

ORIGINAL ARTICLE

Wild relatives of potato may bolster its adaptation to new niches under future climate scenarios

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Abstract

Food production strategies and patterns are being altered in response to climate change. Enhancing the adaptation of important food crops to novel climate regimes will be critical to maintaining world food supplies. Climate change is altering the suitability of production areas for crops such as potato (*Solanum tuberosum* L.) making future productivity, resilience, and sustainability of this crop dependent on breeding for climate adaptation, including through the introgression of novel traits from its wild relatives. To better understand the future production climate envelopes of potatoes, and the potential of its wild relatives to contribute to adaptation to these environments, we estimated the climate of potato in four future climate scenarios and overlapped the current climate of 72 wild relative species and potato with these future climates. We discovered a shift of up to 12.5% by potato from current to novel climate by 2070 and varying magnitudes of overlap by different wild relatives with potato, primarily driven by the extent of endemism. To address the threat of novel climate on potato production and with the wealth of data available for the agrobiodiversity in potato wild relatives, we systematically developed a prioritization value inspired by the logic of the breeder's equation for locating potentially beneficial species possessing local adaptability, climatic plasticity, and interspecific crossability. In doing so, 26 unique species by discrete climate combinations are found, highlighting the presence of unique species to use in adapting potato to changing local climates. Further, the 20 highest prioritized values belong to diploid species, enforcing the drive to shift into diploid breeding by the potato research community, where introgression of the local climate adaptability traits may be more streamlined.

KEYWORDS

climate change, crop improvement, food security, localization, plant breeding

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1 | INTRODUCTION

Global food security is threatened by climate change, impacting production and land use change (Foley et al., 2011; Mehrabi et al., 2020; Ramankutty et al., 2018). Extreme climatic events and shifts have and continue to place pressure on crop cultivars by introducing abiotic and biotic stresses to novel production regimes (Lesk et al., 2016). Future projections provide a way to create realistic assessments of means and variances of future climate scenarios. Adaptation strategies include: (i) sourcing varieties that are adapted to the expected future local climate, (ii) assessing crop wild relatives for naturally evolved adaptations, (iii) changing the crops grown in a particular area, (iv) defining different agroecosystems for existing crops, (v) substantially changing agronomic practices such as row spacing, irrigation and planting date, and (vi) abandoning current production locations with human population moving to areas amenable to current practices/cultivars (Burke et al., 2009; Heider et al., 2021; Pironon et al., 2019; Ramirez-Villegas & Khoury, 2013; Sloat et al., 2020). Despite research exploring the potential for shifts in existing production zones or toward zones forecasted for potato production compatibility (Hijmans, ; Leemans & Solomon, 1993), such shifts present potential tradeoffs (Tanentzap et al., 2015). Therefore, the least disruptive option is utilizing agrobiodiversity for adapting crops to the changing environments with breeding techniques (Borlaug, 1983; Dempewolf et al., 2017; Jansky et al., 2013). Utilizing wild relative species, as well as landrace and heirloom varieties, provides a potential mechanism for alleviating the abiotic stresses expected with climatic shifts through evolved traits including tolerance to salinity, drought, and temperature extremes (Bailey-Serres et al., 2019; Ramankutty et al., 2018). The focus on specific environmental factors has led to large redundancy and overlap in personal (e.g., breeding programs) and institutional collections (e.g., genebanks), resulting in the overcollection of some species and undercollection of others (Dempewolf et al., 2017).

Potato (*Solanum tuberosum* L.) is the most important tuber for human consumption (>1 billion people annually; FAOSTAT, 2017). The tubers of potato provide a rich and complex source of carbohydrates and essential nutrients, including dietary fiber, vitamins, minerals, protein, and antioxidants (Bach et al., 2012). Potato thrives in a relatively narrow climate niche, for example, tuberization has been empirically shown to diminish at temperatures above 17 °C, negatively impacting productivity (Haverkort, 1990; Hijmans, ; Stol et al., 1991). Future yield projections under climate change

indicate a likely production decline in major potato growing regions (Dahal et al., 2019; Raymundo et al., 2018). Changes in potato agronomic practices (e.g., pesticides, fertilizers, and irrigation) have increased the geographic range of production and production per unit area (Devaux et al., 2014; Hijmans, 2001, ; Murchie et al., 2009). Such agronomic practices may help mitigate the impacts of climate change induced production decline and crop improvement can champion these efforts by providing new crop varieties that are more resilient to abiotic stresses.

Potato breeding has generally seen steady improvement with occasional flurries of activity, one such time of rapid improvement was after the late blight epidemics of the 19th century (Jansky & Spooner, 2018). Most selections were made from open pollinated populations as specific crosses of cultivars were rarely successful until the mid-20th century (Bradshaw & MacKay, 1994; Comai, 2005; Jansky & Thompson, 1990; Krantz, 1924, 1946). Improvement in potato yield in the last century was mostly due to agronomics while improvements in quality traits have been attributed to genetics. Potato is a clonally propagated, autotetraploid crop with a narrow genetic base compared to its wild relatives (Spooner et al., 2014), making breeding difficult despite recent efforts to incorporate new diversity (Jansky, 2009) via introgression with potato wild relatives (hereafter PWR). Modern cultivars of potato possess relatively little difference in the percentage of heterozygous loci nor the frequency of homozygous loci from cultivars developed in the past two-centuries (Hirsch et al., 2013; Vos et al., 2015). Additionally, cultivar turnover is very slow in many regions, for example with cultivars in North America being grown for 40–50 years (reviewed in Singh et al., 2020). Using PWR has helped to introduce genetic diversity and valuable agronomic traits, most importantly disease resistance into breeding lines (Castañeda-Álvarez et al., 2015; Hijmans, 2001; Jansky et al., 2013; Zhang et al., 2017).

PWR are a highly diverse set of species found in *Solanum* section *Petota* (Castañeda-Álvarez et al., 2015). These species have a range of ploidy and meiotic behavior (disomic, polysomic, and mixed-somic inheritance), occasionally causing meiotic problems when crossed with the crop (Key, 1970). Many attributes of the PWR have been defined, including their ploidy, mating system, germplasm classification, endosperm balance number, phylogenetic relationships, and geographic ranges in order to operationalize their use in breeding (Castañeda-Álvarez et al., 2015; Hijmans, 2001; Spooner & Hetttersheid, 2007; Spooner & Hijmans, 2001; Zenil-Ferguson et al., 2019). The goal of plant breeding is to

move the population mean of a given trait to a more beneficial value for the particular human use it is intended, the speed with which this can be done is often measured using the breeder's equation (Lush, 1943), which conceptualizes efficiency after accounting for genetic variance and selection intensity. The framework has not been explored in the context of climate change projections and crop wild relatives and could expedite selection of donor species. An estimated breeding value (EBV) is the potential of an individual as a genetic parent, considering the heritability of a given trait under selection (Bernardo, 2020). Typically, EBVs are obtained from narrow breeding populations of a single crop species by multiplying the narrow-sense heritability (calculated either by variance decomposition or parent–offspring regression) by the difference between the parent performance and population mean, which provides an estimate of how the progeny of a specific parental line may perform when compared to the alternative parent. We propose that EBVs could also be calculated for crop wild relative species with the use of the breeder's equation, as long as the phenotype of interest is clearly defined. With this, species and populations instead of individual parents can be identified to extend past heritability to additionally incorporate biological factors (e.g., ploidy, mating system), evolutionary factors (e.g., phylogenetic relationship), and ecological factors (e.g., species environmental niche) in a hierarchical way through interspecific hybridization. Functionally, this adjustment to the breeder's equation would specify a ranking of wild relative species for a discretely described climate to incorporate to each locally relevant breeding program.

Here, we focus on assessing crop wild relatives for naturally evolved adaptations, which is broadly focusing on agrobiodiversity, and has a recognized role in mitigating the threat to crops (Dempewolf et al., 2017). The uncertainty of future climatic conditions creates a situation where breeders must efficiently and effectively prioritize the best potential species to create interspecific populations from and to ameliorate shift-induced stress on production. Therefore, the objectives of this study were to (i) model the shift in climatic conditions expected for potato in the future (2050 and 2070) at a global scale, (ii) model the current climate niche of 72 PWRs, (iii) assess overlaps between the climate niches of PWRs and the novel/future conditions expected for potato, (iv) propose a formalized approach to prioritize PWRs for use in breeding based on their potential for future climate adaptation in specific climatic zones (Pironon et al., 2020). Conceptually, this is similar to envirotyping (Xu, 2016) and enviromics (Resende et al., 2020), but instead of working with breeding populations, here crop wild relatives are explored. This work could serve as a model for

other important crops which are likely to suffer reduced productivity due to climate change.

2 | METHODS

2.1 | Data acquisition

Potato production occurrences ($N = 726,103$) were compiled from the year 2000 land use census data at a 5 arc-minutes resolution (Monfreda et al., 2008), while occurrences for the 72 PWR ($N = 37,250$; Table S1) were compiled from previous gap analysis that prioritized PWR (Castañeda-Álvarez et al., 2015). Climate data were retrieved from WorldClim 2.0 (<https://www.worldclim.org/data/cmip6/cmip6climate.html>) for the years 1970–2000 (hereafter “current climate,” Fick & Hijmans, 2017) at a 5 arc-minutes (~10km) resolution (Eyring et al., 2016). Future climate projections are based on the sixth assessment report (AR6) of the Intergovernmental Panel on Climate Change (IPCC) that uses various shared socioeconomic pathways (SSPs) for different global climate models (GCMs) (IPCC, 2021). Nineteen variables provided by WorldClim were utilized to ensure full capture of mean and variance of temperature and precipitation conditions across and between seasonal shifts for potato and each of its PWRs (Table S2). The same variables were collected for the 2050 and 2070 time periods (averages for 2041–2060 and 2061–2080, respectively) according to two shared socioeconomic pathways (SSPs) of SSP2-4.5 (considered a medium effort to curb emissions) and SSP5-8.5 (considered low to no effort to curb emissions) and eight GCMs (global climate models). The eight GCMs were BCC-CSM2-MR, CNRM-CM6-1, CNRM-ESM2-1, CanESM5, IPSL-CM6A-LR, MIROC-ES2L, MIROC6, and MRI-ESM2-0. Current and future climatic information were extracted for each potato and PWR occurrence point using the `extract` function in the raster package of R. Data for the Köppen–Geiger climate classes of PWR and life history traits were derived from Fumia et al. (2022). The Köppen–Geiger divides climate regimes into a discrete three-tiered system (five main, 30 sub and sub–sub tiers) based on main climate, seasonal precipitation, and temperature (reviewed in Rubel & Kottek, 2010). Further, the regression coefficients for climate niche diversity as well as phylogenetic relatedness were sourced for PWR from Fumia et al. (2022).

2.2 | Climate comparisons

We performed principal component analysis (PCA) to identify the climate niches of the cultivated potato at

current and future time points and compare to the current climate niche of its 72 wild relatives using the 19 bioclimatic variables using the R packages *ade4*, *grDevices*, and *sp*. Climate niches were built using convex polygons around the occurrence points of each species in the principal component climatic space from PC1 (46.4% variance explained) and PC2 (22.2% variance explained) in the joint analysis of species. The technique of convex hull was chosen for quantifying the niche space over alternatives as it does not rely on point density (important because occurrence point sampling is uneven in geographic space) and is conceptually simple and readily interpretable. However, this technique is sensitive to outliers; therefore, the analyses were repeated discarding six different selections of outliers based on Mahalanobis distances (values ranging from 5 to 10) between each occurrence point and the centroid of the species climatic niche, as in Pironon et al. (2019). We estimated the current and future climatic conditions of potato and the current climatic conditions of the 72 PWRs. To estimate the impact of life history traits, species with the same mating system/ploidy combinations were first aggregated, then polygons were drawn around the combined data. The climatic change of potato was estimated as the percentage of the total area of the polygon representing future climatic conditions that is not intersected by the total area of the polygon representing current climatic conditions. We described novel climate as the expected future climate space that is not intersected by the current climate space, indicating a climatic zone of high insecurity facing future potato production. We then analyzed how current PWR climatic niches overlap with this novel climate space in order to estimate the potential contribution of each PWR to potato's adaptation under climate change.

2.3 | CWR prioritization score

We developed a PWR prioritization (PWRP) score inspired by the logic of the breeder's equation (BE) (Bernardo, 2020; Lush, 1943; Lynch & Walsh, 1998; Walsh & Lynch, 2018). Specifically, we conceptualized the PWR species niche overlap with future and current potato climatic conditions at different time points as phenotypes, analogous to the response to selection, which we call climate response potential (Table 1). Considering this, we calculated the PWRP utilizing the format of the BE (Figure 1).

Instead of having a response in progeny, we predict the response in a species over time, this presents a potential capacity for climate adaptability and thus a higher

score in a specific environment means a higher utility as a donor species, this is represented as *PWRP*. Instead of selection intensity (traditionally the phenotypic variance selected on), we use the proportion of a specific Koppen–Geiger climate class as the phenotype which varies by species (Figure S1). This shows future potential adaptability in that specific discrete climate class and is now represented as *applicability* (*a*) (Figure 1). The Koppen–Geiger class system (Rubel & Kottek, 2010) provides climate zones that are useful when defining the range of a particular breeding program and knowing the discrete class provides a shorthand for localization of valuable breeding germplasm. Therefore, *applicability* (*a*) serves as a honing value from the current occurrence of a given PWR in a specific discrete climate class as a percentage of occurrences in that class over the total number of occurrences of that species (Koppen–Geiger Climates, Figure S1). Further, to highlight the ability to localize valuable germplasm this discretizing allows for a correction of the PWRP response to represent 0 where a species does not exist and would be unlikely to offer phenotypic advancement to cultivated potato in that climate, to greater than 0 where the species solely exists in that specific climate.

Instead of heritability, we have a two-tiered component involving crossing potential and climatic plasticity. *Environmental plasticity* (*ep*) represents the correlation between the percentage overlap of a PWR species over the current climate of potato growing regions with the percentage overlap of a PWR species over the future forecasted climate of potato growing regions (adjusted for each SSP and year combination) (Figure 1). Due to the interspecific nature of potential crosses, we adjust the correlation between time points with crossability using two aspects: (1) to adjust for the evolutionary role in climatic diversity, we use the regression coefficient for niche divergence among PWR species with different life history trait interactions (see Fumia et al., 2022); and (2) to adjust for the evolutionary role in crossability, we use the chloroplast genome genetic distance between all PWR and *S. tuberosum* (Fumia et al., 2022), representing the *evolutionary history* (*eh*) (Figure 1). The *evolutionary history* (*eh*) represents the regression output of life-history trait influence upon climatic variation as specifically the intercept +or - the slope value by a PWRs life-history trait combination (Fumia et al., 2022). The ordinary least squares regression referred to uses the count of climate classes as the response with individual life-history trait combinations as the predictors (e.g., asexual diploid, self-compatible diploid, self-incompatible diploid, and self-compatible polyploid), of which the associated slope value is used in *eh* dependent upon this biology of the PWR species. Additionally applied in *eh* is phylogenetic distance,

TABLE 1 Top two species' PWRP values under SSP 4.5 in 2050 for each climate class. Green represents a change in the top two or a rank change in alternative SSP and year scenarios. The presence of these species indicates they may be the most suitable parents for crossing to potato to improve adaptation to future climates in the noted climate class

Koppen-Geiger Climate	Species	Value	
Af	Tropical Rainforest	<i>Solanum colomcianum</i>	0250
		<i>Solanum longiconicum</i>	0.234
Am	Tropical Monsoon	<i>Solanum Garcia-barrigae</i>	0.417
		<i>Solanum longiconicum</i>	0.361
As	Tropical Savanna Dry-Summer	<i>Solanum andreanum</i>	0.039
		<i>Solanum hougassi</i>	0.034
Aw	Tropical Savanna Dry-Winter	<i>Solanum chilliasense</i>	1.646
		<i>Solanum neocardenasii</i>	0.501
Bsh	Hot Semi-Arid	<i>Solanum olmosense</i>	1.032
		<i>Solanum paucissectum</i>	0.767
BSk	Cold Semi-Arid	<i>Solanum gracilifrons</i>	1.705
		<i>Solanum ctumazaense</i>	1.678
BWh	Hot Desert	<i>Solanum buancabambense</i>	0.184
		<i>Solanum cajamarquense</i>	0.173
BWk	Cold Desert	<i>Solanum acroscopicum</i>	0.464
		<i>Solanum medians</i>	0.175
Cfa	Humid Subtropical	<i>Solanum commersonii</i>	0.798
		<i>Solanum chacoense</i>	0.766
Cfb	Temperate oceanic	<i>Solanum neocardenasii</i>	2.013
		<i>Solanum pillabuatense</i>	1.836
Cfe	Subpolar oceanic	<i>Solanum incasicum</i>	1.869
		<i>Solanum buesii</i>	1.103
Csa	Hot-summer Mediterranean	<i>Solanum stoloniferum</i>	0.070
		<i>Solanum iopetalum</i>	0.008
Csb	Warm-summer Mediterranean	<i>Solanum andreanum</i>	0.466
		<i>Solanum columbianum</i>	0.168
Cwa	Monsoon humid subtropical	<i>Solanum chacoense</i>	0.401
		<i>Solanum hougasii</i>	0.305
Cwb	Subtropical highland	<i>Solanum neorossii</i>	1.784
		<i>Solanum gandarillasii</i>	1.540
Cwe	Cold subtropical highland	<i>Solanum venturii</i>	0.106
		<i>Solanum brevicaule</i>	0.057
ET	Polar Tundra	<i>Solanum neovavilovii</i>	1.780
		<i>Solanum limbaniense</i>	1.285
Top-2 Change with a Change in Scenario			
Top-2 Do Not Change with a Change in Scenario			

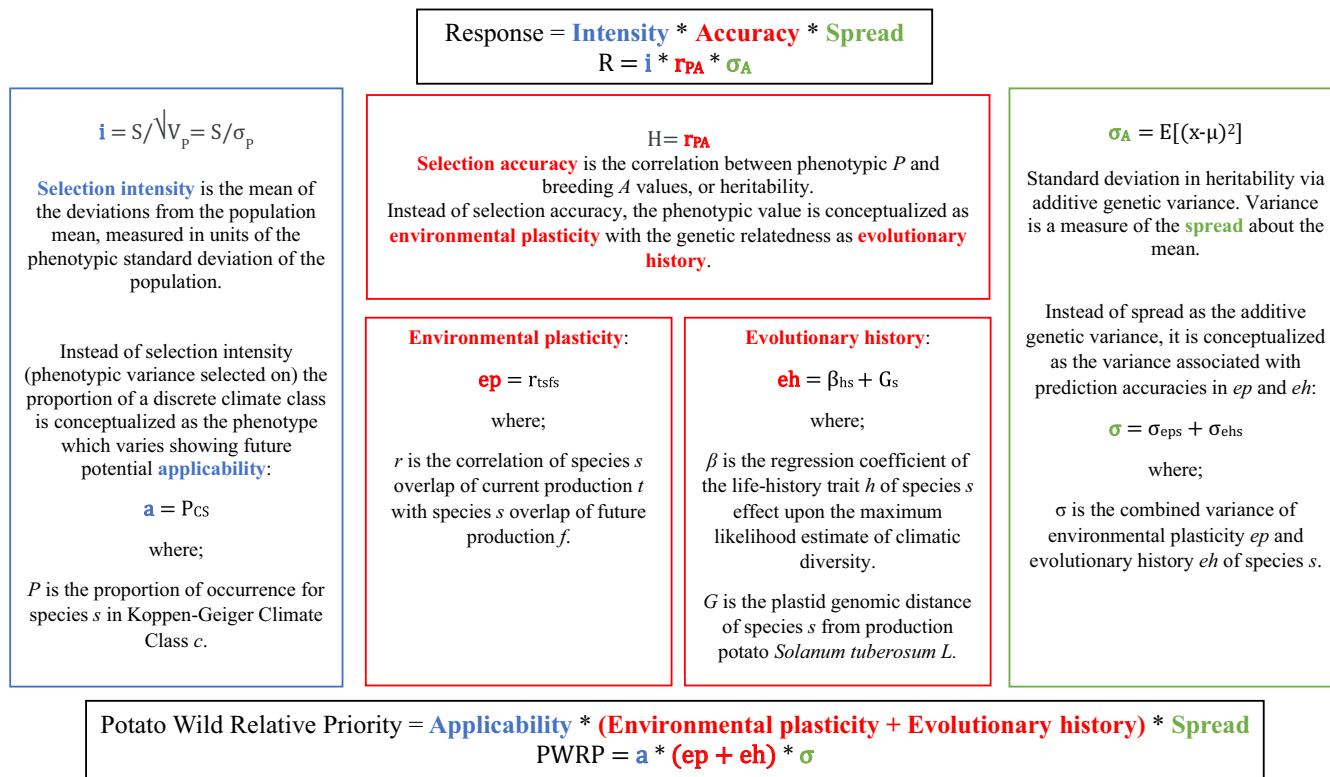


FIGURE 1 Flow chart conceptualizing the Potato Wild Relative Prioritization (PWRP) score by using the logic of the Breeder's Equation (BE). Instead of having a response in progeny, there is a predicted response in a species over time. This presents a potential capacity for climate adaptability and thus a higher score in a specific environment means a higher utility as a donor species

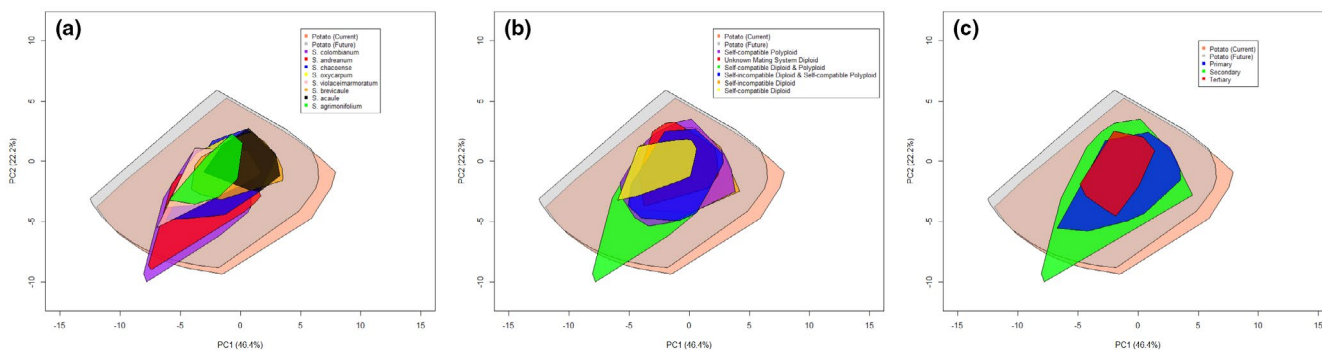


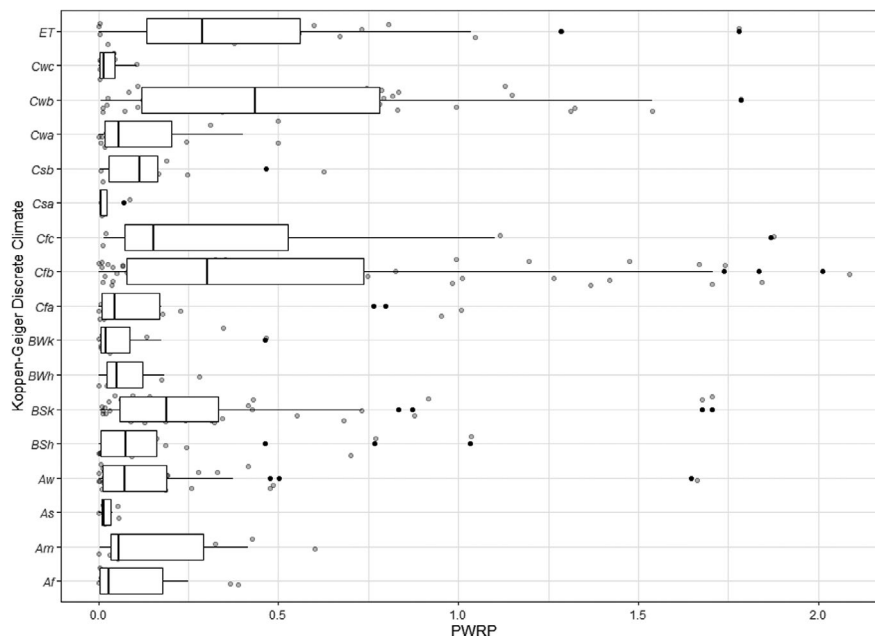
FIGURE 2 Principal component analysis of environmental space of PWR under SSP 8.5 in 2070 grouped as (a) top-8 overlapping PWR, (b) life history traits, and (c) genepool

calculated as the Bayesian predicted plastid genomic distance from cultivated potato (*S. tuberosum*) from Fumia et al. (2022), but this metric could be replaced with any metric of phylogenetic relatedness. Instead of additive genetic variance, we conceptualize this as the variance associated with *environmental plasticity* (ep) and *evolutionary history* (eh), representing the *spread* (σ). *Spread* (σ) accounts for the variation in attributes of ep , as determined by the standard deviation among the different GCMs used in climate projections, and eh , as determined by the standard deviation of the regression intercept +or - the standard deviation of the slope value (Figure 1).

3 | RESULTS

Under future projected climates there is both a clear overlap with those climates used by potato through mating system/ploidy and novel climate space available (Figure 2). Following the SSP 4.5, we predict a 7% climatic shift in potato growing regions by 2050, increasing to 8.4% in 2070. Following a scenario of low effort to curb greenhouse gas emissions (SSP 8.5), we find an 8.7% climatic shift in potato growing regions by 2050, increasing to 12.5% in 2070. Considering global climatic shifts, ~6–12% of the future projected climate space of

FIGURE 3 Boxplot of PWRP for each climate class under SSP 8.5 2070



potato growing regions will be novel, depending on the climate model and emission scenario considered. The above changes in the climatic niche of potato production regions are primarily shifts along PC1, mostly formed by temperature variables (Table S2). This novel climate space is partially occupied by PWR species that possess self-compatible, diploid populations, which in general have the largest ranges and exist in novel climates relative to the current extent of potato. These self-compatible, diploid PWRs exist in the current climate primarily identified by lower PC1 (temperature) and PC2 (precipitation) values (Table S1). It was unexpected that self-compatible diploid species were in the novel climate space as their climate niche is expected to be smaller than other ploidy-mating system combinations (Fumia et al., 2022), this indicates that the specialized nature of the self-compatible diploid populations is becoming more important and more represented in future climate predictions.

The range in the size of climate space varied from the narrowest PWR (*Solanum gracilifrons* Bitter) found in a single small valley near Colcabamba, Peru, to the broadest climate niche of potato, an effect of domestication. PWRs exist in a large number of discrete climate classes (Figure S1), ranging from narrow endemic species occurring in single climate classes (e.g., *Solanum salasianum* Ochoa) to those which exist in over half of the major biomes of earth and 15 climate classes (e.g., *Solanum chacoense* Bitter). The current climatic niche of PWRs shows substantial variation between the predicted novel climates from the global climate models (GCMs) in the future (2050 and 2070) in the different emission scenarios (SSP 4.5 and 8.5) when overlapped with current and future niches of

potato production. As expected, there is more shift in the climate niche at the later time point 2070 and under the more severe emission scenario SSP 8.5 (Figure S2). The largest range seen among the examined species is the domesticated potato. The range expansion of the domestic compared to the PWR can be observed in the number of Koppen–Geiger climate classes where potato occurs relative to PWR species (Figure S1) as well as the total area covered within the climate spaces (Figure 2).

Under future projected climates there is clear overlap of novel climate space by individual PWRs (Figure 2b). In SSP 4.5 in 2050, there was an average overlap of 47.5% by PWRs with the future projected climate of potato production regions, decreasing to 47% in 2070. In SSP 8.5 in 2050, there was an average overlap of 47.1% by PWRs with the future projected climate of potato production regions, decreasing to 45.7% in 2070. PWRs, specifically the top-8 identified (Figure S3), exhibit the adaptation to a higher degree of lower PC1 and PC2. Here, the species that show the most change and most potential for future use in novel space are *S. colombianum* and *S. andreanum*, both possessing populations of self-compatible diploids as well as driving the novel climate space of the secondary gene pool (Figure 2c).

The matrix of prioritization values (PWRP) shows clear variation in PWR regarding utility for breeding with potato for adaptation to climate change (Figure 3; Table 2). The species that showed the best potential for use in adaptation to unique climates were *Solanum neocardenasii*, *Solanum incasicum*, and *Solanum pillahuatense* (Table 1). However, when the end goal shifts, the species with the highest overall PWRP when compared to all other species shifts to *Solanum colombianum* (Table 2). As expected,

TABLE 2 80 Highest valued PWRP (SSP 8.5 in 2070). The table shows the highest scoring species by climate combinations for the worst-case scenario in 2070

Potato Wild Relative Species	Köppen-Geiger Climate	PWRP Value
<i>Solanum colombianum</i>	Temperate oceanic	2.086
<i>Solanum incasicum</i>	Subpolar oceanic	1.877
<i>Solanum pillahuatense</i>	Temperate oceanic	1.844
<i>Solanum neorossii</i>	Subtropical highland	1.784
<i>Solanum neovavilovii</i>	Polar tundra	1.779
<i>Solanum ayacuchense</i>	Temperate oceanic	1.740
<i>Solanum salasianum</i>	Temperate oceanic	1.706
<i>Solanum gracilifrons</i>	Cold Semi-Arid	1.704
<i>Solanum contumazaense</i>	Cold Semi-Arid	1.677
<i>Solanum neocardenasii</i>	Temperate oceanic	1.668
<i>Solanum chilliasense</i>	Tropical Savanna Dry-Winter	1.663
<i>Solanum gandarillasii</i>	Subtropical highland	1.540
<i>Solanum oxycarpum</i>	Temperate oceanic	1.476
<i>Solanum andreanum</i>	Temperate oceanic	1.420
<i>Solanum albornozii</i>	Temperate oceanic	1.369
<i>Solanum venturii</i>	Subtropical highland	1.324
<i>Solanum burkartii</i>	Subtropical highland	1.313
<i>Solanum limbaniense</i>	Polar tundra	1.287
<i>Solanum huancabambense</i>	Temperate oceanic	1.265
<i>Solanum acroglossum</i>	Temperate oceanic	1.196
<i>Solanum okadae</i>	Subtropical highland	1.149
<i>Solanum agrimonifolium</i>	Subtropical highland	1.130
<i>Solanum buesii</i>	Subpolar oceanic	1.115
<i>Solanum rhomboideilanceolatum</i>	Polar tundra	1.046
<i>Solanum olmosense</i>	Hot Semi-Arid	1.037
<i>Solanum longiconicum</i>	Temperate oceanic	1.010
<i>Solanum commersonii</i>	Humid Subtropical	1.009
<i>Solanum lesteri</i>	Subtropical highland	0.994
<i>Solanum tarnii</i>	Temperate oceanic	0.994
<i>Solanum hastiforme</i>	Temperate oceanic	0.984
<i>Solanum chacoense</i>	Humid Subtropical	0.951
<i>Solanum chiquidenum</i>	Cold Semi-Arid	0.917
<i>Solanum cajamarquense</i>	Cold Semi-Arid	0.877
<i>Solanum polyadenium</i>	Subtropical highland	0.835
<i>Solanum verrucosum</i>	Subtropical highland	0.832
<i>Solanum flahaultii</i>	Temperate oceanic	0.825
<i>Solanum chacoense</i>	Subtropical highland	0.817
<i>Solanum acroscopicum</i>	Polar tundra	0.806
<i>Solanum hintonii</i>	Subtropical highland	0.791
<i>Solanum demissum</i>	Subtropical highland	0.788
<i>Solanum brevicaule</i>	Subtropical highland	0.780
<i>Solanum paucissectum</i>	Hot Semi-Arid	0.769

TABLE 2 (Continued)

Potato Wild Relative Species	Köppen-Geiger Climate	PWRP Value
<i>Solanum morelliforme</i>	Subtropical highland	0.765
<i>Solanum paucissectum</i>	Temperate oceanic	0.747
<i>Solanum bulbocastanum</i>	Subtropical highland	0.745
<i>Solanum cantense</i>	Cold Semi-Arid	0.732
<i>Solanum cantense</i>	Polar tundra	0.732
<i>Solanum huancabambense</i>	Hot Semi-Arid	0.702
<i>Solanum hastiforme</i>	Cold Semi-Arid	0.681
<i>Solanum medians</i>	Polar tundra	0.670
<i>Solanum cajamarquense</i>	Temperate oceanic	0.635
<i>Solanum iopetalum</i>	Subtropical highland	0.627
<i>Solanum andreanum</i>	Warm-summer Mediterranean	0.625
<i>Solanum longiconicum</i>	Tropical Monsoon	0.601
<i>Solanum raphanifolium</i>	Polar tundra	0.599
<i>Solanum raphanifolium</i>	Temperate oceanic	0.592
<i>Solanum nubicola</i>	Temperate oceanic	0.573
<i>Solanum microdontum</i>	Subtropical highland	0.562
<i>Solanum bombycinum</i>	Polar tundra	0.557
<i>Solanum stoloniferum</i>	Cold Semi-Arid	0.552
<i>Solanum stoloniferum</i>	Subtropical highland	0.534
<i>Solanum rhomboideilanceolatum</i>	Temperate oceanic	0.522
<i>Solanum violaceimarmoratum</i>	Temperate oceanic	0.506
<i>Solanum hougasii</i>	Monsoon humid subtropical	0.499
<i>Solanum chacoense</i>	Monsoon humid subtropical	0.499
<i>Solanum agrimonifolium</i>	Tropical Savanna Dry-Winter	0.484
<i>Solanum olmosense</i>	Tropical Savanna Dry-Winter	0.478
<i>Solanum morelliforme</i>	Temperate oceanic	0.471
<i>Solanum limbaniense</i>	Temperate oceanic	0.467
<i>Solanum acroscopicum</i>	Cold Desert	0.466
<i>Solanum burkartii</i>	Temperate oceanic	0.453
<i>Solanum violaceimarmoratum</i>	Subpolar oceanic	0.443
<i>Solanum chomatophilum</i>	Temperate oceanic	0.442
<i>Solanum hjertingii</i>	Cold Semi-Arid	0.430
<i>Solanum medians</i>	Cold Semi-Arid	0.428
<i>Solanum acaule</i>	Subtropical highland	0.427
<i>Solanum garcia-barrigae</i>	Tropical Monsoon	0.427
<i>Solanum oxycarpum</i>	Subtropical highland	0.422
<i>Solanum neocardenasii</i>	Tropical Savanna Dry-Winter	0.415
<i>Solanum neocardenasii</i>	Subtropical highland	0.415

these species are associated with the Oceanic climate (Cfb) or Subpolar oceanic climate (Cfc), characterized by narrow annual temperature ranges (Rubel & Kottek, 2010). The next top scoring species are found in extremely different climates. *Solanum neorossi* and *Solanum neovavilovii* possess high PWRP values associated with the climates

Subtropical highland climate (Cwb) and Polar tundra (ET), respectively (Table 2). Furthermore, when looking at the species with the top 20 highest PWRP, all species are either diploid or possess diploid populations. Additionally, when considering the top two species per Köppen–Geiger climate (17 discrete climates), there are 26 unique species

identified for applicability in any given climate (Table 1). Additionally, more than half of the 80 highest valued PWRPs correspond with species identified for Temperate oceanic (24) and Subtropical highland (21), highlighting the agrobiodiversity available for localized crop improvement in these discrete climate niches (Table 2) where only ~10% of current potato production occurs, 7.7% and 2.4%, respectively (Figure S1). Broadly useful species, identified in multiple climates as viable options, include *S. andrea-num*, *S. brevicaule*, *S. chacoense*, *S. colombianum*, *S. hougassii*, and *S. longiconicum*; furthermore, PWR do not occur in every discrete climate of potato, however, the similarity of discrete climates along PC1 and PC2 can be identified for approximate matches (Table S3).

4 | DISCUSSION

4.1 | Climatic shift and adaptation strategies

The projected shifts in climate envelopes introduce hurdles for the sustainable production of potato in current growing regions. There are currently 370 million tons and 17 million hectares of potato in production (FAOSTAT, 2017). If we consider the worst-case scenario for 2070 and assume production is evenly distributed across the climate polygons, there will be a maximum of roughly 44 million tons, or 2.1 million hectares, of potato that will need to be produced in a new climate given the expectation of a 12% climatic shift for potato production regions from current year to 2070. This shift is similar to other major crop species such as sunflower (Mehrabi et al., 2019) and common bean (Ramirez-Cabral et al., 2016). Shifting climate can be addressed through either bringing new land into production or intensifying production on the remaining land, creating a change in the production system where adapted cultivars will be a key component. The shift in climate of potato production places at risk about 10 million tons more than the international production of dry beans and roughly one-third of the international banana production area (FAOSTAT, 2017). Future climate shifts of potato growing regions occur along a lower PC1 (temperature) and higher PC2 (precipitation) gradient while PWRs primarily exist in lower PC1 and lower PC2 (Figure 2) gradients. Therefore, PWRs are more likely to provide the ability to ameliorate stresses associated with lower climatic shifts along PC1 (temperature) and PC2 (precipitation). A limitation of our analysis is the assumption that production will remain in the same location and same production intensity. This assumption was made based on the specialized equipment and processing facilities that accompany large scale potato production. Historically,

there have been production shifts (e.g., New York to Idaho in the United States; Lucier, 1991), but such shifts require large capital investment, often being driven by outside infrastructure and are therefore difficult to predict. The least disruptive option for growers and processors would be to use PWR for genetic improvement of production cultivars to increase productivity on existing cultivated lands rather than expanding production to new areas (Dias et al., 2016). This strategy also avoids forcing potato growing regions to find a new viable crop.

4.2 | Agroecological niche and prioritization of potato wild relative species

A consideration when prioritizing agrobiodiversity is the identification of traits that are useful to agricultural production in specific regions and agroecosystems, these can differ from those that provide adaptability to populations in natural ecosystems (Fumia et al., 2022). In this study, the traits influencing climate adaptability and plasticity as well as crossability to cultivated species were combined in the prioritization, similar conceptually to envirotyping (Xu, 2016) and enviromics (Resende et al., 2020). However, rather than finding the best cultivar for an environment, here we prioritize species with localized climate adaptation for specific climate/production niches found throughout the world (Table 1, Figure 2). Different global regions have different potential donor species for abiotic stress adaptation, for example, *S. colombianum* was identified as a useful donor species in Af (Tropical Rainforest) and Csb (Warm-Summer Mediterranean), as it likely contains the potential to provide adaptability to increased temperatures thus helping to alleviate diminished tuberization and yields that have been documented under high late season temperatures (Haverkort, 1990; Hijmans, ; Stol et al., 1991). Further, in coastal regions where increased salinity is expected via salt-water intrusion, localized adaptability from *Solanum neocardenasii* in Cfb (Temperate Oceanic) could be introduced to ameliorate the abiotic stress. These examples are generalizable to any climate where there are data, in each case a donor species can be selected for generating locally adapted lines in an effort to curb current and future local niche stresses to production. However, selection can be interpolated with associating climate likeness in principal component space (Table S2). In the global potato breeding community, there should be emphasis on prioritizing discrete Köppen–Geiger climate classes for selection where the shift of specific bioclimatic variables is greatest, such as the shift of mean annual temperature (Figure S7) and combine with discrete climates of high production (Figure

S1). Leveraging both of these climatic classifiers allows us to focus on a locale (Koppen-Geiger discrete climate class) and then identify plasticity (Bioclim). This score provides the breeder with a starting-point species identified to have the highest plasticity, localized adaptability, and crossability based on phylogenetic distance. Moreover, prioritized species can be further filtered to account for known biotic resistances, similar to sunflower prioritization (Mehrabi et al., 2019). For example, considering the species (e.g., *S. colombianum* and *S. andreanum*) with the highest climate plasticity (largest climate niche), but adjusting the selection to consider documented *Phytophthora infestans* resistance found in *S. andreanum* while avoiding the overwhelming susceptibility to the disease in *S. colombianum* (Khuiti et al., 2015). Although our study incorporates a proxy for crossability using phylogenetic distance, historical crossing success can and should be taken into account when selecting a species. For example, the tetraploid individuals of *S. colombianum* and *S. andreanum* have mixed crossing success with tetraploid *S. tuberosum*, where a cross with the former has moderate success of seed set as the female plant (Jackson & Hanneman, 1999; Watanabe & Peloquin, 1991). But these species possess diploid and polyploid cytotypes in the same eco-region of Ecuador and Colombia (Correll, 1962). This reinforces the difficulty of finding a selection that is not limited to the species or population level, but to the accession level where high variance is identified for other traits of interest such as resistance to soft rot (Chung et al., 2011). While this study explored potato, the method can be expanded to any crop.

4.3 | Use of PWR in potato breeding: Is diploid potato the future?

Historically, interspecific breeding, while used, was limited due to the creation of populations without local adaptability and with meiotic instability, leading to cycles of recombination to remove linkage drag and increasing the length of time needed to introgress a trait (Bradshaw & MacKay, 1994; Jansky & Peloquin, 2005; MacKay, 2005). Moreover, this has led to the development of complex crossing schemes requiring additional generations before testing (Hijmans et al., 2007; Köhler et al., 2010; Peloquin et al., 1999). While there are occasional interploidy crosses that have become cultivars (Buso et al., 2000), particularly with the use of wild relatives, this strategy of bridge crosses does not work for every species. One potential way to overcome this is to work with species prioritized for local adaptation and to work at the diploid rather than tetraploid level. The top prioritized PWR are diploid, however, cultivated potato is tetraploid with polysomic inheritance, leading to complex segregation patterns during

breeding. This means that additional resources have to be expended to find favorable genotypes (Little & Little, 1945, 1958; McCord et al., 2012). Further, there are additional challenges that occur in interploidy hybridization between PWR and potato, often requiring additional steps such as ploidy reduction, bridge crosses, and re-polyploidization (Jansky, 2006; Ortiz & Peloquin, 1991; Peloquin et al., 1989; Santini et al., 2000; Serquén & Peloquin, 1996). This extended breeding cycle is exacerbated by the standard intensive breeding process of progeny testing (De Jong & Tai, 1991). Such challenges suggest that the move toward diploid germplasm (Jansky et al., 2016) should be accelerated to keep within resource constraints and improve response time to climatic shifts, using the most promising PWR (diploid). Potato breeding is focused on clonal selection, where extreme outliers are important because they can become a cultivar and their outlier nature is not lost through sexual recombination. Since outlier selection is important, breeders rely upon selecting populations that exhibit the greatest phenotypic variation, with diploid populations often expressing larger variation than tetraploid populations (Jansky & Spooner, 2018). While there is great potential to more rapidly breed in diploids, there are also problems with increased genetic load and inbreeding depression (Bachem et al., 2019; Jansky et al., 2016), but these could be overcome by creating an inbred-hybrid system (Zhang et al., 2019). Using these diploid PWR as parental species in diploid breeding programs not only increases genetic diversity, but also introduces climate resilience and plasticity. Increases in the extremes of a segregating diploid population support the production and identification of broadly or specifically eco-adapted individuals. In doing so, interspecific hybrids may possibly be selfed to achieve homozygous climate adaptation traits and thus, significantly decrease the resource intensity currently associated with potato breeding programs. PWR contain species that satisfy these requirements for many different climate classes, in prioritizing by specific class, a short list can be identified that will provide climate adaptability and inform specific breeding designs to reach goals under different temporal constraints. An interesting question for future work would be to identify if the timeframe for de novo domestication of wild potatoes would be faster than introgression due to meiotic incompatibilities, particularly with respect to climate adaptation.

4.4 | Limitations

Cultivated potato is produced in irrigated and dryland systems, which are not separated in this study. This limitation implies that the large range in climate space of cultivated potato (Figure 2) when compared to PWR is due

to a combination of changes in genetics and agronomic practices (e.g., irrigation, fertilization, and pest control), which expand the production niche. Despite this potential overestimation of the climate niche of cultivated potato, the PWRP metric is disentangled from niche size through the use of the correlation between current overlap and future overlap. Furthermore, convex hull, while able to smooth over geographic features and detach analysis from specific error, may inaccurately estimate production loss due to climatic shift and the assumption of equal density. The interpretation of this is that when species are prioritized using this metric they are very likely to hold the abiotic stress tolerance within the climate class of interest. Additionally, although this study uses 72 wild relative species of potato, it does not incorporate the genetic diversity and potential adaptability traits available in landrace varieties, an area ripe for future investigation (Heider et al., 2021), while also avoiding current potato germplasm resources due to the difficulty of assessing abiotic stress in potato from polysomic genetics and high heterozygosity (Handayani et al., 2019). Lastly, PWRP is a metric to improve selection of germplasm for interspecific breeding in a local niche, but does not consider how this selection may alter the final potato product from the current local market preference. The goal is introgression of adaptability traits while maintaining quality traits (e.g., texture, color, nutritional value), however, how the theory meets practice requires empirical testing within potato breeding programs.

5 | CONCLUSION

Potato has become a staple part of the diet of at least a billion people across the globe. Future cultivation is threatened by an increasingly stochastic climate; we projected that up to 12.5% of the current cultivated potato climate will shift into novel regions by 2070. This is a tremendous threat to livelihoods and food production; however, we also identified a clear path to future climate adaptation using PWR genetic resources. Actualizing the finding here would be facilitated by moving breeding systems to diploid germplasm as suggested by Janskey et al. (2016). We have proposed a way of prioritizing species to use in adapting production potato to local climates and specifically finding diploid PWR species, providing support for diploid breeding for streamlined improvement of potato toward abiotic stress adaptability. This may help develop more efficient breeding schemes that will increase the potential of new cultivars to be pre-adapted to the appropriate climate regimes to address the long lag time in agricultural research and development. This study provides a pathway for rapidly increasing the adaptability

and climate tolerance of critical food crops in the face of climate change. Proactive research is essential to meeting world food needs and needs to be actively pursued for a range of staple foods.

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REFERENCES

- Bach, S., Yada, R. Y., Bizimungu, B., & Sullivan, J. A. (2012). Genotype by environment interaction effects on fibre components in potato (*Solanum tuberosum* L.). *Euphytica*, *187*, 77–86. <https://doi.org/10.1007/s10681-012-0734-9>
- Bachem, C. W., van Eck, H. J., & de Vries, M. E. (2019). Understanding genetic load in potato for hybrid diploid breeding. *Molecular Plant*, *12*(7), 896–898. <https://doi.org/10.1016/j.molp.2019.05.015>
- Bailey-Serres, J., Parker, J. E., Ainsworth, E. A., Oldroyd, G. E. D., & Schroeder, J. I. (2019). Genetic strategies for improving crop yields. *Nature*, *575*, 109–118. <https://doi.org/10.1038/s41586-019-1679-0>
- Bernardo, R. (2020). Reinventing quantitative genetics for plant breeding: something old, something new, something borrowed, something BLUE. *Heredity*, *125*(6), 375–385. <https://doi.org/10.1038/s41437-020-0312-1>
- Borlaug, N. E. (1983). Contributions of conventional plant breeding to food production. *Science*, *219*(4585), 689–693.
- Bradshaw, J. E., & Mackay, G. R. (1994). Breeding strategies for clonally propagated potatoes. *Potato Genetics*, 467–497.

- Burke, M. B., Lobell, D. B., & Guarino, L. (2009). Shifts in African crop climates by 2050, and the implications for crop improvement and genetic resources conservation. *Global Environmental Change*, 19(3), 317–325. <https://doi.org/10.1016/j.gloenvcha.2009.04.003>
- Buso, J. A., Boiteux, L. S., & Peloquin, S. J. (2000). Evaluation under long-day conditions of 4x–2x progenies from crosses between potato cultivars and haploid Tuberosum x *Solanum chacoense* hybrids. *Annals of Applied Biology*, 136(1), 35–40.
- Castañeda-Álvarez, N. P., de Haan, S., Juárez, H., Khoury, C. K., Achicanoy, H. A., Sosa, C. C., Bernau, V., Salas, A., Heider, B., Simon, R., Maxted, N., & Spooner, D. M. (2015). Ex situ conservation priorities for the wild relatives of potato (*Solanum* L. Section Petota). *PLoS One*, 10(4), e0122599. <https://doi.org/10.1371/journal.pone.0122599>
- Chung, Y. S., Holmquist, K., Spooner, D. M., & Jansky, S. H. (2011). A test of taxonomic and biogeographic predictivity: resistance to soft rot in wild relatives of cultivated potato. *Phytopathology*, 101(2), 205–212. <https://doi.org/10.1094/PHYTO-05-10-0139>
- Comai, L. (2005). The advantages and disadvantages of being polyploid. *Nature Reviews Genetics*, 6(11), 836–846. <https://doi.org/10.1038/nrg1711>
- Correll, D. S. (1962). The potato and its wild relatives.
- Dahal, K., Li, X.-Q., Tai, H., Creelman, A., & Bizimungu, B. (2019). Improving potato stress tolerance and tuber yield under a climate change scenario – A current overview. *Frontiers in Plant Science*, 10, 563. <https://doi.org/10.3389/fpls.2019.00563>
- De Jong, H., & Tai, G. (1991). Evaluation of potato hybrids obtained from tetraploid-diploid crosses I. *Parent-Offspring Relationships*. *Plant Breeding*, 107, 177–182.
- 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>
- Devaux, A., Kromann, P., & Ortiz, O. (2014). Potatoes for sustainable global food security. *Potato Research*, 57, 185–199.
- Dias, L. C., Pimenta, F. M., Santos, A. B., Costa, M. H., & Ladle, R. J. (2016). Patterns of land use, extensification, and intensification of Brazilian agriculture. *Global Change Biology*, 22(8), 2887–2903. <https://doi.org/10.1111/gcb.13314>
- Eyring, V., Bony, S., Meehl, G. A., Senior, C. A., Stevens, B., Stouffer, R. J., & Taylor, K. E. (2016). Overview of the Coupled Model Intercomparison Project Phase 6 (CMIP6) experimental design and organization. *Geoscientific Model Development*, 9, 1937–1958. <https://doi.org/10.5194/gmd-9-1937-2016>
- 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>
- Foley, J. A., Ramankutty, N., Brauman, K. A., Cassidy, E. S., Gerber, J. S., Johnston, M., & Balzer, C. (2011). Solutions for a cultivated planet. *Nature*, 478(7369), 337–342.
- Food and Agriculture Organization of the United Nations (2017). *FAOSTAT statistical database*. FAO.
- Fumia, N., Rubinoff, D., Zenil-Ferguson, R., Khoury, C. K., Pironon, S., Gore, M. A., & Kantar, M. B. (2022). I Interactions between breeding system and ploidy affect niche breadth in *Solanum*. *Royal Society Open*. <https://dx.doi.org/10.1098/rsos.211862>
- Handayani, T., Gilani, S. A., & Watanabe, K. N. (2019). Climatic changes and potatoes: How can we cope with the abiotic stresses? *Breeding Science*, 69(4), 545–563. <https://doi.org/10.1270/jsbbs.19070>
- Haverkort, A. J. (1990). Ecology of potato cropping systems in relation to latitude and altitude. *Agricultural Systems*, 32(3), 251–272. [https://doi.org/10.1016/0308-521X\(90\)90004-A](https://doi.org/10.1016/0308-521X(90)90004-A)
- Heider, B., Struelens, Q., Faye, É., Flores, C., Palacios, J. E., Eyzaguirre, R., de Haan, S., & Dangles, O. (2021). Intraspecific diversity as a reservoir for heat-stress tolerance in sweet potato. *Nature Climate Change*, 11(1), 64–69. <https://doi.org/10.1038/s41558-020-00924-4>
- Hijmans, R. J. (2001). Global distribution of the potato crop. *American Journal of Potato Research*, 78, 403–412. <https://doi.org/10.1007/BF02896371>
- Hijmans, R., Gavrilenko, T., Stephenson, S., Bamberg, J., Salas, A., & Spooner, D. M. (2007). Geographical and environmental range expansion through polyploidy in wild potatoes (*Solanum* section Petota). *Global Ecology and Biogeography*, 16, 485–495. <https://doi.org/10.1111/j.1466-8238.2007.00308.x>
- Hijmans, R. J., Jacobs, M., Bamberg, J. B., & Spooner, D. M. (2003). Frost tolerance in wild potato species: Assessing the predictivity of taxonomic, geographic, and ecological factors. *Euphytica*, 130(1), 47–59.
- Hirsch, C. N., Hirsch, C. D., Felcher, K., Coombs, J., Zarka, D., Van Deynze, A., De Jong, W., Veilleux, R. E., Jansky, S., Bethke, P., Douches, D. S., & Buell, C. R. (2013). Retrospective view of North American potato (*Solanum tuberosum* L.) breeding in the 20th and 21st centuries. *G3 (Bethesda)*, 3(6), 1003–1013.
- IPCC (2021) *Climate change 2021: The physical science basis. Contribution of working group I to the sixth assessment report of the intergovernmental panel on climate change* [Masson-Delmotte, V., P. Zhai, A. Pirani, S.L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M.I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J.B.R. Matthews, T.K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, and B. Zhou (eds.)]. Cambridge University Press. In Press.
- Jackson, S. A., & Hanneman, R. E. (1999). Crossability between cultivated and wild tuber-and non-tuber-bearing *Solanums*. *Euphytica*, 109(1), 51–67.
- Jansky, S. H. (2006). Overcoming hybridization barriers in potato. *Plant Breeding*, 125, 1–12. <https://doi.org/10.1111/j.1439-0523.2006.01178.x>
- Jansky, S. (2009). Breeding, genetics, and cultivar development. In L. Kaur & J. Singh (Eds.), *Advances in potato chemistry and technology* (pp. 27–62). Academic Press.
- Jansky, S. H., Charkowski, A. O., Douches, D. S., Gusmini, G., Richael, C., Bethke, P. C., Spooner, D. M., Novy, R. G., De Jong, H., De Jong, W. S., Bamberg, J. B., Thompson, A. L., Bizimungu, B., Holm, D. G., Brown, C. R., Haynes, K. G., Sathuvalli, V. R., Veilleux, R. E., Miller, J. C., ... Jiang, J. (2016). Reinventing potato as a diploid inbred line-based crop. *Crop Science*, 56(4), 1412–1422. <https://doi.org/10.2135/cropsci2015.12.0740>
- Jansky, S. H., Dempewolf, H., Camadro, E. L., Simon, R., Zimnoch-Guzowska, E., Bisognin, D. A., & Bonierbale, M. (2013). A case for crop wild relative preservation and use in potato. *Crop Science*, 53(3), 746–754. <https://doi.org/10.2135/cropsci2012.11.0627>
- Jansky, S. H., & Peloquin, S. J. (2005). Advantages of wild diploid *Solanum* species over cultivated diploid relatives in potato breeding programs. *Genetic Resources and Crop Evolution*, 53, 669–674.

- Jansky, S. H., & Spooner, D. M. (2018). The evolution of potato breeding. *Plant Breeding Reviews*, 41, 169–214.
- Jansky, S. H., & Thompson, D. M. (1990). The effect of flower removal on potato tuber yield. *Canadian Journal of Plant Science*, 70(4), 1223–1225. <https://doi.org/10.4141/cjps90-151>
- Key, J. M. (1970). Significance of mating systems for chromosomes and gametes in polyploids. *Hereditas*, 66(2), 165–176. <https://doi.org/10.1111/j.1601-5223.1970.tb02342.x>
- Khiutti, A. L. E. X., Spooner, D. M., Jansky, S. H., & Halterman, D. A. (2015). Testing taxonomic predictivity of foliar and tuber resistance to *Phytophthora infestans* in wild relatives of potato. *Phytopathology*, 105(9), 1198–1205.
- Köhler, C., Scheid, O., & Erilova, A. (2010). The impact of the triploid block on the origin and evolution of polyploid plants. *Trends in Genetics*, 26(3), 142–148.
- Krantz, F. A. (1924). *Potato breeding methods*, Vol. 25. University Farm.
- Krantz, F. A. (1946). *Potato breeding methods. III, A suggested procedure for potato breeding (No. 04; USDA, FOLLETO 2112.)*
- Leemans, R., & Solomon, A. M. (1993). Modeling the potential change in yield and distribution of the earth's crops under a warmed climate. *Climate Research*, 3, 79–96. <https://doi.org/10.3354/cr003079>
- Lesk, C., Rowhani, P., & Ramankutty, N. (2016). Influence of extreme weather disasters on global crop production. *Nature*, 529, 84–87. <https://doi.org/10.1038/nature16467>
- Little, T. M. (1945). Gene segregation in autotetraploids. *Botanical Review*, 11, 60. <https://doi.org/10.1007/BF02861164>
- Little, T. (1958). Gene segregation in autotetraploids. II. *Botanical Review*, 24(5), 318–339. <https://doi.org/10.1007/BF02872438>
- Lucier, G. (1991). *US Potato Statistics, 1949-89 (No. 829)*. US Department of Agriculture, Economic Research Service.
- Lush, J. L. (1943). *Animal breeding plans. Animal breeding plans.*, (Edn 2).
- Lynch, M., & Walsh, B. (1998). *Genetics and analysis of quantitative traits*, Vol. 1 (pp. 535–557). Sinauer.
- MacKay, G. (2005). Propagation by traditional breeding methods. In M. Razdan, & A. Mattoo (Eds.), *Genetic improvement of Solanaceae crops*, Volume 1, Potato (pp. 65–81). Science Publishers, Inc., Enfield, NH.
- McCord, P., Zhang, L., & Brown, C. (2012). The incidence and effect on total tuber carotenoids of a recessive zeaxanthin epoxidase allele (Zep1) in yellow-fleshed potatoes. *American Journal of Potato Research*, 89, 262–268.
- Mehrabi, Z., McDowell, M. J., Ricciardi, V., Levers, C., Martinez, J. D., Mehrabi, N., Wittman, H., Ramankutty, N., & Jarvis, A. (2020). The global divide in data-driven farming. *Nature Sustainability*, 4(2), 154–160. <https://doi.org/10.1038/s41893-020-00631-0>
- Mehrabi, Z., Pironon, S., Kantar, M. B., Ramankutty, N., & Rieseberg, L. (2019). Shifts in the abiotic and biotic environment of cultivated sunflower under future climate change. *OCL*, 26, 9. <https://doi.org/10.1051/ocl/2019003>
- Monfreda, C., Ramankutty, N., & Foley, J. A. (2008). Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Global Biogeochemical Cycles*, 22(1), <https://doi.org/10.1029/2007GB002947>
- Murchie, E. M., Pinto, M., & Horton, P. (2009). Agriculture and the new challenges for photosynthesis research. *New Phytologist*, 181, 532–552. <https://doi.org/10.1111/j.1469-8137.2008.02705.x>
- Ortiz, R., & Peloquin, S. J. (1991). A new method of producing 4x hybrid true potato seed. *Euphytica*, 57, 103–107. <https://doi.org/10.1007/BF00023067>
- Peloquin, S. J., Boiteux, L. S., & Carputo, D. (1999). Meiotic mutants in potato: valuable variants. *Genetics*, 153(4), 1493–1499. <https://doi.org/10.1093/genetics/153.4.1493>
- Peloquin, S. J., Jansky, S. H., & Yerck, G. L. (1989). Potato cytogenetics and germplasm utilization. *American Potato Journal*, 66, 629–638. <https://doi.org/10.1007/BF02853983>
- Pironon, S., Borrell, J. S., Ondo, I., Douglas, R., Phillips, C., Khoury, C. K., Kantar, M. B., Fumia, N., Soto Gomez, M., Viruel, J., Govaerts, R., Forest, F., & Antonelli, A. (2020). Toward unifying global hotspots of wild and domesticated biodiversity. *Plants*, 9(9), 1128. <https://doi.org/10.3390/plants9091128>
- Pironon, S., Etherington, T. R., Borrell, J. S., Kühn, N., Macias-Fauria, M., Ondo, I., Tovar, C., Wilkin, P., & Willis, K. J. (2019). Potential adaptive strategies for 29 sub-Saharan crops under future climate change. *Nature Climate Change*, 9(10), 758–763. <https://doi.org/10.1038/s41558-019-0585-7>
- Ramankutty, N., Mehrabi, Z., Waha, K., Jarvis, L., Kremen, C., Herrero, M., & Rieseberg, L. H. (2018). Trends in global agricultural land use: implications for environmental health and food security. *Annual Review of Plant Biology*, 69, 789–815. <https://doi.org/10.1146/annurev-arplant-042817-040256>
- Ramirez-Cabral, N. Y. Z., Kumar, L., & Taylor, S. (2016). Crop niche modeling projects major shifts in common bean growing areas. *Agricultural and Forest Meteorology*, 218, 102–113. <https://doi.org/10.1016/j.agrformet.2015.12.002>
- Ramirez-Villegas, J., & Khoury, C. K. (2013). Reconciling approaches to climate change adaptation for Colombian agriculture. *Climatic Change*, 119(3), 575–583. <https://doi.org/10.1007/s10584-013-0792-6>
- Raymundo, R., Asseng, S., Robertson, R., Petsakos, A., Hoogenboom, G., Quiroz, R., Hareau, G., & Wolf, J. (2018). Climate change impact on global potato production. *European Journal of Agronomy*, 100, 87–98. <https://doi.org/10.1016/j.eja.2017.11.008>
- Resende, R. T., Piepho, H. P., Rosa, G. J., Silva-Junior, O. B., e Silva, F. F., de Resende, M. D. V., & Grattapaglia, D. (2020). Enviromics in breeding: applications and perspectives on envirotypic-assisted selection. *Theoretical and Applied Genetics*, 134(1), 95–112.
- Rubel, F., & Kottek, M. (2010). Observed and projected climate shifts 1901–2100 depicted by world maps of the Köppen-Geiger climate classification. *Meteorologische Zeitschrift*, 19, 135–141. <https://doi.org/10.1127/0941-2948/2010/0430>
- Santini, M., Camadro, E. L., Marcellán, O. N., & Erazzú, L. E. (2000). Agronomic characterization of diploid hybrid families derived from crosses between haploids of the common potato and three wild Argentinian tuber-bearing species. *American Journal of Potato Research*, 77, 211–218. <https://doi.org/10.1007/BF02855788>
- Serquén, F. C., & Peloquin, S. J. (1996). Variation for agronomic and processing traits in *Solanum tuberosum* haploids × wild species hybrids. *Euphytica*, 89, 185–191. <https://doi.org/10.1007/BF00034604>
- Singh, R. P., Chintagunta, A. D., Agarwal, D. K., Kureel, R. S., & Kumar, S. J. (2020). Varietal replacement rate: Prospects and challenges for global food security. *Global Food Security*, 25, 100324.
- Sloat, L. L., Davis, S. J., Gerber, J. S., Moore, F. C., Ray, D. K., West, P. C., & Mueller, N. D. (2020). Climate adaptation by crop

- migration. *Nature Communications*, 11(1), 1–9. <https://doi.org/10.1038/s41467-020-15076-4>
- Spooner, D. M., Ghislain, M., Simon, R., Jansky, S. H., & Gavrilenko, T. (2014). Systematics, diversity, genetics, and evolution of wild and cultivated potatoes. *The Botanical Review*, 80(4), 283–383. <https://doi.org/10.1007/s12229-014-9146-y>
- Spooner, D. M., & Hetterscheid, W. (2007). *Origins, evolution, and group classification of cultivated potatoes*. Chapter 13, 285–307.
- Spooner, D. M., & Hijmans, R. (2001). Potato systematics and germplasm collecting, 1989–2000. *American Journal of Potato Research*, 78, 237–268. <https://doi.org/10.1007/BF02875691>
- Stol, W., de Koning, G. H. J., Haverkort, A. J., Kooman, P. L., van Keulen, H., & Penning de Vries, F. W. T. (1991). *Agro-ecological characterization for potato production. A simulation study at the request of the International Potato Center (CIP), Lima, Peru*. CABO-DLO, Report 155.
- Tanentzap, A. J., Lamb, A., Walker, S., & Farmer, A. (2015). Resolving conflicts between agriculture and the natural environment. *PLoS Biology*, 13(9), e1002242. <https://doi.org/10.1371/journal.pbio.1002242>
- Vos, P. G., Uitdewilligen, J. G., Voorrips, R. E., Visser, R. G., & van Eck, H. J. (2015). Development and analysis of a 20K SNP array for potato (*Solanum tuberosum*): an insight into the breeding history. *Theoretical and Applied Genetics*, 128(12), 2387–2401. <https://doi.org/10.1007/s00122-015-2593-y>
- Walsh, B., & Lynch, M. (2018). *Evolution and selection of quantitative traits*. Oxford University Press.
- Watanabe, K., & Peloquin, S. J. (1991). The occurrence and frequency of 2n pollen in 2x, 4x, and 6x wild, tuber-bearing *Solanum* species from Mexico, and Central and South America. *TAG Theoretical and Applied Genetics*, 82(5), 621–626. <https://doi.org/10.1007/BF00226800>
- Xu, Y. (2016). Envirotyping for deciphering environmental impacts on crop plants. *Theoretical and Applied Genetics*, 129(4), 653–673. <https://doi.org/10.1007/s00122-016-2691-5>
- Zenil-Ferguson, R., Burleigh, J. G., Freyman, W. A., Igić, B., Mayrose, I., & Goldberg, E. E. (2019). Interaction among ploidy, breeding system and lineage diversification. *New Phytologist*, 224, 1252–1265. <https://doi.org/10.1111/nph.16184>
- Zhang, C., Wang, P., Tang, D., Yang, Z., Lu, F., Qi, J., Tawari, N., Shang, Y., Li, C., & Huang, S. (2019). The genetic basis of inbreeding depression in potato. *Nature Genetics*, 51, 374–378. <https://doi.org/10.1038/s41588-018-0319-1>
- Zhang, H., Mittal, N., Leamy, L. J., Barazani, O., & Song, B. H. (2017). Back into the wild—Apply untapped genetic diversity of wild relatives for crop improvement. *Evolutionary Applications*, 10(1), 5–24. <https://doi.org/10.1111/eva.12434>

SUPPORTING INFORMATION

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