



HAL
open science

Discussion: Prioritize perennial grain development for sustainable food production and environmental benefits

Lee R Dehaan, James A Anderson, Prabin Bajgain, Andrea Basche, Douglas J Cattani, Jared Crain, Timothy E Crews, Christophe David, Olivier Duchene, Jessica Gutknecht, et al.

► To cite this version:

Lee R Dehaan, James A Anderson, Prabin Bajgain, Andrea Basche, Douglas J Cattani, et al.. Discussion: Prioritize perennial grain development for sustainable food production and environmental benefits. *Science of the Total Environment*, 2023, 895, pp.164975. 10.1016/j.scitotenv.2023.164975 . hal-04145160

HAL Id: hal-04145160

<https://isara.hal.science/hal-04145160v1>

Submitted on 28 Jun 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Journal Pre-proof

Discussion: Prioritize perennial grain development for sustainable food production and environmental benefits

Lee R. DeHaan, James A. Anderson, Prabin Bajgain, Andrea Basche, Douglas J. Cattani, Jared Crain, Timothy E. Crews, Christophe David, Olivier Duchene, Jessica Gutknecht, Richard C. Hayes, Fengyi Hu, Jacob M. Jungers, Søren Knudsen, Wenqian Kong, Steve Larson, Per-Olof Lundquist, Guangbin Luo, Allison J. Miller, Pheonah Nabukalu, Matthew T. Newell, Lennart Olsson, Michael Palmgren, Andrew H. Paterson, Valentin D. Picasso, Jesse A. Poland, Erik J. Sacks, Shuwen Wang, Anna Westerbergh



PII: S0048-9697(23)03598-2

DOI: <https://doi.org/10.1016/j.scitotenv.2023.164975>

Reference: STOTEN 164975

To appear in: *Science of the Total Environment*

Received date: 2 March 2023

Revised date: 2 June 2023

Accepted date: 15 June 2023

Please cite this article as: L.R. DeHaan, J.A. Anderson, P. Bajgain, et al., Discussion: Prioritize perennial grain development for sustainable food production and environmental benefits, *Science of the Total Environment* (2023), <https://doi.org/10.1016/j.scitotenv.2023.164975>

This is a PDF file of an article that has undergone enhancements after acceptance, such as the addition of a cover page and metadata, and formatting for readability, but it is not yet the definitive version of record. This version will undergo additional copyediting, typesetting and review before it is published in its final form, but we are providing this version to give early visibility of the article. Please note that, during the production process, errors may be discovered which could affect the content, and all legal disclaimers that apply to the journal pertain.

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^f, Christophe David^f, Olivier Duchene^f, Jessica Gutknecht^g, Richard C. Hayes^h, Fengyi Huⁱ, Jacob M. Jungers^b, Søren Knudsen^j, Wenqian Kong^k, Steve Larson^l, Per-Olof Lundquist^m, Guangbin Luoⁿ, Allison J. Miller^o, Pheonah Nabukalu^p, Matthew T. Newell^q, Lennart Olsson^r, Michael Palmgrenⁿ, Andrew H. Paterson^k, Valentin D. Picasso^s, Jesse A. Poland^t, Erik J. Sacks^u, Shuwen Wang^a, and Anna Westerbergh^m

^aThe Land Institute, 2440 E. Water Well Rd, Salina, Kansas, USA 67401

^bDepartment of Agronomy and Plant Genetics, University of Minnesota, 1991 Upper Buford Circle, St. Paul, MN, USA 55108

^cDepartment of Agronomy and Horticulture, University of Nebraska-Lincoln, 1875 N. 38th St, 279 PLSH, Lincoln, NE, USA 68583-0915

^dDepartment of Plant Science, University of Manitoba, 66 Dafoe Rd, Winnipeg, MB, Canada R3T 2N2

^eDepartment of Plant Pathology, Kansas State University, 1712 Claflin Rd, 4024 Throckmorton PSC, Manhattan, KS, USA 66506

^fISARA, Agroecology and Environment Research Unit, 23 rue Jean Baldassini, 69364 Lyon, France

^gDepartment of Soil, Water, and Climate, University of Minnesota, 1991 Upper Buford Cir, Falcon Heights, MN, USA 55108

^hNSW Department of Primary Industries, Wagga Wagga Agricultural Institute, 322 Pine Gully Rd, NSW 2795, Australia

ⁱState 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

^jCarlsberg Research Laboratory, J. C. Jacobsens Gade 4, 1799, 1778, Copenhagen, Denmark

^kUniversity of Georgia, Athens, USA

^lUSDA-ARS, Forage and Range Research, 696 North 1100 East, Logan, Utah, USA 84321

^mDepartment of Plant Biology, Uppsala BioCenter, Linnean Center for Plant Biology in Uppsala, Swedish University of Agricultural Sciences, Box 7080, 750 07, Uppsala, Sweden

ⁿDepartment of Plant and Environmental Sciences, University of Copenhagen, Denmark

^oSaint Louis University and Donald Danforth Plant Science Center, 975 N Warson Rd, Olivette, MO, USA 63132

^pNESPAL, University of Georgia, 2356 Rainwater Rd, Tifton, Georgia, USA 31793

^qNSW Department of Primary Industries, Cowra Agricultural Research Station, 296 Binni Creek, Cowra NSW 2794, Australia

[†]Lund University Centre for Sustainability Studies, P.O. Box 170, SE-221 Lund, Sweden

[§]University of Wisconsin-Madison, USA.

[‡]King Abdullah University of Science and Technology, Thuwal 23955, Saudi Arabia

[¶]University of Illinois at Urbana-Champaign, USA

*Correspondence: dehaan@landinstitute.org, The Land Institute, 2440 E. Water Well Rd, Salina, Kansas, USA 67401

Journal Pre-proof

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 we argue these may be mitigated by implementation of recent technological advances in crop breeding and genetics such as low-cost genotyping, genomic selection, and genome editing. With aggressive research investment in the development of new perennial grain crops, they can be developed and deployed to provide atmospheric greenhouse gas reductions.

Keywords: soil quality, climate change, carbon sequestration, genome editing, intermediate wheatgrass, 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, the first extensive review of past efforts to develop perennial grains using species in the grass family was published (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 profits 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 1920s. 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 favorable alleles in new high-yielding perennial grains.

In the 20 years following the 2002 review by 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 (Craham 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 relatively 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 and future decades.

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 F₂ 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 ha⁻¹ harvest⁻¹, similar to the yield of replanted annual rice, which is also harvested twice per year (Zhang et al., 2022). After the first season, perennial rice resulted in substantial savings on labor and other inputs, which boosted net 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).

Since its release to farmers in 2018, farmer acceptance has been strong, and perennial rice cultivation is increasing rapidly. Although still less than 0.1% of the area of total rice production in China, 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 grain feasibility

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 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 Alleviating concerns about the yield potential of perennials

The feasibility of breeding herbaceous perennial plants with high grain yield has been understandably questioned, since on average both wild and domestic herbaceous perennial plants tend to have lower seed production 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 favoring 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 (Smaile, 2015), the large competitive structures (e.g., large roots, tall stems) of wild perennials may simply provide a larger pool of resources from which to reallocate 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 evidence of increased soil carbon and improved soil quality under perennial crops selected for maximum above ground yield is 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 and Long, 2009; Heaton et al., 2008), showing that winter survival need not come at the cost of aboveground production.

3.2 Other perennial grains are being developed to follow the success of perennial rice

Smaje (2015) 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. 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, past critics discounted the high productivity of woody perennials as a “special case” where the yield of trees is irrelevant to high-yield perennials 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 labor requirement (Charles, 2022). We would respond by pointing out that there are other perennial grain candidates, such as perennial sorghum, where the annual progenitor also ratoons. All perennial crops in development have unique advantages that may make them special cases in various ways, such as current use as forage crops or valuable by-products such as honey or fiber. With every candidate crop having unique advantages, we cannot confidently predict which will be easiest to achieve, and we contend that the best way to determine which crops are feasible to develop is to attempt

many projects at once (DeHaan et al., 2016). 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).

Just as all annual grain crops have unique advantages and disadvantages in terms of growing environment and end uses, there is an array of perennial grain crops currently under various stages of development for a variety of initial target environments and uses. Every crop in the making faces a unique set of challenges and presents distinct advantages. As mentioned above, perennial grain sorghum has the same advantage as perennial rice, where the annual parent (*Sorghum bicolor*) was able to ratoon, but the hybrids with perennial *Sorghum halepense* have thus far lacked strong winter hardiness in the temperate environment (Cox et al, 2018). Following the model of perennial rice, perennial sorghum lines are now being introduced to tropical environments, but years of work remain to integrate the perennial habit with locally adapted germplasm. Perennial silflower (*Silphium integrifolium*) is being developed by domesticating a forb native to the USA. While this species has large seeds and high yield for a wild plant, insect pests and diseases present in its native range have presented a unique challenge for the breeding program (Price et al., 2022). Sainfoin (*Onobrychus viciifolia*) is a forage legume that is just beginning domestication at The Land Institute. Its seeds are quite large, and yields are already substantial in dry regions, but thorough testing of the grain must be completed to determine if it is safe for human consumption. Perennial flax domestication is starting with perennial species of *Linum*. Although the perennial species grow vigorously in the target environment, improvement through breeding must be made for a wide array of traits, including growth form, seed size, germination, and early maturity (Tork et al., 2019). Perennial barley development is a possibility either through wide hybridization between annual barley (*Hordeum vulgare*) and the perennial *Hordeum bulbosum* or through direct domestication of the perennial. While the wide hybridization approach has been difficult due to low recombination between the annual and perennial chromosomes, direct domestication of *H. bulbosum* is now a real possibility due to the detailed genomic information which is available for barley (Chapman et al., 2022). With knowledge of the genetic control of

the critical domestication traits of barley, analogous changes in the wild perennial might be rapidly induced by mutagenesis or genome editing.

3.3 *Breeding is increasing yields of intermediate wheatgrass*

Efforts to improve the grain yield of perennial intermediate wheatgrass (*Thinopyrum intermedium*) 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 project 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. 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. Never was the seed from more than one breeding cycle planted in a given trial. From this assembled data, they concluded, “Based on an analysis of these results, there is no evidence of progress towards higher grain yields” (Cassman and Connor, 2022). No details regarding the methods of their analysis are presented, and the data which they analyzed was irrelevant to the question of yield progress, leaving their conclusions without merit.

There are three primary reasons that the data used by Cassman and Connor (2022) were 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). High GXE for traits such as grain yield across distances of 1000 km is expected, but fortunately not an insurmountable barrier for breeding. The clear solution is to, as in annual crops, have regional breeding programs which develop locally adapted varieties. Indeed, in the case of intermediate wheatgrass, three geographically diverse breeding programs are now in operation.

Intermediate wheatgrass has a history of remarkably rapid response to selection. 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). On a percentage basis, the yield gains have been roughly 20 to 30% per cycle, with cycle length varying from 2 to 4 years, for an average progress of about 10% per year.

While a young breeding program for a crop with initially low yields is expected to make large percentage gains, yield increases from selection are often linear. Thus, future gains should only be roughly extrapolated from past gains in terms of yield per area, rather than as percentage increases. Yield on an area basis in the trials mentioned above was increasing about 23 kg ha⁻¹ year⁻¹. For wheat varieties released in the USA Southern Plains between 1992 and 2014, yield increase was 1.1% year⁻¹, or 17 kg ha⁻¹ year⁻¹ (Rife et al., 2019). Thus, we see that when evaluated with a proper statistical design, even the earliest intermediate wheatgrass selection programs with meager resources were exceeding wheat breeding

progress on a percentage basis and at least matching it in terms of absolute yield increase per year. Using modern genomic selection to perform one cycle per year could increase yield progress to 58 kg ha⁻¹ year⁻¹, if current trends continue (Bajgain et al. 2022).

While traditional breeding produced 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 for rapid domestication of intermediate wheatgrass feasible (Chapman et al., 2022; DeHaan et al., 2020). 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 (Cain 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 (*Triticum aestivum*) 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. Opportunities and Risks

While new perennial grain crops could aid in addressing the greatest environmental challenge of our time, climate change, the protracted nature of the work required to breed the crops, formulate productive cropping systems, and study the potential risks and benefits inherent in the production of perennial grain

crops means that sustained upfront investment will be required before positive outcomes are achieved.

Therefore, concurrent with the breeding of new perennial grain crops, experimental testing of the potential benefits of perennial grain cropping systems is underway, producing promising results thus far, while some uncertainties remain.

Research results currently support the capacity for perennial grains to substantially increase soil carbon, which would reduce atmospheric carbon dioxide while simultaneously enhancing soil quality (Crews and Rumsey, 2017). Increases in soil carbon storage under perennial cropping is driven by two mechanisms: reducing the regular disturbances, which exacerbate mineralization losses, that are associated with annual crop establishment (Crews et al., 2016) while simultaneously increasing carbon input through the potentially larger biomass production of perennial crops (Newell and Hayes, 2017) and increased belowground allocation (Sprunger et al., 2019). Soil carbon accumulation under perennial cropping has been found to improve soil health parameters, including greater microbial biomass and respiration (Means et al., 2022), greater microbial abundance and mycorrhizae indicators (Duchene et al., 2020), N mineralization (McKenna et al., 2020), and increased particulate carbon accumulation (van der Pol et al., 2022). Furthermore, perennial cover will generally result in reduced soil erosion and greater climate resilience through increased water infiltration and storage (Asbjornsen et al., 2014). However, many properties are expected to be sensitive to management and may vary according to crop species. Transitions between various perennial crops, which may involve soil disturbance, may be particularly critical points where the benefits of perennial cropping could be compromised (Ryan et al., 2018).

Perennial grain cropping has significant potential to reduce emissions of nitrous oxide from production fields. The perennial grain intermediate wheatgrass has been shown to consistently reduce both soil moisture and nitrate pools (Culman et al. 2013; Jungers et al., 2019; Reilly et al., 2022), which are two primary drivers of nitrous oxide emissions. While there are theoretical reasons to anticipate reduced emissions of nitrous oxide from perennial crop fields, variation is expected and optimal crop management schemes will be necessary to maximize the benefits, as has been observed in the more extensively studied perennial biofuel crops (Bai et al., 2022).

The potential impact of perennial grains on the potent greenhouse gas methane is uncertain, although there have been some intriguing results. Because unsaturated upland soils have capacity to remove methane from the atmosphere, deeply rooted perennial grain crops which can dry the soil at depth have been observed to increase the methane sink capacity of fields in comparison to annual grains (Kim, et al., 2021). Perennial rice makes possible a range of no-till and flooding management regimes, (Zhang et al., 2022) so the crop could potentially reduce methane emissions. However, some intermittent flooding techniques have led to dramatic increases in nitrous oxide emissions (Kritee et al., 2018). Clearly, more research is needed to develop management approaches for diverse perennial grain cropping systems to enable consistent greenhouse gas reductions.

New crops inherently come with new risks. While perennial rice can be sold directly into conventional markets, many perennial grain crops in development will be treated as novel foodstuffs, requiring development of new supply chains and unique consumer products. The commercial success of a new crop often requires the coordination of dozens of factors, including items such as quality seed, weed control methods, appropriate field equipment, access to processing facilities, and expertise for every step from seed handling to harvest and recipe formulation (Jolliff and Snapp, 1988). Failure in any critical factor will jeopardize the success of the new crop. Perennial grain crops may carry some unique risks, such as the challenge of managing pests and disease without the simple techniques of annual tillage and crop rotation (Cox et al., 2005). However, these risks may be offset by unique advantages, such as greater inherent pest and disease resistance (Glover et al., 2010), savings on costs to manage a crop that does not require annual planting, and reduced risk of establishment failure when the crop is regenerating from overwintering structures.

For a new crop to succeed, a substantial societal investment in breeding, agronomic research, and early supply chain coordination is essential. A primary risk is that critical components for the success of the new crop will not be available. To achieve success, commercialization and plant breeding efforts must be coordinated to develop strategically diversified production systems and supply chains (Runck et al., 2014). Thus, the greatest threat to the effort is the ebb and flow of funding cycles and market interest in diverse

products with ecological benefits. The antidote to this risk will be sustained commitment from funders to strategically support the multifaceted effort to develop new crops over a timeframe of more than a decade.

5. Conclusions

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 such as genome resequencing, genomic selection, and genome editing to the development of perennial crops is demonstrating the ability to rapidly develop and introduce new perennial crops, (Runck et al., 2014) often waiting only on funding to accelerate the work. 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.

References

- Adhikari, L.; Shrestha, S.; Wu, S.; Crain, J.; Gao, L.; Evers, B.; Wilson, D.; Ju, Y.; Koo, D.H.; Hucl, P.; Pozniak, C.; et al. A high-throughput skim-sequencing approach for genotyping, dosage estimation and identifying translocations. *Scientific Reports* 2022, 12, <https://doi.org/10.1038/s41598-022-19858-2>.
- Asbjornsen, H.; Hernandez-Santana, V.; Liebman, M.; Bayala, J.; Chen, J.; Helmers, M.; Ong, C.K.; Schulte, L.A. Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services 2014, 29, 101-125, <https://doi.org/10.1017/S1742170512000385>.

- Bai, J.; Luo, L.; Aixin, L.; Lai, X.; Zhang, X.; Yu, Y.; Wang, H.; Wu, N.; Zhang, L. Effects of biofuel crop switchgrass (*Panicum virgatum*) cultivation on soil carbon sequestration and greenhouse gas emissions: A review, *Life* 2022, 12, 2105, <https://doi.org/10.3390/life12122105>.
- Bajgain, P.; Zhang, X.; Jungers, J.M.; DeHaan, L.R.; Heim, B.; Sheaffer, C.C.; Wyse, D.L.; Anderson, J.A. 'MN-Clearwater', the first food-grade intermediate wheatgrass (*Kernza* perennial grain) cultivar. *Journal of Plant Registrations* 2020, 14, 288-297, <https://doi.org/10.1002/plr2.20042>.
- Banks, P.M.; Xu, S.J.; Wang, R.C.; Larkin, P.J. Varying chromosome composition of 56-chromosome wheat × *Thinopyrum intermedium* partial amphiploids. *Genome* 1993, 36, 207-215, <https://doi.org/10.1139/g93-029>.
- Broussard, W.; Turner, R.E. A century of changing land-use and water quality relationships in the continental US. *Frontiers in Ecology and the Environment* 2009, 7, 302-307, <https://doi.org/10.1890/080085>.
- Cacho, J.F.; Negri, M.C.; Zumpf, C.R.; Campbell, P. Introducing perennial biomass crops into agricultural landscapes to address water quality challenges and provide other environmental services. *Wiley Interdisciplinary Reviews: Energy and Environment* 2018, 7, e275, <https://doi.org/10.1002/wene.275>.
- Cassman, K.G.; Connor, D.J. Progress Towards Perennial Grains for Prairies and Plains. *Outlook on Agriculture* 2022, 51, 32-38, <https://doi.org/10.1177/00307270211073153>.
- Chapman, E.A.; Thomsen, H.C.; Tulloch, S.; Correia, P.M.; Luo, G.; Najafi, J.; DeHaan, L.R.; Crews, T.E.; Olsson, L.; Lundquist, P.O.; Westerbergh, A. Pedas, P.R.; Knudsen, K.; Palmgren, M. Perennials as future grain crops: opportunities and challenges. *Frontiers in Plant Science* 2022, 13, <https://doi.org/10.3389/fpls.2022.898769>.
- Charles, D. Could this Cheaper, More Climate-friendly Perennial Rice Transform Farming? NPR 2022, <https://www.npr.org/sections/goatsandsoda/2022/11/07/1134796649/could-this-cheaper-more-climate-friendly-perennial-rice-transform-farming> (accessed on 8 Dec. 2022).
- Cox, C.M.; Garrett, K.A.; Bockus, W.W. Meeting the challenge of disease management in perennial grain cropping systems. *Renewable Agriculture and Food Systems* 2005, 20, 15-24, <https://doi.org/10.1079/RAF200495>.

- Cox, S.; Nabukalu, P.; Paterson, A.H.; Kong, W.; Auckland, S.; Rainville, L.; Cox, S.; Wang, S. High proportion of diploid hybrids produced by interspecific diploid× tetraploid Sorghum hybridization. *Genetic Resources and Crop Evolution*, 2018, 65, 387-390, <https://doi.org/10.1007/s10722-017-0580-7>.
- Cox, T.S.; Bender, M.; Picone, C.; Van Tassel, D.; Holland, J.B.; Brummer, E.C.; Zoeller, B.E.; Paterson, A.H.; Jackson, W. Breeding perennial grain crops. *Critical Reviews in Plant Sciences* 2002, 21, 59-91, <https://doi.org/10.1080/0735-260291044188>.
- Cox, T.S.; Van Tassel, D.L.; Cox, C.M.; DeHaan, L.R. Progress in breeding perennial grains. *Crop and Pasture Science* 2010, 61, 513-521, <https://doi.org/10.1071/CP10201>.
- Crain, J.; DeHaan, L.; Poland, J. Genomic prediction enables rapid selection of high-performing genets in an intermediate wheatgrass breeding program. *The Plant Genome*, 2021, 14, <https://doi.org/10.1002/tpg2.20080>.
- Crews, T.E.; Blesh, J.; Culman, S.W., Hayes, R.C.; Jansen, E.S.; Mack, M.C.; Peoples, M.B.; Schipanski, M.E. Going where no grains have gone before: From early to mid-succession. *Agriculture, Ecosystems & Environment* 2016, 223, 223-238, <https://dx.doi.org/10.1016/j.agee.2016.03.012>.
- Crews, T.E.; DeHaan, L.R. The strong perennial vision: A response. *Agroecology and Sustainable Food Systems* 2015, 39, 500-515, <https://doi.org/10.1080/21683565.2015.1008777>.
- Crews, T.E.; Rumsey, B.E. What agriculture can learn from native ecosystems in building soil organic matter: A review. *Sustainability* 2017, 9, 578, <https://doi.org/10.3390/su9040578>.
- Culman, S.W.; Snapp, S.S.; Olenburger, M.; Basso, B.; DeHaan, L.R., et al. Soil and water quality rapidly responds to the perennial grain Kernza wheatgrass. *Agronomy Journal* 2013, 105, 735-744, <https://doi.org/10.2134/agronj2012.0273>.
- Daigh, A.L. Bioenergy cropping systems effects on soil quality. *Soil Survey Horizons* 2011, 52, 31-34, <https://doi.org/10.2136/sh2011.2.0031>.
- DeHaan, L.; Christians, M.; Crain, J.; Poland, J. Development and evolution of an intermediate wheatgrass domestication program. *Sustainability* 2018, 10, <https://doi.org/10.3390/su10051499>.

- DeHaan, L.; Larson, S.; López-Marqués, R.L.; Wenkel, S.; Gao, C.; Palmgren, M. Roadmap for accelerated domestication of an emerging perennial grain crop. *Trends in Plant Science*, 2020, 25, 525-537, <https://doi.org/10.1016/j.tplants.2020.02.004>.
- DeHaan, L.R.; Van Tassel, D.L. Gourmet grasslands: Harvesting a perennial future. *One Earth* 2022, 14-17, <https://doi.org/10.1016/j.oneear.2021.12.012>.
- DeHaan, L.R.; Van Tassel, D.L.; Anderson, J.A.; Asselin, S.R.; Barnes, R.; Baute, G.J.; Cattani, D.J.; Culman, S.W.; Dorn, K.M.; Hulke, B.S.; Kantar, M.; Larson, S.; Marks, M.D.; Miller, A.J.; Poland, J.; Ravetta, D.A.; Rude, E.; Ryan, M.; Wyse, D.; Zhang, X. A pipeline strategy for grain crop domestication. *Crop Science* 2016, 56, 917-930, <https://doi.org/10.2135/cropsci2015.06.0356>.
- DeHaan, L.R.; Van Tassel, D.L.; Cox, T.S. Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems* 2005, 20, 5-14, <https://doi.org/10.1079/RAF200496>.
- DeHaan, L.R.; Wang, S.; