage, P. A., Killian, A., Loza, M. I., Whitmore, M. B., & Smith, A. B. (2016). A systematic assessment of threats affecting the rare plants of the United States. *Biological Conservation*, *203*, 260–267. https://doi.org/10.1016/j.biocon.2016.10.009

Herrero, M. P., & Johnson, R. R. (1980). High temperature stress and pollen viability of maize. *Crop Science*, *20*(6), 796–800. https://doi.org/10.2135/cropsci1980.0011183x002000060030x

Hirabayashi, K., Murch, S. J., & Erland, L. A. E. (2022). Predicted impacts of climate change on wild and commercial berry habitats will have food security, conservation and agricultural implications. *Science of The Total Environment*, *845*, 157341. https://doi.org/10.1016/j.scitotenv.2022.157341

Hummer, K. E., Williams, K. A., & Bushakra, J. M. (2019). North American crop wild relatives of temperate berries (*Fragaria* L., *Ribes* L., *Rubus* L., and *Vaccinium* L.). In S. L. Greene, K. A. Williams, C. K. Khoury, M. B. Kantar, & L. F. Marek (Eds.), *North American crop wild relatives. Vol. 2: Important species* (pp. 283–327). Springer. https://doi.org/10.1007/978-3-319-97121-6_9

IPCC. (2022). *The intergovernmental panel on climate change*. https://www.ipcc.ch/

IPCC. (2023). *AR6 Synthesis Report: Climate Change 2023 — IPCC*. https://www.ipcc.ch/report/sixth-assessment-report-cycle/

Jarvis, A., Lane, A., & Hijmans, R. J. (2008). The effect of climate change on crop wild relatives. *Agriculture, Ecosystems & Environment*, *126*, 13–23. https://doi.org/10.1016/j.agee.2008.01.013

Jenderek, M. M., Yeater, K. M., Ambruzs, B. D., & Magby, J. T. (2022). Pretreatment *Prunus avium* (L) L. dormant buds increased viability after cryogenic storage. *Cryobiology*, *106*, 164–166. https://doi.org/10.1016/j.cryobiol.2022.03.001

Jiang, Y., Lahlali, R., Karunakaran, C., Warkentin, T. D., Davis, A. R., & Bueckert, R. A. (2019). Pollen, ovules, and pollination in pea: Success, failure, and resilience in heat. *Plant, Cell & Environment*, *42*(1), 354–372. https://doi.org/10.1111/pce.13427

Keith, L. M., Sugiyama, L. S., Brill, E., Adams, B. L., Fukada, M., Hoffman, K. M., Ocenar, J., Kawabata, A., Kong, A. T., McKemy, J. M., Olmedo-Velarde, A., & Melzer, M. J. (2022). First report of coffee leaf rust caused by *Hemileia vastatrix* on coffee (*Coffea arabica*) in Hawaii. *Plant Disease*, *106*, 761. https://doi.org/10.1094/PDIS-05-21-1072-PDN

Keller, E. R. J., Zanke, C. D., Senula, A., Breuing, A., Hardeweg, B., & Winkelmann, T. (2013). Comparing costs for different conservation strategies of garlic (*Allium sativum* L.) germplasm in genebanks. *Genetic Resources and Crop Evolution*, *60*, 913–926. https://doi.org/10.1007/s10722-012-9888-5

Khoury, C. K., Brush, S., Costich, D. E., Curry, H. A., de Haan, S., Engels, J. M. M., Guarino, L., Hoban, S., Mercer, K. L., Miller, A. J., Nabhan, G. P., Perales, H. R., Richards, C., Riggins, C., & Thormann, I. (2021). Crop genetic erosion: Understanding and responding to loss of crop diversity. *New Phytologist*, *233*, 84–118. https://doi.org/10.1111/nph.17733

Khoury, C. K., Carver, D., Barchenger, D. W., Barboza, G. E., van Zonneveld, M., Jarret, R., Bohs, L., Kantar, M., Uchanski, M., Mercer, K., Nabhan, G., Bosland, P. W., & Greene, S. L. (2020). Modelled distributions and conservation status of the wild relatives of chile peppers (*Capsicum* L.). *Diversity and Distributions*, *26*(2), 209–225. https://doi.org/10.1111/ddi.13008

