






INVITED REVIEW

Adapting perennial grain and oilseed crops for climate resiliency

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Abstract

Climate change is threatening the status quo of agricultural production globally. Perennial cropping systems could be a useful strategy to adapt agriculture to a changing climate. Current and future perennial row crop systems have many and varied applications and these systems can respond differently than annuals to agricultural challenges resulting from climate change, such as shifting ranges of plant, pathogen, and animal species and more erratic weather patterns. To capitalize on attributes of perennial systems that assist in our ability to adapt to a changing world, it is important we fully consider the component parts of agroecosystems and their interactions, including species, genotype and genotypic variance, environment and environmental variance, adaptive management strategies, and farm socioeconomics. We review the current state of perennial grain and oilseed crops for integration into row crop agriculture and summarize the potential for current and future systems to support multiple environmental benefits and adaptation to climate change. We then propose a plant breeding strategy that incorporates the complexity of common domestication traits as they relate to future perennial crop improvement and adaptation and highlight digital technologies that can advance these goals. Evaluation of genetic gain during the development of new perennial crops and systems can be improved using research designs that span an environmental gradient that captures the forecasted shift in climate for a region, which we demonstrate by reanalyzing existing data. Successful development and deployment of perennial crops as a climate adaptation strategy depends on grower adoption, scalability, and sustainable modifications to markets and supply chains.

Abbreviations: GHG, greenhouse gas; TLI, the intermediate wheatgrass population; UAS, unmanned aerial systems.

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1 | INTRODUCTION

In many industrialized societies there has been an increase in annual crop production on large farms that account for much of the world's production (Riccardi et al., 2018). Major 20th century innovations in crop development and production—including the invention of synthetic nitrogen and pesticides, understanding of genetics, advancements in farm machinery, and computing—have all contributed to increased agricultural output often at the expense of the environment, including increased greenhouse gas (GHG) emissions (Garnett et al., 2013; Tilman et al., 2011). In recent decades, awareness and response to increasingly volatile climates, increasing global population, and the need to increase ecosystem services from agricultural land has shifted selection goals within breeding programs (Jordan et al., 2007; Runge et al., 2003; Tilman et al., 2002). Direct warming and other climate change disruptions add a massive layer of added pressure to agricultural production and the need for robust ecosystem services and function (IPCC, 2019).

Food security across scales is deeply impacted by climate change with altered local growing season dynamics, an increase in extreme events, as well as the presence of biotic and abiotic stresses that may not have been previously present at a given location (Foley et al., 2011; Lesk et al., 2016; Mehrabi et al., 2020; Ramankutty et al., 2018). Because of their potential to be low input, low disturbance, and less sensitive to precise timing of infield management that could be disrupted by a given weather pattern, perennial crops and cropping systems have been proposed as a strategy for enhancing resilience to climate change (Glover et al., 2010). Perennial systems can also improve food security and address other environmental challenges such as soil loss and water pollution (Chapman et al., 2022; Glover et al., 2010).

Perennial systems have potential to enhance ecosystem services from agricultural land compared to annual crops (Asbjornsen et al., 2014; Costanza et al., 2014). Much of this potential is based on research conducted in natural perennial grassland ecosystems (e.g., nutrient cycling and C sequestration of tallgrass prairie; Tilman et al., 2012). The benefits of perennials in the context of climate change are clear and include attributes that mitigate adverse environment impacts via reduced GHG emissions (e.g., reduced tillage, more efficient N uptake, and dual-use potential; Jungers et al., 2015; Jungers, Eckberg et al., 2017; Jungers et al., 2021; Ryan et al., 2018), climate regulation (Weißhuhn et al., 2017), reduced nutrient loss to waterways (Asbjornsen et al., 2014), and increases in biodiversity (Shulte et al., 2017). Perennial crops also support climate change adaptation via temporal yield stability and resiliency to extreme climate events (Lehmann, Ammunét et al., 2020; Lehmann, Bossio et al., 2020; Leisner, 2020; Sanford et al., 2021). There has been further work

Core Ideas

- Many agronomic and horticultural crops are perennials, which survive for years or decades after establishment.
- Perennial crops are uniquely positioned to reduce the impacts of changing climates on growers.
- Perennial crops are uniquely positioned to increase the ecological and social benefits of agriculture.
- Perennial grain and oilseeds must be able to withstand increasingly erratic weather and shifts in disease, weed, and pest pressures.
- Perennial grains and oilseed crops will play a more important role in sustainable and profitable agricultural production in the future.

on diverse management strategies to understand how ecosystem services could become part of the agricultural mainstream (Basche et al., 2016; Shulte et al., 2017).

Creating realistic predictions of future climates helps agriculturalists and policymakers set goals to maintain food production and ecosystem function under global climate change. These predictions must accurately forecast changes in temperatures, volatility in temperature patterns such as freeze/thaw cycles, reduced snowpack, extreme events such as floods, storms, and droughts, and altered distributions of pests and diseases. Adaptation strategies broadly fit into two main categories, genetics (e.g., developing new crops, introgression of novel traits, genome engineering, breeding for resilience through genetic diversity) and management strategies (e.g., changing crop ecoregions, changing agronomic and horticultural practices), that could build resilience to climate change in agroecosystems (Burke et al., 2009; Heider et al., 2021; Pironon et al., 2019; Ramirez-Villegas & Khoury, 2013; Sloat et al., 2020). There are numerous potential adaptation strategies, and there is work being done to explore computational methods to limit the number of systems that need to be empirically tested (Runck, Streed et al., 2022).

For perennial systems to be able to achieve multiple goals of growers, society, and markets, there is a need to improve germplasm, improve agronomics, improve horticultural practices, and understand environmental variation, because each of these have different temporal requirements enabling implementation on the landscape. Perennial crops typically have longer breeding and selection cycles, which makes it more difficult to maintain genetic gain at the necessary rate of change. There is a need to have clearer strategies and selection criteria for different levels of perenniality as some systems are short lived (2–3 years), while others are in production for relatively longer periods of time (20–30 years). These systems have

different management dynamics, different levels of vulnerability to a rapidly changing climate, and different time scales for testing new breeding material.

This article focuses on methodological approaches that can help realize the potential of perennial cropping systems to provision food and ecosystem services under an increasingly volatile climate. We emphasize the potential for incorporating perennial grain and oilseed crops into cropping systems found in regions supporting row crop agriculture. To explore this topic, we review the current use of perennials in agriculture, the role of perennial systems in protecting soil and water in the context of climate change, the implications for plant breeding in these systems, and how to improve plant breeding using digital technologies. We demonstrate different study designs and analyses that can help explore these systems and finally outline how to commercialize and support grower and market adoption of emerging perennial crops at scale.

2 | CURRENT STATE OF PERENNIAL AGRICULTURAL LANDSCAPES

2.1 | Widespread perennial systems

Perennial crops have been a part of the agricultural landscape for thousands of years, but in recent decades there has been a concerted effort to expand the application of perennials from more traditional orchard and forage uses to more recently developed perennial grain and oilseed uses (Glover et al., 2010; Table 1). Current iterations of perennial systems can take many forms, with the most common perennial systems being orchards, pastures, biofuel feedstocks, and perennial grains. Overall, perennial species account for ~15% of all harvested cropland across the globe (Food and Agriculture Organization of the United Nations, 2022). As with annual crops, most perennial crop species from all use categories, including fruits, nuts, berries, and forage, are grown in regions outside of wild relatives' ranges (e.g., Heinitz et al., 2019; Hummer et al., 2019; Wang et al., 2021) and there is usually more suitable areas than the major production areas (Mahaut et al., 2022). For example, suitability analyses have found that edaphically and climatically feasible ranges of cool season fruits are fourfold larger than current centers of production (McCarthy et al., 2022). Efforts to promote and expand the use of perennial crops is in the context of a growing reliance on very few annual crops: maize (*Zea mays* L.), wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), soybean (*Glycine max* [L.] Merr.), and barley (*Hordeum vulgare* L.), which together occupy 60%–75% of all harvest croplands (Monfreda et al., 2008; Thenkabail et al., 2016; Waha et al., 2020).

2.2 | Developing perennial systems

A major new effort has focused on perennial species to create commercial-scale perennial grains and oilseeds (DeHann et al., 2016; Kantar et al., 2016), with research looking to increase the pace of new crop development (Coe et al., 2020; Østerberg et al., 2017) and identify strategies for strategically locating new crops on the landscape (Runck et al., 2014). In addition, developing techniques to evaluate perennial crop germplasm for new traits (e.g., ecosystem services and environmental resiliency) while simultaneously optimizing management and maintaining genetic diversity. A major challenge with some perennial crops is that their markets are simultaneously being developed (e.g., emerging crops) or are small; therefore, limited information on consumer preference, economics, and other factors can prevent the definition of clear breeding targets. Tightly linking production to market demand also has opportunities to increase grower economic security.

2.3 | The benefit of perennial crops on soil and water as an approach to climate adaptation

Highly functioning soil and water resources can buffer agricultural productivity against warming and fluctuating climate conditions (Qiao et al., 2022). Perennial crops have been shown to improve soil functioning and water regulation through their extensive root system, long growing seasons, and lack of annual tillage or soil disturbance for typical production (Asbjornsen et al., 2014). Thus, growing perennial crops on marginal soils has the potential to repair soil quality (fertility, texture, and organic matter; Cosentino et al., 2007; Monti & Zatta, 2009), preventing desertification and providing an opportunity for more land to produce provisioning benefits (Barbosa et al., 2015; Fernando et al., 2018; Monti & Zegada-Lizarazu, 2016; Wayman et al., 2014). For example, improving soil structure can increase infiltration rates in soils vulnerable to surface compaction, reducing surface water runoff, and promoting water uptake by crops (Fatichi et al., 2020). Increasing soil organic matter contents can increase water holding capacity and increase crop water uptake (Basso et al., 2018; Williams et al., 2016). Pastures and forage crops are well known for their ecosystem service benefits (e.g., soil health), and have large ranges that encompass many different cropping systems (Aponte et al., 2019; Martin et al., 2020; Teixeira et al., 2021). The perennial grain Kernza is one example of the potential for perennial crops to improve soil quality and water regulation (Audu et al., 2022; Rakkar et al., 2023; Reilly et al., 2022; van der Pol et al., 2022). The ability of

TABLE 1 Status of a subset of perennial crops.

Crop	Use	Native range	Status	Citation
Alfalfa— <i>Medicago sativa</i> L.	Forage	Mediterranean Sea	~15 million US acres (2021)	Tautges et al. 2018
Almonds— <i>Prunus amygdalus</i> Batsch	Nuts	Central Asia	1.3 million US acres (2021)	Wang et al. 2021
Grapes— <i>Vitis vinifera</i> L.	Fruit	Central Asia	~900,000 US acres (2021)	Heinitz et al. 2019
<i>Citrus spp.</i> L.	Fruit	South and Southeast Asia	~635,500 acres (2021)	Zhong and Nicolosi, 2020
Apple— <i>Malus domestica</i> Borkh.	Fruit	Central Asia	~290,000 acres (2021)	Luby et al. 2001
Blueberry— <i>Vaccinium sect. Cyanococcus</i> Rydb.	Berry	North America	~100,000 US acres (2017)	Hummer et al. 2019
Strawberry— <i>Fragaria × ananassa</i> Duchesne	Berry	North America	~49,000	Edger et al. 2019
Cranberry— <i>Vaccinium subg. Oxycoccus</i> (Hill) A. Gray	Fruit	Eastern North America	~38,000	Neyhart, Kantar et al. 2022.
Intermediate wheatgrass (Kernza)— <i>Thinopyrum intermedium</i> (Host) Barkworth & D. R. Dewey	Grain for flour production	Western Asia	~4000 acres	DeHaan et al. 2018
Switchgrass— <i>Panicum virgatum</i> L.	Cellulosic bioenergy	North American tallgrass prairie	~1000 US acres (2017)	Lovell et al. 2021
<i>Silphium integrifolium</i> Michx.	Oil seed	North American tallgrass prairie	Experimental	Van Tassel et al. 2017

Note: Acreage is from USDA quickstats—<https://quickstats.nass.usda.gov> with the exception of intermediate wheatgrass which comes from Jungers et al. 2022.

perennials to provide these ecosystem benefits is one reason they are a powerful climate adaptation tool.

Perennials also have a longer growing season than annuals, thus allowing these crops to capture and utilize water that is available outside the typical annual crop growing season (Vico & Brunzell, 2018). Utilization of water that is unavailable to annual crops can reduce nutrient losses to surface water and groundwater. Research has shown that intermediate wheatgrass grown for grain can reduce NO₃ leaching to groundwater—thus protecting rural drinking water sources while generating an economic return for farmers (Huddell et al., 2023; Jungers et al., 2019; Reilly et al., 2022). Similarly, Randall and Mulla (2001) showed that subsurface field drainage volume and nitrate N losses were 30–50 times higher beneath annual crops compared with perennial crops.

In summary, there is potential for perennial agriculture to provide adaptation to climate change through provisioning of ecosystem services related to soil and water. To maximize the benefits related to ecosystem services there is a need to explicitly focus on roots and rooting characteristics to make sure benefits outlined above are supported. Therefore, breeding and selecting for root biomass, architecture, or other traits associated with these ecosystem services, in conjunction with improvement of aboveground agronomic and horticultural traits, will be important in the development and improvement of perennial crops.

2.4 | Challenges facing agricultural adaptation to climate change

Climate is one of the major factors that affects key areas in the agricultural supply chain, as it impacts many aspects related to crop growth (Rötter & van de Geijn, 1999), biotic threats (Surówka et al., 2020), and even decisions such as postharvest storage which directly affects markets and consumption (Magan et al., 2011). Numerous studies have attempted to forecast the possible drastic effects of climate change on these considerations (Adams et al., 1998; Frazier et al., 2022; Mora et al., 2018; Pirinon et al., 2019). These studies have shown conflicting results depending on the scale explored. Some geographies show improvements, while others show many compounded negative impacts. A major highlight of these studies is the need to explore regional capacity to develop adaptation strategies.

While all plants are impacted by climate change, crops are more susceptible because of artificial selection for specific outcomes (e.g., increased seed to vegetative biomass ratio) in specific environments, and thus may have lost traits that would allow them to respond to new conditions (Gepts, 2004). When the environment changes, steps must be taken to re-optimize cropping systems (Challinor et al., 2010). One option is to move crops between regions (translocation), which will depend on range shifts for agricultural species, where the various crops are currently farmed, supply chains

that would have to be altered, and if the crops are culturally acceptable in the new regions (e.g., is it part of the current cultural palate) (Pironon et al., 2019). Disease and pest distribution will change while crop distributions change (Chaloner et al., 2021). Changing distributions will impact infection potential, this will require new descriptions of interactions between pathogens and crops (Chaloner et al., 2021; DeLucia et al., 2012; Shaw & Osborne, 2011). Predictions for tropical areas (even under conservative emission scenarios) indicate that major production regions could experience novel climate conditions not yet experienced on earth (Fumia et al., 2022; Pugh et al., 2016), which makes the translocation of species unfeasible unless appropriate adaptation techniques (e.g., breeding) occur (Corlett, 2012). For many temperate regions, climate change is expected to increase temperatures and decrease available moisture at lower latitudes, which is a situation where the success of crop translocation is more likely as there are many warm season species that can be moved without disrupting current infrastructure (Pugh et al., 2016). There are also instances where there will be increased precipitation and temperature (Polsky et al., 2000), this will require nuanced approaches that are geography specific. For agricultural regions at higher latitudes, a longer growing season may offer some gains in agricultural productivity (Motha & Baier, 2005). While this tropical/temperate comparison in terms of climate change effects on agriculture is very crude, it allows for an appreciation of how changes in average conditions could affect current agricultural crops differently in different geographies. Translocation of perennial crops is often more difficult (Compagnoni et al., 2021; Koch et al., 2021; Usinowicz & Levine, 2021).

2.5 | Valuation of ecosystem services and adjusting conception of tradeoffs

Producing food and other agricultural outputs in ways that meet human demands while minimizing detrimental impacts on nature in the face of climate change will require agriculture to become more resilient. This will require making explicit goals that were once implicit. For example, since World War II, sometimes explicit but often implicit goal of agriculturalists has been to prioritize selection targets that increase production, which has led the focus of breeding programs to increase or protect yield (Baenziger et al., 2006). While this goal has greatly helped to increase food production across the world, it has often ignored tradeoffs with other agricultural services (Dennison et al., 2003). Because the dominant orthodoxy has been that yield is most important (especially after specific quality metrics are met; e.g., baking quality traits in wheat), little effort has been placed into exploring trait relationships that are unrelated to yield per se. Examples of this include other human benefits including nutrition (Sands et al., 2009) or environmental outcomes (Mandolesi et al., 2022).

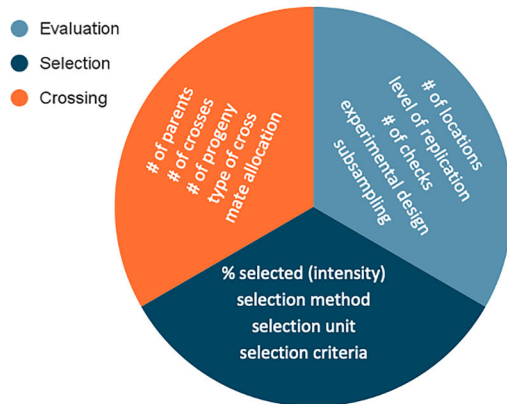
Some perennial crops might be especially well suited for providing a specific ecosystem service, while other crops might be more general and effective at providing a suite of services. It is unlikely that there will be a single crop that can support all the ecosystem services that we have outlined, and this is especially true under climate change. Strategically placing certain crops on the landscape to achieve geographically specific outcomes (e.g., perennial grass crops on slopping fields prone to soil erosion) in ways that result in diverse agroecosystems is one way to capitalize on the potential of perennial crops (Shulte et al., 2017). Plant breeding for adaptation will require co-prioritization of multiple outcomes to achieve benefits simultaneously. As a result, plant breeders will need to communicate to a wider range of stakeholders to identify the best selection targets and collaboratively develop a robust system for prioritizing these newly explicit outputs. It will also require explicitly factoring into breeding programs the interaction between environmental benefits and classical production-based goals (Dennison et al., 2003). While it is necessary to have plant material that has novel characteristics, having a clear market is necessary for widespread adoption (Lanker et al., 2020), in some cases adoption can occur quickly (Khanna et al., 2017) in others it does not, this exemplifies the need for policy to work in close concert with production (Scott et al., 2022).

3 | BREEDING PERENNIAL CROPS

Perennial crops have a different life cycle than annual crops, which means that while gain (for any trait explored) per cycle may be similar, gain per unit time is often substantially lower. Many of the technologies that have shown to be beneficial to annuals (e.g., genomic selection) are necessary but lacking for longer lived species (Cros et al., 2015; Wong & Bernardo, 2008). The range of cycle times (1–7 years) creates challenges to crop improvement for perennial species, as does the need for multiple harvests before it becomes clear which genotype is the best performer (Figure 1). Identifying the optimal time to invest in technology is key to operationalizing new breeding programs defined by longer lived species.

Breeding for perennial systems requires several different techniques. One set of techniques is often associated with *de novo* domestication, while others translate modern annual crop breeding techniques for a different set breeding goals in perennial crops. Often perennial crops have much shallower bases of genotypic and phenotypic knowledge. Additionally, perennial systems have yield measurements at different time-points (e.g., multiple harvests or extended juvenile period), which changes selection criteria and in turn alters breeding timelines (Figure 2). Many of the techniques that are widely associated with technologically advanced breeding (e.g., genomics and phenomics) are of even greater use in long lived perennial crops. This is because many of the

(a) Breeding Scheme



(b)

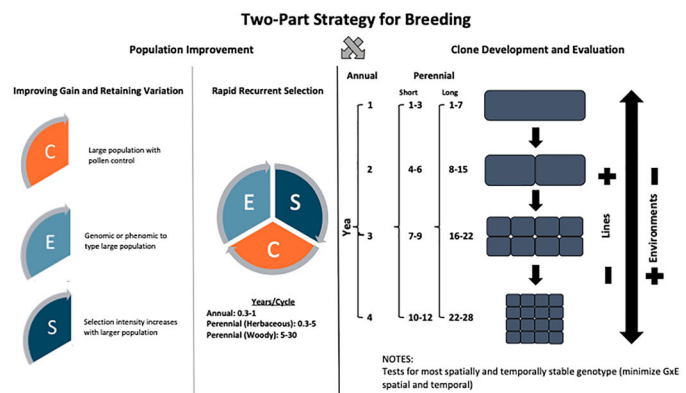
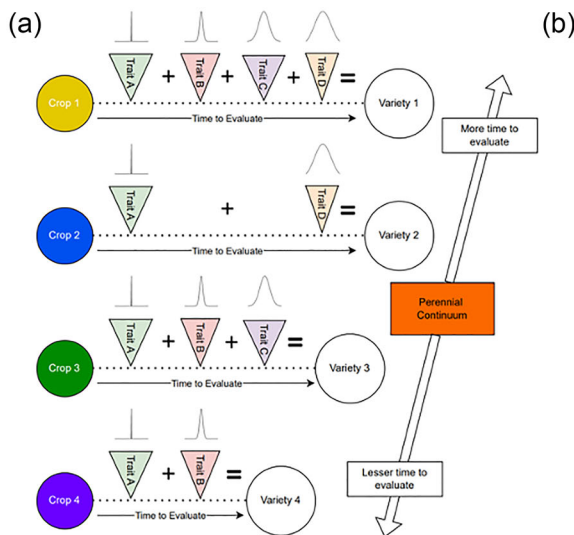


FIGURE 1 A major challenge in perennial crop breeding is the increased length of time a cycle of selection takes, in terms of how to measure productivity over several years on the same plant. In this study, we explore (A) generalized portions of a breeding program and (B) specific alterations in order to identify the best perennial genotype under different cycle times, however in order to properly account for temporal variation, original germplasm plots should be maintained for the entire breeding/selection cycle in order to account temporal stability for traits of interest.



(b)

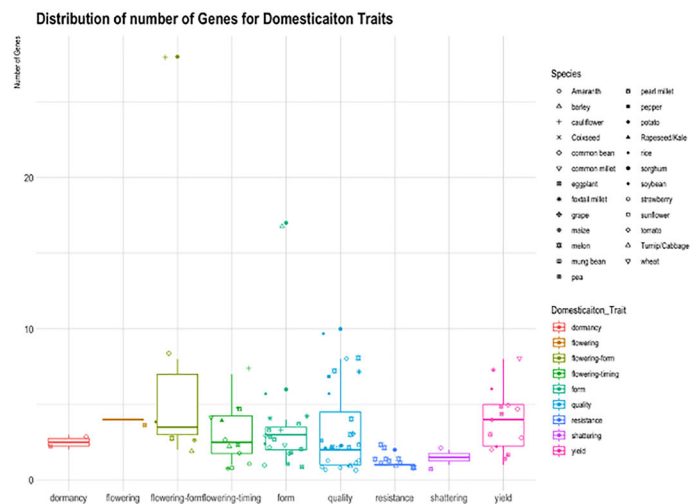


FIGURE 2 When creating a de novo domestication program or for introduction of a crop to a new agroecosystem it is important to understand the limitations. Panel (A) shows that you are limited not by the number of traits, but by the most complex trait. Panel (B) shows what the expected complexity of domestication traits is in common crops. Understanding the complexity is important for making decisions about investment and for having good estimates of how long it will take to bring a new crop to market. Citations for the number of genes involved found in Table S1.

logistical problems associated with turnaround time of lab and data analysis are less of an issue due to the longer lifespan of perennials (e.g., longer amount of time to make selection decisions), also the benefits of more efficient selection are more important as there are fewer generations of selections during a breeding career.

With respect to de novo domestication there is a well-known process and set of traits (e.g., flowering time, non-shattering, removal of dormancy) that make crops function well in modern production systems and are broadly similar across a wide range of cultivated taxa (Kantar et al., 2017; Meyer & Purugganan, 2013; Meyer et al., 2012; Purug-

ganan, 2019). While selecting for key known traits, selection for linked traits (genetic hitchhiking) and indirect selection will occur (Gepts, 2004). While domestication of current commodities took thousands of years (Allaby et al., 2008; Wilcox, 1998), experimental evidence shows that selection for key traits can drastically speed up the process (Hillman & Davies, 1990; Kantar et al., 2016). Empirical evidence of de novo domestication is limited to a few case studies where commercial cultivars have been released: intermediate wheat-grass (Bajgain, Zhang, Jungers et al., 2020) and pennycress (Phippen et al., 2022); and those that have made progress but are yet to release commercial material such as perennial

TABLE 2 Examples of priority traits for perennial crops.

Crop	Trait 1	Trait 2	Trait 3	Trait 4
<i>Acacia koa</i> A. Gray	Disease tolerance	Plant architecture (straight)	Wood quality (curly)	Yield
Kernza (<i>Thinopyrum intermedium</i>) (Host) Barkworth & D. R. Dewey)	Seed size	Free threshing	Shatter resistance	Short stature
<i>Silphium integrifolium</i> Michx.	Uniform maturity	Number heads per plant	Seeds per head	Seed size

sunflower (Ekar et al., 2019) and silphium (Price et al., 2021). It is also important to remember that breeding time is measured in generations of the plant, not in years. De novo domestication of these species required different investments of resources and different lengths of time to reach the market. This has led to a continuum of domestication, along which crop traits that make farming easier have been improved to varying levels. Market factors and the production system strongly influence the traits that are selected upon to advance a given species towards a form that is more adapted to cultivation. During de novo domestication, ideotype breeding has often been used (Donald, 1968; Rasmussen, 1987). The ideotype is a way to discretize the continuous nature of many domestication syndrome traits, by clearly defining key ranges for quantitative traits. For example, we can see that different methods of selection may be optimal due to the differences in genetic architecture and plant morphology for different species (Table 2)

In general, the rate of domesticating or adapting species is limited not by the number of traits, but by the most complex trait (Figure 2). Complex traits require more time to improve than simple ones. Complexity of a single trait can vary substantially across species and between annuals and perennials. Quantifying this complexity is important to identify bottlenecks of breeding for both domestication and climate adaptation. A promising method for the quick adaptation of existing crop wild relatives is gene-editing, as demonstrated in case studies of tomato and ground cherry (Lemmon et al., 2018). However, consumer acceptance of gene-editing is unlikely to be acceptable for the entire global and infeasible for semidomesticated, orphan, or landrace species because of their limited information (Del Valle-Echevarria et al., 2021). Further, for many traits specific genes and causative mutations are not known so it would be difficult to operationalize gene editing. There will also be a clear need to optimize prediction across a range of tested and unknown production environments (Neyhart, Gutierrez et al., 2022).

3.1 | Defining and measuring genetic gain for perennial crops under climate change

Assessing and achieving germplasm improvement within the context of adapting perennial crops to climate change is challenging for both breeding and agronomic development.

This section discusses strategies to identify, measure, and interpret traits that lead to adaptation to the pressures of climate change. These processes may be undertaken to improve stability across fluctuations in weather, pathogen, and pest pressures that affect both plant performance and the ability of growers to undertake management.

Genetic gain, a core concept, is the improvement in average phenotypic value of a population due to selection over breeding cycles (Rutkowski, 2019). This definition begs the question of what phenotypes are valuable and useful for breeding. Because of the biological and functional diversity of perennials, defining genetic gain in a general sense is challenging. For example, a woody ornamental might be valued for long-term erosion control and foliage aesthetics, while an herbaceous grain might need to establish quickly and produce grain that threshes easily (Bajgain, Zhang, & Anderson, 2020; Carlson & Smart, 2022). Perennial crops serve multiple ecological, agronomic, horticultural, and social purposes, which may not be positively correlated, may not emerge concurrently, and may result from difficult-to-measure traits. Additionally, desirable perennial crops must deliver reliable performance across erratic weather, pathogen, and pest pressures—all of which are expected to become more extreme with climate change (IPCC, 2022). Finally, perennial crop breeding is fragmented across species and functions, inhibiting transfer of knowledge across species systems. While the same could be said of annual crops the problem is less acute due to more breeders working in that space. The concept of agronomic gain from management practices (Saito et al., 2021) provides a framework to synthesize disparate outcomes and goals.

Early selection criteria that correspond to long-term performance are critical to achieve timely gains due to perennials' longer breeding cycles (Hayes et al., 2018). Willow (*Salix* spp. L.) breeding demonstrates the utility of these indices for improving multiple outcomes that are achieved after years of growth. Willow is grown for the environmental benefit of erosion control and wildlife habitat, the social benefit of a windbreak, and for economic value as a biofuel feedstock. All these outcomes are enhanced with rapid establishment and the production of large amounts of high-density biomass (Carlson & Smart, 2022). Typically, large, segregating breeding populations are planted in single plant plots in replicated or augmented design for early phenotypic evaluation and selection (Kopp et al., 2001; Macalpine et al., 2010). Early

selection occurs on secondary traits that are predictive of desirable traits of established plants: plant height, stem diameter, stem density, wood chemical composition, and disease resistance are strongly correlated with biomass yield in later years (Kopp et al., 2001). By applying index selection methods, these traits serve as early selection criteria for inclusion in advanced yield trials, where total biomass yield will be measured over multiple coppice (harvest) cycles. Direct selection of genotypes in advanced yield trials are then moved to multi-environment trials or commercialized. This secondary trait approach is especially important for those traits that aid climate adaptation, like rooting patterns, that are very challenging to measure directly and are strongly influenced by environments. The digital technologies section discusses measurement of these traits in more detail.

In perennial crops, genetic gain is interpreted differently from that of annual crops. For instance, willow plantations can remain productive for more than 20 years (Keoleian & Volk, 2005), long enough to experience extreme weather events and measurable shifts in average climate conditions. Another aspect is that while it takes a long time to select the desirable genotype it can take even longer to evaluate to fully understand if the genotype will respond well to the long productivity, meaning that it can take an entire career to evaluate a single breeding cycle. Additionally, many important agronomic, horticultural, and productivity traits show genetic-by-weather-year interactions in perennial crops (Bajgain, Zhang, & Anderson, 2020). Therefore, stability of selection indices must be considered a selection criterion. This is especially true across weather conditions, as evidence suggests that plant specialization to spatial environments (e.g., soil conditions) can improve productivity (Ewing et al., 2019; MacQueen et al., 2022).

Fitting such improved crops into socioeconomic systems is also essential and may dovetail well with multiple environmental trials that are essential to assessing stability. Thus far, we have emphasized early selection indices of agronomic, horticultural, and environmental outcomes to predict genetic gain in perennial crops. Annual crops and management are increasingly being developed and assessed using distributed, on-farm, and participatory methods (Colley et al., 2021; Snapp et al., 2019) that feature multiple disparate environments. One of the ways annual crop breeding has been so successful has been the use of widespread collaborative multi-environment trials, that specifically define target environmental regions (Atlin et al., 2000). When applied to perennial crops, these experimental methods allow the collection of qualitative data describing, for example, potential use cases, agronomic traits including weed suppression, or other grower preferences that are essential to grower adoption (Mungai et al., 2016) and thus are critical components of genetic gain. Agricultural scientists, growers, industry, and other stakeholders may then more easily assess promising

lines for the multiple roles they play on the landscape and within social systems (Saito et al., 2021).

Breeding perennial crops for disease resistance under future climates may be challenging. Currently, some perennial grain crops have genes that confer resistance to major diseases of annual wheat, such as Fusarium head blight (Bajgain et al., 2019), as well other fungal and viral pathogens that commonly infect annual cereal crops (Li & Wang, 2009). Increasing the acreage of new perennial crops could disrupt a pathogen's live cycle by limiting its ability to mutate and propagate during the summer and overwinter in cold seasons, thus potentially limiting on annual crops. However, the lack of widespread geographic evaluation of perennial grain and oilseed crops means that some organisms may exist in potential production regions that have not yet been identified as pests for these crop (McDonald & Stukenbrock, 2016). Moreover, many pests in annual rowcrop systems can be partially controlled via tillage and frequent crop rotation, yet these tools will be limited and perhaps unavailable for multiple continuous years of perennial crop production, thus increasing the reliance on genetic resistance (Ryan et al., 2018). Uncertainty around geographic ranges, phenology, and distribution patterns of crop diseases under changing climates are significant (Ristaino et al., 2021) and therefore, presents a moving target for plant breeders working on improving genetic resistance of perennial crops to plant pathogens.

3.2 | Digital technologies to advance breeding of perennials

Artificial intelligence and machine learning, in particular, are becoming central to the analysis of agricultural data (Basso & Antle, 2020; Harfouche et al., 2019). Long growing seasons and the need to monitor perennials while dormant outside the growing season can introduce technical challenges to digital data collection of perennials. Data collection hardware, usually including wireless connectivity, must be robust in a large range of environmental stresses (temperature, storms, animals). These challenges can be overcome as new sensing hardware and data analytic techniques provide a way to generate and analyze data in a wide range of systems with many different goals in addition to dealing with data privacy concerns (Runck, Joglekar et al., 2022). New technology allows for more complex measurements that can better account for variation within and between seasons. Enabling technologies for on-farm and on-station research trials include sensors (biophysical and bioclimatic data), imaging (plant growth, plant physiology), and experiment management platforms (data archiving and analysis). These new technologies can also be used to measure ecosystem services provided by perennial crops. These data will also aid with robust and accurate forecasts of agricultural outcomes and provide validations for

these forecasts. While there is increased capacity to generate these data and the data have been shown to have utility, there will be a need to increase the capacity to operationalize these data within public and small scale commercial endeavors.

Advancements in remote sensing with unmanned aerial systems (UAS) have dramatically reduced phenotyping and screening costs, enabling cost-effective testing in multiple environments. UAS can measure traits such as canopy volume that correspond to (1) productive outcomes such as biomass production, grain yield, and plant height (Adak et al., 2021), (2) adaptive outcomes including phenology of greening and senescence that predict adaptation to long-term trends of lengthening growing seasons (Caruso et al., 2019), and (3) resilience outcomes including resistance to disease pressure under different weather conditions (Torreson et al., 2017). As UAS are limited to assessing aboveground traits, similar advances in screening belowground traits such as root architecture, exudation patterns, and resistance to diseases are critical for continuing genetic gains in perennial crops. These traits correspond both to aboveground resilience to weather extremes and to ecosystem service outcomes of perennial crops including improved carbon sequestration that may provide additional revenues to growers, enhance food security, and mitigate climate change (Droste et al., 2020; Oldfield et al., 2019; Williams et al., 2016).

Methods are being developed, such as ground penetrating radar and light detection and ranging, to understand how to use remote sensing to estimate belowground biomass and understand biotic and abiotic stress (Bellvert et al., 2021; Ferrara et al., 2014; George et al., 2019). In addition, the application of near-infrared spectroscopy in characterizing forage properties (Norman et al., 2020), digital images as well as machine learning models in measuring grain characteristics (Bajgain & Anderson, 2021; Bajgain et al., 2022), and other phenomics and automation tools (Rubin et al., 2022) have shown promise in expediting domestication, improvement, and adaptation of perennial crops.

3.3 | Understanding limitations and opportunities of experimental designs for perennial systems

Another modification to the typical crop development and evaluation system required for perennials is related to experimental design. Classic experimental designs focus on things that are easy to measure and analyze, but these measurements are often not determinants of the most important goals of a given system and do not give the most generalizable answer (Osmolovskaya et al., 2018). The most common sets of designs in agricultural science are blocked designs, both complete and incomplete (Gomez & Gomez, 1984). Many other designs have been used mostly due to limi-

tations in experimental material: these include augmented designs (Federer & Raghavarao, 1975), mother-baby trials (Snapp, 2002), and alpha-lattice designs (Patterson & Williams, 1976). These designs are very useful because they provide a way to effectively test hypotheses for a range of questions related to genetics, management, or delivery of ecosystem services. However, these designs also suffer from logistical limitations such as limitations in ability to phenotype and limitations of sites to fully take advantage of environmental variation. Further, there is often not enough information in experimental designs and metadata to make use of complex analysis (Hufnagel et al., 2020). To make best use of these opportunities, there is a need to understand the current and potential approaches to combining experimental techniques, data sources, and statistical techniques to advance genetic gain. Newer methods of analysis and experimentation can help reconcile the need for robust data while fully embracing different goals (White et al., 2016).

3.4 | Avoiding pseudoreplication in perennial research

Management and analysis of field data evaluating novel perennial crop lines requires careful model specification that may not be required in annual crop systems. While not specific to perennials, due to space and time constraints one of the major pitfalls often confronted in analyzing complex field trial data of perennial crops is pseudoreplication, where replicates are treated as independent even though they are part of the same experimental unit, that is, measurements on a single plant or population are not independent across years. Classic methods of partitioning variance such as split-plot in time do not account for the true variance structure and lack of independence between measurements, and thus increase the chance of false positive findings. Instead, the entire life cycle of the system must be considered the experimental unit. A major problem when exploring perennial systems is that within any experimental design, the experimenter is sampling the same plots with each successive harvest (i.e., subsequent years) thereby not representing independent site-years common to field research with annual crops. This is an example of pseudoreplication, where classical methods of analysis (e.g., analysis of variance or ordinary least squares regression) will have their assumptions violated and thus decrease the accuracy of the analysis.

The most straightforward method for dealing with this is multilevel modeling. This class of models has a defined hierarchical structure that can account for differences in error structure (Qian et al., 2010). At the observational level (i.e., the first level), like an ordinary least square regression, a mixed model predicts a biological response with one or more independent variables. However, unlike nonhierarchi-

cal regressions, multilevel models include random variables that cluster related observations (e.g., samples coming from the same plot) to account for the lack of independence (Qian et al., 2010; Qian, 2017). Multilevel models must have at least two levels, where each level can have its own set of predictors. Misspecification of the model may lead to incorrectly rejecting the null hypothesis when substantial between cluster variation is present (i.e., high intraclass correlation). For example, consider a common analysis of a multiyear trial of annual crops where site and year are fixed but blocking is random without repeated measurements (equations will be shown in the notation of the R package lme4; Bates, 2010):

$$\text{yield} \sim \text{site} + \text{year} + \text{soiltexture} + \text{fertilizerrate} + (1 | \text{block}) \quad (1)$$

Here, this model in Equation (1) contains two levels. The first is the observational level where yield responds to variable fertilizer application rates. The second is the blocking level which accounts for random differences in the yield response among blocks. We can also include a predictor associated with each block, such as soil texture, to help explain at least some of the variation in the response due to blocking.

We can now modify the equation such that site and year are random:

$$\text{yield} \sim \text{precipitation} + \text{soil texture} + \text{fertilizer rate} + (1 | \text{site/block}) + (1 | \text{year/block}) \quad (2)$$

Alternatively, in Equation (2), we now have three levels. The first is still the observational level which characterizes the yield response. The second is also still the blocking level, but now we include a third level for location and year as fully crossed random effects. We can also include site-level predictors such as precipitation.

Within this framework for perennial crops, repeated measures can be correctly modeled using a plot identification factor given that plots are repeatedly sampled from year to year (Equation 3). In the first iteration, site and time might be fixed with a plot nested within the block. This allows the yield response in time to vary randomly between plots. Likewise, we may even include a plot level variable such as a preplant soil nutrient status:

$$\text{yield} \sim \text{site} + \text{year} + \text{soil texture} + \text{fertilizer rate} + \text{prelant nutrient status} + (1 | \text{block/plot_id}) \quad (3)$$

We can further refine this three-level model by keeping site and time fixed but adding year as the random slope (Equation 4), which allows the yield response to vary in time between experimental treatments as follows:

$$\text{yield} \sim \text{site} + \text{year} + \text{soil texture} + \text{fertilizer rate} + \text{prelant nutrient status} + (\text{year} | \text{block/plot_id}) \quad (4)$$

Lastly, we could build a four-level model by introducing the site as a random rather than fixed effect with no random slope (Equation 5) or with year as the random slope (Equation 6). Implementing either of these models will depend on what type of inference the researcher wants to make. We can also add a site level predictor back into the model.

$$\text{yield} \sim \text{precipitation} + \text{year} + \text{soil texture} + \text{fertilizer rate} + \text{prelant nutrient status} + (1 | \text{site/block/plot_id}) \quad (5)$$

$$\text{yield} \sim \text{precipitation} + \text{year} + \text{soil texture} + \lim_{x \rightarrow \infty} \text{fertilizer rate} + \text{prelant nutrient status} + (\text{year} | \text{site/block/plot_id}) \quad (6)$$

Selecting the correct model specification will ensure that the model matches the experiment and identifies the most accurate answer (Figure 3). To emphasize the utility of these models, we reanalyzed past data on perennial systems (Jungers, Dehaan et al., 2017) using the originally applied model analogous to Equation (1) and a model accounting for repeated measures analogous to Equation (3). The experiment compared biomass yield of four perennial crops—three intermediate wheatgrass populations (TLI) and switchgrass—each grown with and without alfalfa as an intercrop. The experimental design was a completely randomized block design with four replicates conducted across six sites over three years. In the incorrect model, grain yield of the “TLI” $p = 0.03$, however, when properly accounting for covariance structure and nonindependence of repeated samples, TLI evidence to reject the null hypothesis was weakened ($p = 0.052$). While the result is small in this example, it may not always be and is important to check to help eliminate false positives that could lead to misplaced effort (Table S2; Supporting Information 1 and 2). It is important to use disciplinary knowledge as well as statistical knowledge to build evidence for future experiments. Multilevel models can be complex, and so it is important to confirm its necessity by first assessing intraclass correlation. This class of models has been used in selection of multi-harvest trials among perennial crops using various covariance structures for different experimental unit levels (Piepho et al., 2004; Piepho & Eckl, 2014; De Faveri et al., 2015; Smith et al., 2007). In this study, we have described the importance of accounting for year-to-year correlations when analyzing yields of perennial crops through time, but it should be noted that there can be mortality and recruitment of individuals within an experimental

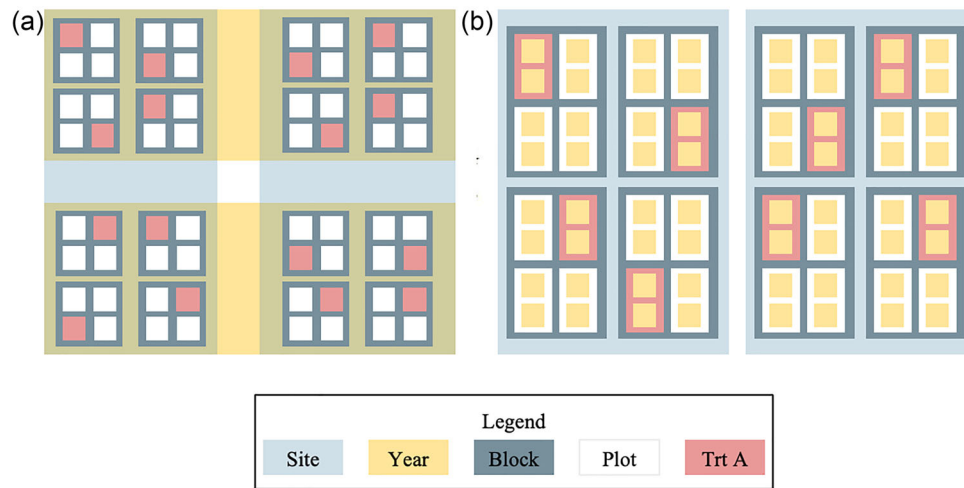


FIGURE 3 Comparison repeated measures analysis of identical field layouts with different statistical analyses based on the nature of perennial cropping systems. (A) This image illustrates a fully crossed model in a randomized complete design, modeling this image accounts for treatments, blocks and years, but does not account for any repeated sampling in each plot, so it is an incorrect model for perennial systems and (B) A depiction of the correct model, where the repeated measurements were collected across different years within a single plot, this is illustrated with the multiple boxes for years within each plot. Properly accounting for the sources of variation in the complex models associated with perennial systems changes the significance reducing false positives (Table S2). This has large implications for which systems get pursued and which may be scaled. Just like in green eggs and ham (represented here by Sam I am; Seuss, 1960) researchers will likely only appreciate new analyses and designs once they are tried. Trt, treatment.

unit for some perennial crops in field trials. Such turnover can alter the age structure and genetic makeup of the population within experimental units, which could influence yield and other response variables measured through time. Research is needed to quantify this source of variability and compare it to others related to changes in yields through time in perennial crops.

4 | NONRESEARCH CONSIDERATIONS FOR ADAPTATION: COMMERCIALIZATION, ADOPTION, AND SCALING OF PERENNIALS IN FOOD SYSTEMS

While scientific work establishing new management and genetics to adapt perennials to climate change is essential, releasing new or better-adapted varieties does not mean that farmers will adopt new practices or that consumers will purchase new ingredients and products. Therefore, the success of a new perennial crop rapidly deployed to keep pace with climate change will require concurrent work on consumer research, commercialization plans, supply chain modifications, and a strategy to provide these new crops and ingredients to various stakeholders—from farmers to end users. Widespread adoption and commercial viability of perennial cropping systems require success in a complex and risky set of activities. These “niche” perennial solutions must be rapidly incorporated into a relatively path-dependent agri-

food regime under the landscape level pressures of climate change, commodities markets, and consumer preferences. Greater incorporation of perennial crops into agricultural systems is likely to involve the following:

1. Strategic and robust technology transfer, adoption, and diffusion to carry the novel technologies, best management practices, and cultural shifts that bring new perennial crops from the controlled laboratory and test plot environment to broad commercial production.
2. Cascading innovations in harvesting, storage, and processing equipment and methods, product development, business and supply chain structure, finance, and marketing.

These activities are critical to the process of supporting the adoption, commercialization, and scaling of novel perennial crops.

Just as the targets and methodologies of basic science must adapt to the variable and uncertain impacts of climate change, so too should the targets and methodologies of commercializing novel perennial crops adapt to these pressures. Climate-smart agriculture provides a framework for priority outcomes of the agri-food system that include sustainability, increasing food security, resilience to climate change, and reducing GHG emissions (McCarthy et al., 2018; Bibas et al., 2017; Lipper et al., 2017). To reach these outcomes requires navigating complex tradeoffs in developing and advancing novel perennial crops for a broader set of private and pub-

lic goods. Key transitions in the current agricultural system can help move the needle, for example, moving toward more complex multi-cropping systems that include different species with variable phenology and life history. Further, looking at productivity as a more holistic metric that includes economics, ecosystem services, and sustainability will provide longer term value (Davis et al., 2012; Saito et al., 2021). During these transformations it is imperative that outputs are predictable, with many contingencies built in, having a safe, secure, and diverse food system is the goal.

Developing markets and supply chains for emerging perennial crops is a major barrier to their incorporation into agricultural systems. While historically humans' diets have been very diverse, there was clear homogenization over the 20th century (Khoury et al., 2014) and many crops have fallen out of use. Therefore, it will be imperative that as new crops are introduced, markets are simultaneously created along with supply chains to make sure new products can be distributed (Runck et al., 2014). In some cases, perennial crops can be used as a replacement of annuals that fit the same place in the market (e.g., Kernza; Rahardjo et al., 2018) and leverage existing infrastructure for storage and processing. All of this requires that perennial crops can provide outcomes (largely crop yield) that are economically viable and valued by society and the market.

There are many approaches to generating demand to incorporate perennial products into existing and new food, fuel, and feed products. These can be broadly placed into the categories of full substitution, partial substitution, or complementation. The strategy will be different for each introduced crop but understanding that the focus must be multifaceted and flexible will be key to success. The degree of substitutability in resulting products presents challenges and opportunities for novel perennial crops (e.g., high substitutability flax and wheat). However, there are market constraints on the yield that will be required over the life of the stand (Bell et al., 2008). Many major constraints on the marketing and adoption of perennial crops are related to policies. For example, in the United States, there are complex crop insurance requirements associated with harvestable groundcover (Moore et al., 2019; Wachter et al., 2019). There are no current subsidy programs associated with perennial grains, but there are some new policies that allow for ecosystem service production (Lichtenberg, 2021). Another potential avenue will be carbon credits if perennials are a persistent part of the landscape (Englund et al., 2022). Currently the best example of a commercialized perennial grain is Kernza, which shows there can be marketplace complementation, adoption, and a price premium (Lanker et al., 2020; Jordan et al., 2021). Kernza was helped by concurrent market development and creation of distribution networks (Gutknecht et al., in review).

Finding optimal locations for growing and processing emerging perennial crops is another challenge. One option is

to target perennial crop production on lands adjacent to agricultural fields that have been retired from crop production because they cannot support profitable annual agriculture. Implementing perennial crop production in those areas will allow for lands near skilled farmers to be able to be brought into production, albeit possibly at risk of habitat loss. Another approach is to identify specific fields that are currently in annual crop production but generate relatively low net economic returns. Such fields might result in low yields because soil type or topography might prevent timely planting of annuals, which would give perennials an advantage in closing the yield gap. Perennial crops that provide ecosystem services can be placed on specific lands with targeted ecosystem function needs, such as agricultural land with high rates of groundwater recharge where nitrate leaching to drinking water is a concern (e.g., drinking water; Jager et al., 2022). In fact, many of the researched perennial crops already show a clear ecosystem service benefit over annuals (Table 3). New crops may be hyper-localized before they can grow into more regional or national products. This also argues for targeted breeding efforts to maximize local adaptation within the target species and the need to have large scale networks for data collection and sharing (Ewing et al., 2019; MacQueen, et al., 2022).

Adaptive potential is greatly linked to human behavior changes (Fleming & Vanclay, 2010). For example, the increased uncertainty from climate change may increase risk aversion where farmers may be interested in using more stable varieties which may be more stress tolerant (Anwar et al., 2013). This increased uncertainty makes genetic improvement a particularly attractive solution, using germplasm collections (Heider et al., 2021), crop wild relatives (Fumia et al., 2022), introducing new traits like perenniality (Sanford et al., 2021), and domestication of new crops (DeHaan et al., 2016). While the threat from climate change is generally being addressed by "policy", stakeholder adaptation mechanisms are generally slow moving (Berrang-Ford et al., 2021). This may be due to the expense of shifting infrastructure under rapid adaptation scenarios (Office of Technology Assessment, 1993, Adams et al., 1998). Due to region-dependent forecasting, adaptation approaches are easier to quantify in local studies (Mitchell et al., 1999). Therefore, novel climate change adaptation by developing perennial versions of current annual crops, or optimizing currently used perennial agricultural crops for projected climate change scenarios, requires not only scientific study but stakeholder interaction as well (Runck et al., 2014). More research is needed to match the body of research available regarding climate change impact on annual crops across scale, from local to global. Such studies will remove the blind spot of wrongly dismissing a solution as the effects from climate change are highly varied by location, crop, and management. Perennial crops have always been a part of agricultural systems, however, to make agriculture truly climate resilient

TABLE 3 Application areas of perennials in current food systems.

Crop	Current use	Potential use	Ecosystem value	Citation
Kernza (intermediate wheatgrass)	Contract grain	Commodity grain	Water and soil quality/carbon sink/strengthen microbial communities	Rakkar et al., 2023
Flax— <i>Linum usitatissimum</i> L.	Ornamental	oilseed	Water and soil quality, pollinators	Tork et al., 2019; Tork et al., 2022
Apple (<i>Malus domestica</i> Borkh.), orange (<i>Citrus × sinensis</i> [L.] Osbeck), cherry [<i>Prunus avium</i> L.], grape (<i>Vitis vinifera</i> L.)	Orchard	Intercropping agroforestry system	Water and soil quality, pollinators	Demestihis et al., 2017
Alfalfa, <i>Medicago sativa</i> L.	Pasture	Intercropping system	Water and soil quality, pollinators	Lescourret et al., 2015
Hazelnut, <i>Corylus avellana</i> L.	Harvestable hedgerows	Intercropping system	Water and soil quality	Demchik, et al., 2014
Prairie grass (species like; big bluestem— <i>Andropogon gerardi</i> Vitman, switchgrass— <i>Panicum virgatum</i> L., Indiangrass— <i>Sorghastrum nutans</i> (L.) Nash, and little bluestem— <i>Shizachyrium scoparium</i> [Michx.] Nash)	Pasture	Intercropping system, biofuel	Water and soil quality, native biodiversity	Noe et al., 2016

there is a need to greatly expand their use beyond the current global land use of ~15% (Food and Agriculture Organization of the United Nations, 2022).

An opportunity to overcome “chicken or egg” commercialization barriers, expedite scale up of acreage and supply chains, and potentially de-risk grower adoption of perennial crops lies in strategic landscape deployment where perennials can directly provide ecosystem services. For example, plot-scale research has shown that Kernza can reduce nitrate leaching to groundwater when grown on various soil types in Minnesota (Reily et al., 2022). Researchers, state public health officials, and the Department of Agriculture initiated a project to financially incentivize the replacement of high nitrogen demanding row crops with Kernza in the state’s drinking water supply management areas that were most vulnerable to nitrate leaching. The project provided economic support to farmers to replace annual row crops with Kernza, which allowed researchers to study watershed-scale impacts of such transitions. This program also allowed for a buildup in the supply of Kernza seed and grain for scaling up research and development of food products. Nitrate levels in public drinking water supplies have decreased in these areas and studies are underway to determine the influence of Kernza on this positive public health outcome. Similar opportunities exist to plant perennials in specific regions to (1) reduce nutrient losses to surface waters, (2) prevent soil erosion,

or (3) restore organic matter levels on degraded farmland. Multi-stakeholder partnerships are important for designing and deploying such projects.

5 | CONCLUSIONS

Adapting to climate change will require exploration of future projections as well as embracing new methods for understanding cropping system productivity. Historically agriculture has measured productivity in annualized ways; however, annual measures of productivity of perennial crops are less important than the productivity over the life of the system (Bell et al., 2008). There is a need to increase the speed of research with regards to climate change adaptation measures to deal with the longer life history of perennial species, with a specific focus on new experimental techniques and novel phenotypes.

Increasing perenniality across the landscape is a goal that is gaining more attention to respond to climate change. The benefits to mitigating environmental damage include improving water quality, reducing GHG emissions and providing habitat for many different species. This goal can be achieved while still maintaining food, fuel, and fiber production. However, achieving the benefits of expanding perennial crops, will require a concerted effort. Deliberately implementing technology to maximize the ability to monitor ecosystem services,

improve management, and maximize genetic gain will be essential. To help achieve this, more complex analyses and designs coupled with development of markets, supply chains, and technology transfer tools is required to iteratively expand perennial crops on the landscape and in the marketplace.

AUTHOR CONTRIBUTIONS

Jacob Jungers: Conceptualization; Formal analysis; Methodology; Writing—original draft; Writing—review and editing. **Bryan Runck:** Conceptualization; Supervision; Writing—original draft; Writing—review and editing. **Tai Maaz:** Formal analysis; Methodology; Visualization; Writing—original draft; Writing—review and editing. **Nathan Fumia:** Visualization; Writing—original draft; Writing—review and editing. **Craig Henry Carlson:** Writing—original draft; Writing—review and editing. **Jeffrey Neyhart:** Writing—original draft; Writing—review and editing. **Mitch Hunter:** Writing—original draft; Writing—review and editing. **Prabin Bajgain:** Writing—review and editing. **Jessica Gutknecht:** Writing—original draft; Writing—review and editing. **Michael Kantar:** Conceptualization; Visualization; Writing—original draft; Writing—review and editing.



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The authors declare no conflicts of interest.

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SUPPORTING INFORMATION

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