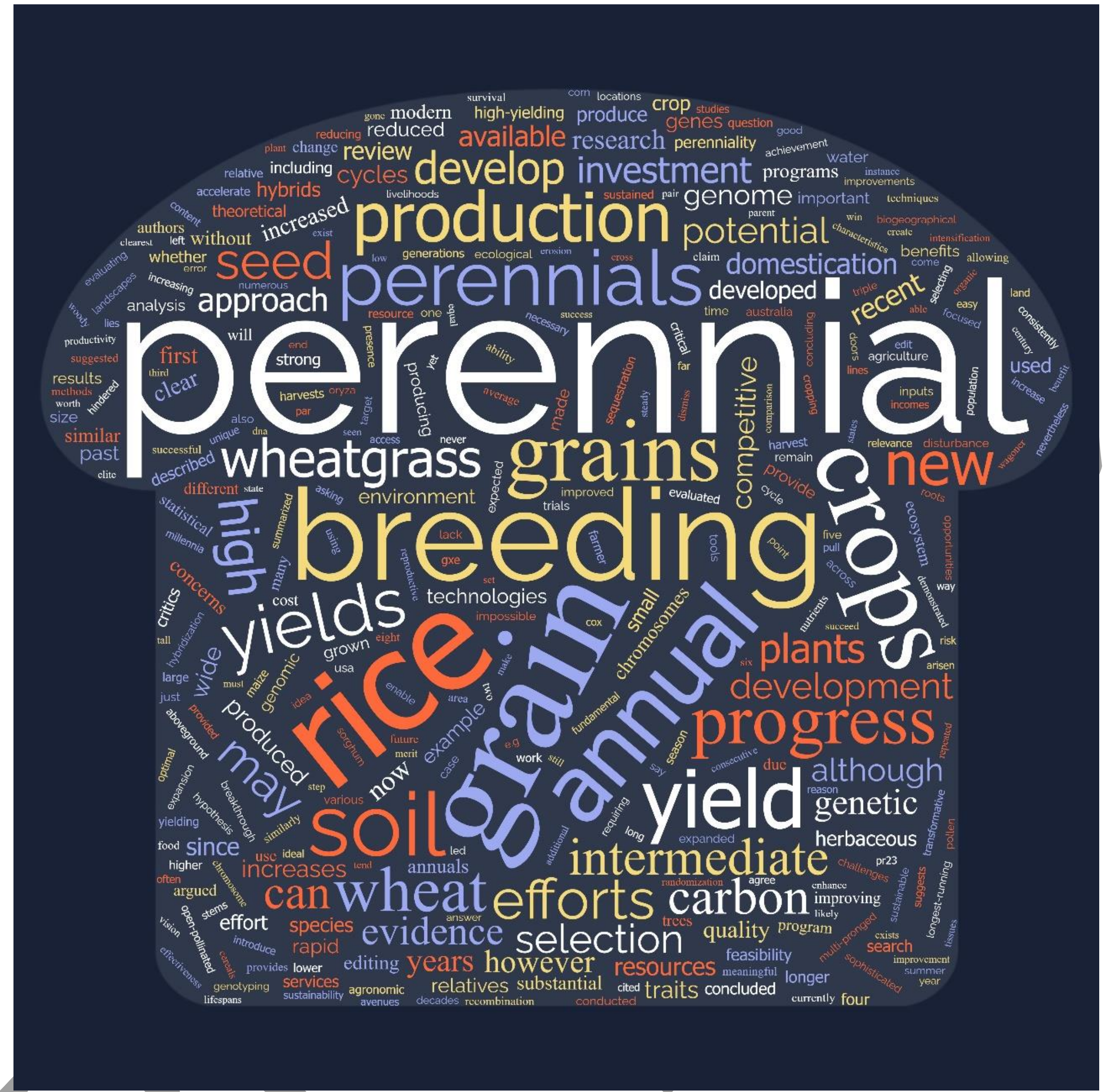
Discussion: Prioritize Perennial Grain Development for Sustainable Food Production and Environmental Benefits