Khoury, C. K., Carver, D., Greene, S. L., Williams, K. A., Achicanoy, H. A., Schori, M., Leon, B., Wiersema, J. H., & Frances, A. (2020). Crop wild relatives of the United States require urgent conservation action. *Proceedings of the National Academy of Sciences*, *117*(52), 33351–33357. https://doi.org/10.1073/pnas.2007029117

Khoury, C. K., Greene, S. L., Krishnan, S., Miller, A. J., Moreau, T., Williams, K. A., Rodriguez-Bonilla, L., Spurrier, C. S., Zalapa, J., & Nabhan, G. P. (2020). Toward integrated conservation of North America's crop wild relatives. *Natural Areas Journal*, *40*(1), 96–100. https://doi.org/10.3375/043.040.0111

Khoury, C. K., Greene, S., Wiersema, J., Maxted, N., Jarvis, A., & Struik, P. C. (2013). An inventory of crop wild relatives of the United States. *Crop Science*, *53*(4), 1496–1508. https://doi.org/10.2135/cropsci2012.10.0585

Kostick, S. A., Norelli, J. L., & Evans, K. M. (2019). Novel metrics to classify fire blight resistance of 94 apple cultivars. *Plant Pathology*, *68*, 985–996. https://doi.org/10.1111/ppa.13012

Kuhnholz, S., & Seeley, T. D. (1997). The control of water collection in honey bee colonies. *Behavioral Ecology and Sociobiology*, *41*(6), 407–422. https://www.jstor.org/stable/4601407

Kybartaite, J., Šernaité, L., Rasiukevièiuté, N., & Valiuškaité, A. (2020). Plants and fungal pathogens under climate change, a review. Optimization of ornamental and garden plant assortment. *Technologies and Environment*, *11*, 37–45.

Lohani, N., Singh, M. B., & Bhalla, P. L. (2021). Short-term heat stress during flowering results in a decline in Canola seed productivity. *Journal of Agronomy and Crop Science*, *208*, 486–496. https://doi.org/10.1111/jac.12534

Lovell, J. T., Bentley, N. B., Bhattarai, G., Jenkins, J. W., Sreedasyam, A., Alarcon, Y., Bock, C., Boston, L. B., Carlson, J., Cervantes, K., Clermont, K., Duke, S., Krom, N., Kubenka, K., Mamidi, S., Mattison, C. P., Monteros, M. J., Pisani, C., Plott, C., … Randall, J. J. (2021). Four chromosome scale genomes and a pan-genome annotation to accelerate pecan tree breeding. *Nature Communications*, *12*(1), 1–12. https://doi.org/10.1038/s41467-021-24328-w

Moore, F. C., Baldos, U., Hertel, T., & Diaz, D. (2017). New science of climate change impacts on agriculture implies higher social cost of carbon. *Nature Communications*, *8*(1), 1–9. https://doi.org/10.1038/s41467-017-01792-x

Nabhan, G. P. (1989). *Enduring seeds: Native American agriculture and wild plant conservation*. North Point Press.

National Climate Task Force. (2021). *Conserving and restoring America the beautiful*. https://www.doi.gov/sites/doi.gov/files/report-conserving-and-restoring-america-the-beautiful-2021.pdf

NOAA. (2022). *Carbon dioxide now more than 50% higher than pre-industrial levels*. https://www.noaa.gov/news-release/carbon-dioxide-now-more-than-50-higher-than-pre-industrial-levels

O'Donnell, M. S., & Ignizio, D. A. (2012). Bioclimatic predictors for supporting ecological applications in the conterminous United States. *US Geological Survey Data Series*, *691*(10), 4–9. https://pubs.usgs.gov/ds/691/ds691.pdf

Oliver, R. (2022). Observations of pollen subs: Part 4 – Nectar, water and humidity. *Scientific Beekeeping*, *00*, 00–00. https://scientificbeekeeping.com/observations-on-pollen-subs-part-4-nectar-water-and-humidity/

Pagter, M., & Arora, R. (2013). Winter survival and deacclimation of perennials under warming climate: Physiological perspectives. *Physiologia Plantarum*, *147*(1), 75–87. https://doi.org/10.1111/j.1399-3054.2012.01650.x

Panis, B., Nagel, M., & Van den Houwe, I. (2020). Challenges and prospects for the conservation of crop genetic resources in field genebanks, in in vitro collections and/or in liquid nitrogen. *Plants*, *9*(12), 1634. https://doi.org/10.3390/plants9121634

Pathak, T. B., Maskey, M. L., Dahlberg, J. A., Kearns, F., Bali, K. M., & Zaccaria, D. (2018). Climate change trends and impacts on California agriculture: A detailed review. *Agronomy*, *8*(3), 25. https://doi.org/10.3390/agronomy8030025

Pathirana, R., & Carimi, F. (2022). Management and utilization of plant genetic resources for a sustainable agriculture. *Plants*, *11*(15), 2038. https://doi.org/10.3390/plants11152038

Pavek, D. S., Lamboy, W. F., & Garvey, E. J. (2003). Selecting in situ conservation sites for grape genetic resources in the USA. *Genetic Resources and Crop Evolution*, *50*(2), 165–173. https://doi.org/10.1023/A:1022947605916

Porter, J. H., Parry, M. L., & Carter, T. R. (1991). The potential effects of climatic change on agricultural insect pests. *Agricultural and Forest Meteorology*, *57*(1-3), 221–240. https://doi.org/10.1016/0168-1923(91)90088-8

Pörtner, H. O., Roberts, D. C., Adams, H., Adler, C., Aldunce, P., Ali, E., … & Birkmann, J. (2022). Climate change 2022: Impacts, adaptation and vulnerability. *IPCC Sixth Assessment Report*. https://policycommons.net/artifacts/2679314/climate-change-2022/3702620/

Postman, J., Hummer, K., Stover, E., Krueger, R., Forsline, P., Grauke, L. J., Zee, F., Ayala-Silva, T., & Irish, B. (2006). Fruit and nut genebanks in the US National Plant Germplasm System. *Hortscience*, *41*(5), 1188–1194. https://doi.org/10.21273/HORTSCI.41.5.1188

Pravallika, K., Arunkumar, C., Vijayakumar, A., Beena, R., & Jayalekshmi, V. G. (2020). Effect of high temperature stress on seed filling and nutritional quality of rice (*Oryza sativa* L.). *Journal of Crop and Weed*, *16*(2), 18–23. https://doi.org/10.22271/09746315.2020.v16.i2.1310

Pusey, P. L., & Curry, E. A. (2004). Temperature and pomaceous flower age related to colonization by *Erwinia amylovora* and antagonists. *Phytopathology*, *94*(8), 901–911. https://doi.org/10.1094/PHYTO.2004.94.8.901

Ramirez-Villegas, J., Khoury, C. K., Achicanoy, H. A., Diaz, M. V., Mendez, A. C., Sosa, C. C., Kehel, Z., Guarino, L., Abberton, M., Aunario, J., Al Awar, B., Alarcon, J. C., Amri, A., Anglin, N. L., Azevedo, V., Aziz, K., Capilit, G. L., Chavez, O., Chebotarov, D., … Zavala, C. (2022). State of ex situ conservation of landrace groups of 25 major crops. *Nature Plants*, *8*(5), 491–499. https://doi.org/10.1038/s41477-022-01144-8

Reeksting, B. J., Taylor, N. J., & van den Berg, N. (2014). Flooding and *Phytophthora cinnamomi*: Effects on photosynthesis and chlorophyll fluorescence in shoots of non-grafted *Persea americana* (Mill.) rootstocks differing in tolerance to Phytophthora root rot. *South African Journal of Botany*, *95*, 40–53. https://doi.org/10.1016/j.sajb.2014.08.004

Riahi, K., van Vuuren, D. P., Kriegler, E., Edmonds, J., O'Neill, B. C., Fujimori, S., Bauer, N., Calvin, K., Dellink, R., Fricko, O., Lutz, W., Popp, A., Cuaresma, J. C., Samir, K. C., Leimbach, M., Jiang, L., Kram, T., Rao, S., Emmerling, J., … Tavoni, M. (2017). The shared socioeconomic pathways and their energy, land use, and greenhouse gas emissions implications: An overview. *Global Environmental Change*, *42*, 153–168. https://doi.org/10.1016/j.gloenvcha.2016.05.009

Riordan, E. C., & Nabhan, G. P. (2019). Trans situ conservation of crop wild relatives. *Crop Science*, *59*(6), 2387–2403. https://doi.org/10.2135/cropsci2019.06.0356

Rodriguez-Bonilla, L., Williams, K. A., Rodriguez Bonilla, F., Matusinec, D., Maule, A., Coe, K., Wiesman, E., Diaz-Garcia, L., & Zalapa, J. (2020). The genetic diversity of cranberry crop wild relatives, *Vaccinium macrocarpon* Aiton and *V. oxycoccos* L., in the US, with special emphasis on National Forests. *Plants*, *9*(11), 1446. https://doi.org/10.3390/plants9111446

Rosa, L., Chiarelli, D. D., Sangiorgio, M., Beltran-Peña, A. A., Rulli, M. C., D'Odorico, P., & Fung, I. (2020). Potential for sustainable irrigation expansion in a 3˚C warmer climate. *Proceedings of the National Academy of Sciences*, *117*(47), 29526–29534. https://doi.org/10.1073/pnas.2017796117

Sadok, W., & Jagadish, S. K. (2020). The hidden costs of nighttime warming on yields. *Trends in Plant Science*, *25*(7), 644–651. https://doi.org/10.1016/j.tplants.2020.02.003

Seeley, T. D. (2009). *The wisdom of the hive: The social physiology of honey bee colonies*. Harvard University Press.

Seeley, T. D. (2019). *The lives of bees: The untold story of the honey bee in the wild*. Princeton University Press.

Shtienberg, D., Manulis-Sasson, S., Zilberstaine, M., Oppenheim, D., & Shwartz, H. (2015). The incessant battle against fire blight in pears: 30 years of challenges and successes in managing the disease in Israel. *Plant Disease*, *99*(8), 1048–1058. https://doi.org/10.1094/PDIS-01-15-0101-FE

Skendžić, S., Zovko, M., Živković, I. P., Lešić, V., & Lemić, D. (2021). Effect of climate change on introduced and native agricultural invasive insect pests in Europe. *Insects*, *12*(11), 985. https://doi.org/10.3390/insects12110985

Sloggett, J. J. (2021). Aphidophagous ladybirds (Coleoptera: Coccinellidae) and climate change: A review. *Insect Conservation and Diversity*, *14*(6), 709–722. https://doi.org/10.1111/icad.12527

Sparks, D., Reid, W., Yates, I. E., Smith, M. W., & Stevenson, T. G. (1995). Fruiting stress induces shuck decline and premature germination in pecan. *Journal of the American Society for Horticultural Science*, *120*(1), 43–53. https://doi.org/10.21273/JASHS.120.1.43

Tadesse, Y., Amare, D., & Kesho, A. (2021). Coffee leaf rust disease and climate change. *World Journal of Agricultural Science*, *17*(5), 418–429.

Taylor, K., Brummer, T., Rew, L. J., Lavin, M., & Maxwell, B. D. (2014). *Bromus tectorum* response to fire varies with climate conditions. *Ecosystems*, *17*(6), 960–973. https://doi.org/10.1007/s10021-014-9771-7

Terrer, C., Jackson, R. B., Prentice, I. C., Keenan, T. F., Kaiser, C., Vicca, S., Fisher, J. B., Reich, P. B., Stocker, B. D., Jungate, B. A., Peñuelas, J., McCallum, I., Soudzilovskaia, N. A., Cernusak, L. A., Talhelm, A. F., Van Sundert, K., Piao, S., Newton, P. C. D., Hovenden, M. J., … Franklin, O. (2019). Nitrogen and phosphorus constrain the CO_2 fertilization of global plant biomass. *Nature Climate Change*, *9*(9), 684–689. https://doi.org/10.1038/s41558-019-0545-2

Thuiller, W., Lavorel, S., Araújo, M. B., Sykes, M. T., & Prentice, I. C. (2005). Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences*, *102*(23), 8245–8250. https://doi.org/10.1073/pnas.0409902102

Towill, L. E. (1999). Cryopreservation of sour cherry (*Prunus cerasus* L.) using a dormant vegetative bud method. *Cryo-Letters*, *20*, 215–222.

USDA. (2021). *Action plan for climate adaptation and resilience*. https://www.sustainability.gov/pdfs/usda-2021-cap.pdf

USDA-ARS GRIN-Global. (2022a). https://npgsweb.ars-grin.gov/gringlobal/query/summary

USDA-ARS GRIN-Global. (2022b). https://npgsweb.ars-grin.gov/gringlobal/search

USDA Climate Hubs. (2021). *2021 Northwest heat dome: Causes, impacts and future outlook*. https://www.climatehubs.usda.gov/hubs/northwest/topic/2021-northwest-heat-dome-causes-impacts-and-future-outlook

USDA Climate Hubs. (2022). *Homepage*. https://www.climatehubs.usda.gov/

USDA Forest Service. Adaptation: 2022 Forest Service climate adaptation plan. (2022). https://www.fs.usda.gov/managing-land/sc/adaptation

USFS & USDA-ARS. (2014). *Joint strategic framework on the conservation and use of native crop wild relatives in the United States. FS-1029*. USDA. https://www.fs.usda.gov/wildflowers/ethnobotany/documents/cwr/FrameworkNativeCropWildRelativesOct2014.pdf

Vano, J. A., Kim, J. B., Rupp, D. E., & Mote, P. W. (2015). Selecting climate change scenarios using impact-relevant sensitivities. *Geophysical Research Letters*, *42*, 5516–5525. https://doi.org/10.1002/2015GL063208

Velásquez, A. C., Castroverde, C. D. M., & He, S. Y. (2018). Plant–pathogen warfare under changing climate conditions. *Current Biology*, *28*(10), R619–R634. https://doi.org/10.1016/j.cub.2018.03.054

Vincent, H., Amri, A., Castañeda-Álvarez, N. P., Dempewolf, H., Dulloo, E., Guarino, L., Hole, D., Mba, C., Toledo, A., & Maxted, N. (2019). Modeling of crop wild relative species identifies areas globally for in situ conservation. *Communications Biology*, *2*(1), 1–8. https://doi.org/10.1038/s42003-019-0372-z

Volk, G. M., Byrne, P. F., Coyne, C. J., Flint-Garcia, S., Reeves, P. A., & Richards, C. (2021). Integrating genomic and phenomic approaches to support plant genetic resources conservation and use. *Plants*, *10*(11), 2260. https://doi.org/10.3390/plants10112260

Volk, G. M., & Walters, C. (2003). Preservation of genetic resources in the national plant germplasm clonal collections. *Plant Breeding Reviews*, *23*, 291–344. https://doi.org/10.1002/9780470650226.ch7

Walters, J., Zavalnitskaya, J., Isaacs, R., & Szendrei, Z. (2022). Heat of the moment: Extreme heat poses a risk to bee-plant interactions and crop yields. *Current Opinion in Insect Science*, *52*, 100927. https://doi.org/10.1016/j.cois.2022.100927

Warschefsky, E. J., & Rieseberg, L. H. (2021). Laying the groundwork for crop wild relative conservation in the United States. *Proceedings of the National Academy of Sciences*, *118*(4), e2024375118. https://doi.org/10.1073/pnas.2024375118

Williams, K. A., & Greene, S. L. (2018). Conservation of crop wild relatives in the USA. In S. L. Greene, K. A. Williams, C. K. Khoury, M. B. Kantar, & L. F. Marek (Eds.), *North American crop wild relatives, Volume 2. Important species*. Springer.

Zeilinger, A. R., Rapacciuolo, G., Turek, D., Oboyski, P. T., Almeida, R. P., & Roderick, G. K. (2017). Museum specimen data reveal emergence of a plant disease may be linked to increases in the insect vector population. *Ecological Applications*, *27*(6), 1827–1837. https://doi.org/10.1002/eap.1569

Zeng, J., Liu, Y., Zhang, H., Liu, J., Jiang, Y., Wyckhuys, K. A., & Wu, K. (2020). Global warming modifies long-distance migration of an agricultural insect pest. *Journal of Pest Science*, *93*(2), 569–581. https://doi.org/10.1007/s10340-019-01187-5

Zhao, H., Li, G., Guo, D., Li, H., Liu, Q., Xu, B., & Guo, X. (2021). Response mechanisms to heat stress in bees. *Apidologie*, *52*(2), 388–399. https://doi.org/10.1007/s13592-020-00830-w

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Volk, G. M., Carver, D., Irish, B. M., Marek, L., Frances, A., Greene, S., Khoury, C. K., Bamberg, J., del Rio, A., Warburton, M. L., & Bretting, P. K. (2023). Safeguarding plant genetic resources in the United States during global climate change. *Crop Science*, 1–23. https://doi.org/10.1002/csc2.21003