Lee DeHaan[1], Jared Crain[1], Jesse Poland[1], Erik Sacks[1], James Anderson[1], Prabin Bajgain[1], Andrea Basche[1], Douglas Cattani[1], Timothy Crews[1], Christophe David[1], Olivier Duchene[1], Jessica Gutknecht[1], Richard Hayes[1], Fengyi Hu[1], Jacob Jungers[1], Soren Knudsen[1], Wenquian Kong[1], Steve Larson[1], Per-Olaf Lundquist[1], Guangbin Luo[1], Allison Miller[1], Pheonah Nabukalu[1], Matthew Newell[1], Lennart Olsson[1], Michael Palmgren[1], Andrew Patterson[1], Valentin Picasso[1], Shuwen Wang[1], and Anna Westerbergh[1]

[1]Affiliation not available

June 27, 2023

Graphical Abstract:



Article Highlights:

Perennial grains would reduce the environmental impact of food production.

Perennial grains can improve soil health and sequester atmospheric carbon.

Success in perennial rice shows feasibility of developing high yield perennials.

Progress in new crop development is severely limited by small research investment.

Genomic tools will accelerate perennial grain development for near-term feasibility.

Discussion: Prioritize Perennial Grain Development for Sustainable Food Production and Environmental Benefits

Lee R. DeHaan[a,*], James A. Anderson[b], Prabin Bajgain[b], Andrea Basche[c], Douglas J. Cattani[d], Jared Crain[e], Timothy E. Crews[a], Christophe David[f], Olivier Duchene[f], Jessica Gutknecht[g], Richard C. Hayes[h], Fengyi Hu[i], Jacob M. Jungers[b], Søren Knudsen[j], Wenqian Kong[k], Steve Larson[l], Per-Olof Lundquist[m], Guangbin Luo[n], Allison J. Miller[o], Pheonah Nabukalu[p], Matthew T. Newell[q], Lennart Olsson[r], Michael Palmgren[n], Andrew H. Paterson[k], Valentin D. Picasso[s], Jesse A. Poland[t], Erik J. Sacks[u], Shuwen Wang[a], and Anna Westerbergh[m]

[a]The Land Institute, 2440 E. Water Well Rd, Salina, Kansas, USA 67401

[b]Department of Agronomy and Plant Genetics, University of Minnesota, 1991 Upper Buford Circle, St. Paul, MN, USA 55108

[c]Department of Agronomy and Horticulture, University of Nebraska-Lincoln, 1875 N. 38th St, 279 PLSH, Lincoln, NE, USA 68583-0915

[d]Department of Plant Science, University of Manitoba, 66 Dafoe Rd, Winnipeg, MB, Canada R3T 2N2

[e]Department of Plant Pathology, Kansas State University, 1712 Claflin Rd, 4024 Throckmorton PSC, Manhattan, KS, USA 66506

[f] ISARA, Agroecology and Environment Research Unit, 23 rue Jean Baldassini, 69364 Lyon, France

[g]Department of Soil, Water, and Climate, University of Minnesota, 1991 Upper Buford Cir, Falcon Heights, MN, USA 55108

[h]NSW Department of Primary Industries, Wagga Wagga Agricultural Institute, 322 Pine Gully Rd, NSW 2795, Australia

[i]State Key Laboratory for Conservation and Utilization of Bio-Resources in Yunnan, Research Center of Perennial Rice Engineering and Technology in Yunnan, School of Agriculture, Yunnan University, 2 Cuihu N Rd, Wuhua District, Kunming, China 650106

[j]Carlsberg Research Laboratory, J. C. Jacobsens Gade 4, 1799, 1778, Copenhagen, Denmark

[k]University of Georgia, Athens, USA

[l]USDA-ARS, Forage and Range Research, 696 North 1100 East, Logan, Utah, USA 84321

[m]Department of Plant Biology, Uppsala BioCenter, Linnean Center for Plant Biology in Uppsala, Swedish University of Agricultural Sciences, Box 7080, 750 07, Uppsala, Sweden

[n]Department of Plant and Environmental Sciences, University of Copenhagen, Denmark

[o]Saint Louis University and Donald Danforth Plant Science Center, 975 N Warson Rd, Olivette, MO, USA 63132

[p]NESPAL, University of Georgia, 2356 Rainwater Rd, Tifton, Georgia, USA 31793

[q]NSW Department of Primary Industries, Cowra Agricultural Research Station, 296 Binni Creek, Cowra NSW 2794, Australia

[r]Lund University Centre for Sustainability Studies, P.O. Box 170, SE-221 Lund, Sweden
[s]University of Wisconsin-Madison, USA.
[t]King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia
[u]University of Illinois at Urbana-Champaign, USA
*****Correspondence: dehaan@landinstitute.org, The Land Institute, 2440 E. Water Well Rd, Salina, Kansas, USA 67401

Abstract

Perennial grains have potential to contribute to ecological intensification of food production by enabling the direct harvest of human-edible crops without requiring annual cycles of disturbance and replanting. Studies of prototype perennial grains and other herbaceous perennials point to the ability of agroecosystems including these crops to protect water quality, enhance wildlife habitat, build soil quality, and sequester soil carbon. However, genetic improvement of perennial grain candidates has been hindered by limited investment due to uncertainty about whether the approach is viable. As efforts to develop perennial grain crops have expanded in past decades, critiques of the approach have arisen. With a recent report of perennial rice producing yields equivalent to those of annual rice over eight consecutive harvests, many theoretical concerns have been alleviated. Some valid questions remain over the timeline for new crop development, but these may be mitigated by implementation of new technologies such as low-cost genotyping, genomic selection, and genome editing.

Keywords: soil quality, climate change, carbon sequestration, genome editing, genomic selection

1. Introduction

The abundant potential of perennial grains, if developed, to address a wide array of global sustainability challenges to agricultural production has long been recognized. In 1990, Wagoner published the first extensive review of past efforts to develop perennial grains using species in the grass family (Wagoner, 1990). The review listed numerous reasons for perennial grain development, including reducing soil erosion, reducing inputs, conserving soil nutrients, building soil health, and improving farmer incomes by reducing costs of inputs and field operations while preserving grain productivity. Although humans have consumed the seeds of perennial grasses for millennia, domestic perennial grains were not developed. As Wagoner described, efforts to develop perennial wheat through wide hybridization between annual cereals and perennial relatives were conducted in the Soviet Union beginning in the 1930s. Efforts later spread to other regions and attempts were made to create perennial versions of other crops by cross-pollination with perennial relatives. These programs generally produced short-lived perennials with yields inferior to annual grains, and there was never a clear commercial opportunity.

In 2002, an exhaustive review of past and potential efforts to breed successful perennial grains was published (Cox et al., 2002). Again, the authors concluded that decades of work had failed to produce yields on par with comparable annual grains. However, they also asserted that important avenues to high grain yield from perennials may have been overlooked. For instance, perennials can often use resources such as water, nutrients and sunlight that are unavailable to many annual crops due to their brief summer lifespans. The authors also described the potential of ongoing efforts to develop perennial rice and perennial sorghum by hybridizing the annual crops with their perennial relatives and suggested that repeated rounds of selection over many generations would enable simultaneous improvement in longevity and seed production traits by combining favourable alleles in new high-yielding perennial grains.

In the 20 years following the 2002 review article (Cox et al., 2002), perennial grain development efforts have grown in number and have attracted expanding attention as an approach to address urgent issues in agriculture. Reports are continuing to show the effectiveness of perennial crops in stabilizing production (Sanford et al., 2021), improving soil quality (Daigh, 2011; DeHaan and Van Tassel, 2022; Emmerling et al., 2017; McGowan et al., 2019), mitigating climate change (Crews and Rumsey, 2017; Jacot et al., 2021), improving wildlife habitat (Graham et al., 2017; Helms et al., 2020; Robertson et al., 2011) and protecting water quality (Cacho et al., 2018; Culman et al., 2013; Jungers et al., 2019; Moore et al., 2019). Evidence of rapid expansion in perennial grain research is seen in a Google Scholar search, where only 5 articles containing the search term “perennial wheat” are returned from the year 2001, compared to 463 articles from 2021. Although the increase is substantial, perennial grain efforts remain insignificant compared with annual crops, as a search for “winter wheat” from 2021 provides more than 24,000 results.

Although efforts to develop new perennial grains remain slight, they have been sufficient to attract critique from authors who regard the vision as being unlikely to succeed and unworthy of expanded investment (Cassman and Connor, 2022; Loomis, 2022; Smaje, 2015). These critiques are helpful, to some extent, as they allow a careful examination of the available evidence for and against greater investment in programs that will require sustained effort over longer time frames than might typically be embraced by funders. Herein we will support our thesis that recent research progress, theoretical considerations, and advances in breeding and genetic technologies have combined to provide justification for an aggressive expansion in perennial grain research in the current decade.

2. Recent progress in perennial rice

Perennial rice currently provides the clearest example of what can be achieved through sustained investment in a perennial grain breeding program. An initial successful cross between annual rice (*Oryza sativa*) and the perennial relative *Oryza longistaminata* was obtained in 1996, and work was invigorated when the first promising F_2 progeny with good seed set and moderately strong rhizome production was identified in 2007 (Zhang et al., 2022). What followed were generations of selfing and selection for plants with increased pollen viability and short rhizomes. As generations advanced, plants were identified that had traits similar to annual rice (height, seed size, and grain set). However, the selected lines retained the ability to regrow vigorously after harvest. Subsequent rounds of backcrossing to various elite rice types have demonstrated the potential to introduce the perennial trait into different genetic backgrounds (Zhang et al., 2022).

In 2018, the first perennial rice variety, PR23, was released to farmers in China. While other rice varieties may have weak “ratooning” (regrowth after harvest), allowing a small second crop, PR23 has capacity for strong regrowth and sustained yield. Evaluated over eight consecutive harvests across four years, the perennial rice produced an average of 6.8 Mg harvest^{-1}, similar to the yield of replanted annual rice (Zhang et al., 2022). After the first season, perennial rice resulted in substantial savings on labour and other inputs, which boosted farmer incomes (Zhang et al., 2022), consistent with earlier predictions made by advocates for perennial grain development (Wagoner, 1990; Cox et al, 2002). Additionally, reduced soil disturbance in perennial rice production provided measurable improvements in soil, as expected. For example, in four years of paddy perennial rice production, soil organic carbon content increased by a substantial 0.95 Mg ha^{-1} (Zhang et al., 2022).

Although the total planted area of perennial rice is still small relative to the global area of rice production, farmer acceptance has been strong, and perennial rice cultivation is increasing rapidly. In 2021, the area planted to perennial rice increased fourfold to 15,522 ha on 44,752 smallholder farms (Zhang et al., 2022.

Perennial rice is a clear example of how readily a new perennial grain can be developed, requiring an investment of less than US$20 million over 15 years (Glover, 2022). As the authors reporting the progress concluded, “perennial rice is a step change with potential to improve livelihoods, enhance soil quality and inspire research on other perennial grains” (Zhang et al., 2022).

3. Responses to concerns about perennial grains

Perennial grain crops have been proposed as a strategy to achieve expanded ecosystem services such as reduced erosion, greater resource use efficiency, reduced nutrient leaching, reduced watershed contamination, improved soil carbon content, and reduced dependence on fertilizer, herbicide, and tillage (Broussard and Turner, 2009; Glover et al., 2010). Although various perennial crops and cropping systems are expected to have a range of impacts on these ecosystem services, there has been little disagreement over the claim that perennial grains producing yields as large as their annual counterparts would have environmental and sustainability benefits. Divergent viewpoints have more frequently arisen concerning whether breeding perennial crops with yields similar to annual crops is a feasible goal. If clear evidence exists that perennial grain crops would be impossible to breed or that the cost of their development would exceed the benefits, then we would agree that research would be better focused elsewhere. Instead, we find compelling recent results that provide multiple lines of support for prioritizing perennial grain breeding.

3.1 Perennials can yield similarly to annuals

Understandably, the feasibility of breeding herbaceous perennial plants with high grain yield has been questioned, since on average both wild and domestic herbaceous perennial plants tend to have lower yields than their annual relatives (Vico et al., 2016). In Wagoner’s 1990 review, forage crops that had been selected for good seed production were found to have yields that might, in ideal circumstances, approach those of annual grains grown in the same region (Wagoner, 1990), but the general trend is clear that herbaceous perennials tend to be lower seed producers than annuals.

However, it would be unscientific conjecture to say that just because something does not currently exist, it can never exist in the future. For instance, maize yields in the USA have increased more than five-fold since the 1920s (Duvick, 2005). How was it possible to dramatically increase the grain production of maize when human-driven selection should have been favouring the highest seed producers for millennia? The answer likely lies in a multi-pronged approach including transitioning from open-pollinated populations to F_1 hybrids, modifying the agricultural environment for optimal growth, and enhancing selection methodology to favor plants that are less competitive while being more stress tolerant, thereby avoiding wasteful competitive responses while growing in high population densities (DeHaan et al., 2005; Denison, 2015; Duvick, 2005). Perennial grain breeders have argued that modern selective breeding, which has reduced competitive waste in annual grain fields, should similarly enable yield increases in perennials (DeHaan et al., 2005). While critics have suggested that the competitive nature of perennials means that they will inherently have lower seed yield (Smaje, 2015), the large competitive structures (e.g., large roots, tall stems) of wild perennials may simply provide a larger pool of resources to reallocate from competitive tissues into harvestable grain (DeHaan et al., 2005). Just because wild perennials allocate more resources on average to competition than seed production, there is no reason to believe that the same must hold true for domesticated perennials (Crews and DeHaan, 2015). The important unanswered question is to what extent can the benefits of perennial cropping be retained while selecting for increased yield, but thus far results are promising (Emmerling et al., 2017; McGowan et al., 2019).

The clearest arguments against investment in perennial grain breeding have focused on theories of resource allocation. One critic has summarized the position, stating, “For seed yields to approach those of annuals, however, plants would have to pull all available resources into seed production at the end of the growing season, as annuals do, making death almost certain” (Denison, 2012). We would suggest that this argument is only valid if “all things are equal” in comparing annuals to perennials. However, all things are not equal. Perennials often have more rapid spring growth and a longer growing season, allowing access to more sunlight (Dohleman and Long, 2009); they may also have longer roots, allowing access to more water and nutrients (Duchene et al., 2020). Indeed, the success described above with perennial rice illustrates that perennial survival with high grain yield has now been achieved, clearly contradicting the claim that high yielding perennials would be faced with “almost certain” death (Denison, 2012) due to a strict trade-off between survival and yield. Further evidence is seen in the perennial grass crop *Miscanthus*, which can yield more aboveground biomass than maize in the Midwest US corn belt (Dohleman, 2009; Heaton et al., 2008), showing that winter survival need not come at the cost of aboveground production.

3.2 High yielding perennials are evidence of what is possible

Smaje has argued that the lack of any successful perennial grain crops arising over the 10,000 years of agriculture suggests that such crops may be impossible (Smaje, 2015). But he then goes on to state that "Nevertheless if sophisticated modern plant breeding techniques can overcome the obstacles hitherto obstructing a perennial grain agriculture, past impediments may lack future relevance" (Smaje, 2015). We agree with this assessment and observe that concerns about the feasibility of high-yielding perennial grains is quickly becoming a historical artifact rather than a contestable hypothesis, as evidenced by the breeding technologies that produced high yielding perennial rice (Zhang et al., 2022) and are now advancing other perennial grains in development.

While perennial rice provides a recent example of a high-yielding perennial, advocates of perennial grains have previously argued that trees with higher reproductive allocation than modern annual grains are evidence that perenniality need not preclude high yields (Van Tassel et al., 2010). However, critics have discounted the high productivity of woody perennials as a "special case" where the yield of trees is irrelevant to high-yield perennial herbs because trees have unique "ecological and biogeographical characteristics" (Smaje, 2015). Since all individual species have unique ecological and biogeographical characteristics, a similar statement could be applied to dismiss the relevance of perennial rice. Indeed, Kenneth Cassman stated in an interview that perennial rice is a special case, since annual rice already ratoons, and rice production has a high labour requirement (Charles, 2022). Ironically, while some detractors have argued that breeding perennial rice developed for the high-yield paddy system took the easy route (Loomis, 2022) and is therefore a less important achievement, other critics have said that breeding perennials for more stressful, lower-yielding environments would be the easiest approach (Cassman and Connor, 2022). Although critics may continue attempting to dismiss the existence of high-yielding fruit trees or perennial rice as irrelevant to the debate, we maintain that these achievements demonstrate that artificial selection can generate perennial crops with high reproductive outputs and are justification for expanding efforts to develop additional highly productive perennial crops (Van Tassel et al., 2010).

3.3 Breeding is increasing yields of intermediate wheatgrass

Efforts to improve the grain yield of perennial intermediate wheatgrass have been ongoing since the 1980s (DeHaan et al., 2018), although until 2010, the project had a small investment, with less than half the effort of a single plant breeder provided each year. Since this is likely the longest-running effort to directly domesticate a wild perennial herbaceous species for use as a grain crop, it is worth asking whether progress is being made. Cassman and Connor (2022) claim to answer this question in the negative. Unfortunately, the methods they used to evaluate progress were unsuitable, leaving their conclusions without merit. Cassman and Connor (2022) compiled a summary in table form of yields obtained in six agronomic trials of intermediate wheatgrass conducted between 2009 and 2018. The trials were performed in four different northern USA states using seed from four different breeding cycles from a program in Kansas. From this assembled data, they concluded, “Based on analysis of these results, there is no evidence of progress towards higher grain yields” (Cassman and Connor, 2022).

There are three primary reasons that the table presented by Cassman and Connor (2022) is insufficient to quantify genetic progress. First, the concept of randomization, which is fundamental to statistical analysis, was ignored. Fisher, a founder of the field of statistics, stressed that “as is the randomization, so is the analysis” (Street, 1990). In this case, because breeding cycles were not randomized across locations, years, or management approaches, there would be no way of evaluating breeding progress without accounting for a host of unknown confounding variables. Secondly, one cannot hope to draw meaningful conclusions about breeding progress from such a small sample size. Before concluding that no evidence of an effect exists in an experiment, the scientist must be cognizant of the risk of Type II error (wrongfully failing to reject the null hypothesis). Failing to account for the sample size necessary to obtain relevant statistical power has been described as a “fatal” error in statistical analysis (Kuzon et al., 1996). Third, the reality of genotype X environment interactions (GXE) has been neglected. The agronomic trials cited were situated between 800 and 1700 km distant from the location of the breeding program that developed the genetic materials used. Complex traits such as grain yield usually have high GXE, so meaningful evaluation of progress for this trait requires experimentation within the target environment. Testing for progress in a non-target environment ignores what is known about the substantial magnitude of GXE in related crops such as wheat (Peterson, 1992).

Intermediate wheatgrass has a history of rapid response to selection, and new genetic and genomic technologies now present opportunities for accelerated grains. Although Cassman and Connor stated that “there is no evidence of progress toward higher [intermediate wheatgrass] grain yields,” one of the papers they cited contains strong evidence of breeding progress in intermediate wheatgrass (Bajgain et al., 2020; Cassman and Connor, 2022). The intermediate wheatgrass variety MN-Clearwater was developed in Minnesota, USA for improved grain production by selecting out of the third breeding cycle from The Land Institute. Evaluated across five locations and two years, this single round of selection in the Minnesota environment increased yield by 230 kg ha^{-1}, or 49% (Bajgain et al., 2020). Other studies of breeding progress conducted in Kansas as part of The Land Institute’s breeding program have shown increases of 150 kg ha^{-1} over two cycles (DeHaan et al., 2014) and 68 kg ha^{-1} $cycle^{-1}$ over five cycles (Tyl et al., 2020). In Canada, breeding produced a steady yield increase of 79 kg ha^{-1} $cycle^{-1}$ over five cycles (Knowles, 1977). When evaluated with a proper statistical design, intermediate wheatgrass breeding programs have consistently produced substantial yield increases, surpassing progress in modern wheat breeding on an annual basis (Rife et al., 2019).

While traditional breeding is producing substantial yield increases in intermediate wheatgrass, new techniques and knowledge of genes controlling domestication traits paired with genome editing are opening doors to breakthroughs in rapid domestication (Lemmon et al., 2018; Li et al., 2018; Yu and Li, 2022; Zhu and Zhu, 2021). In recent years, development of genetic resources has made genome editing (Chapman et al., 2022; DeHaan et al., 2020) for rapid domestication of intermediate wheatgrass feasible. Genomic selection can accelerate breeding in perennials by accurately predicting performance of plants using DNA collected at the seedling stage (McClure et al., 2014; Seyum et al., 2022). This technique is being used to accelerate progress in the domestication of intermediate wheatgrass (Crain et al., 2021) and holds promise for many perennial species. These new methods have potential to accelerate domestication and produce viable new crops in just a decade or two, opening fresh doors of opportunity for developing transformative new crops (Runck et al., 2014).

3.4 New approaches to perennial wheat

As efforts to develop perennial wheat by hybridizing annual wheat with perennial relatives have been attempted on and off for nearly a century, it is worth asking whether this approach to perennial grain development still has merit. Cassman and Connor (2022) summarized work on perennial wheat in Australia, and correctly concluded that "Progress in conducting agronomic research with perennial wheat derivatives in Australia is hindered because no commercial cultivars are yet available…" What was left unmentioned was that virtually no breeding efforts have been undertaken in Australia to develop adapted cultivars (Hayes et al., 2017). This is consistent with a fundamental conclusion of Cassman and Connor: perennial grains have yet to succeed due to "inadequate investment in R&D relative to the magnitude of the challenge" (Cassman and Connor, 2022).

As a wide hybridization effort in an allopolyploid crop, perennial wheat is expected to have a different development trajectory in comparison to simpler introgression projects with diploids such as rice or domestication projects such as intermediate wheatgrass. While breeding is producing steady increases in yield of intermediate wheatgrass, wide hybridization may not produce similar stepwise improvements if the wide hybrids require breakthrough solutions to make them viable.

Perennial rice and now perennial sorghum breeding programs (Cox et al., 2018) have the benefit of recombination between corresponding chromosomes originating from the annual and perennial parents. In wheat, the annual and perennial parents have diverged to the point where chromosomes do not readily pair (Banks et al., 1993). Presumably, chromosomes originating from wheat carry genes that are detrimental to perenniality, while chromosomes from the perennial parent harbor genes limiting critical traits such as seed size (Cox et al., 2002, 2010). Thus, past programs may have been able to obtain plants with moderate perenniality and moderate yield, but without recombination, they have been unable to make much additional progress.

In their 2002 review, Cox et al. suggested that the task of developing perennial wheat could be nearly impossible until new molecular techniques were available (Cox et al., 2002). This idea is proving prophetic, as the necessary tools may now be available for the first time. For example, tracking individual chromosomes and chromosome fragments by cytology was once cost- and time-prohibitive for use in breeding. Now, sequence-based methods can track chromosome presence and absence in wide hybrids at low cost (Adhikari et al., 2022). A reference genome is now available for the perennial parent currently used in perennial wheat hybrids, and with this resource, genome editing could be used to knock out or otherwise edit genes impacting important traits in the hybrids, eliminating the need for genetic recombination (DeHaan et al., 2020; Soto- Gómez et al., 2022). Alternatively, mutagenesis followed by genotyping to search for mutations in critical target genes could be effective (Knudsen et al., 2022). With aggressive application of these tools, a breakthrough in perennial wheat may be imminent.

4. Breeding grain crops for a sustainable future

Perennial grains have been long recognized as having the potential to produce directly edible calories from plants that could be grown without regular soil disturbance and replanting, enabling a trajectory change in sustainable intensification (Pimentel et al., 2012). However, the idea has struggled to gain traction as small efforts with various species have come and gone. Lack of a clear success story and lingering theoretical questions about the biological feasibility of plants with longer lifespans and high seed yields has led some to question the wisdom of continued investment of resources in the effort to develop perennial grains.

Recent successes in breeding and genetics have now demonstrated the feasibility of perennial grain development. Perennial rice, which has produced yields equivalent to annual rice over eight harvests while improving ecosystem services and producer livelihoods, has shown how a perennial grain can create the triple win of food production, profitability, and sustainability. Theoretical concerns about the potential for perennials to produce competitive yields have begun to fade in the face of this clear achievement. Similarly, the application of modern genetic tools including genome sequencing, genomic selection, and genome editing to the domestication of perennial crops is demonstrating transformative the ability to rapidly develop and introduce new perennial crops (Runck et al., 2014). If these and other revolutionary technologies are applied aggressively to the basic biology of perenniality (Chapman et al., 2022; Li et al., 2022) and the creation of new crops, they will be available in time to provide meaningful benefits to such grand challenges as soil quality and carbon sequestration to combat climate change and its impacts on food production (Crews and Rumsey, 2017). The critical need for the ecosystem services of new perennial crops grown in multifunctional landscapes (Jordan et al., 2007) has converged with the technological capacity to develop these crops, so now is the ideal moment to aggressively expand perennial grain research.

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Declaration of competing interest

Declaration of interests

☒ The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: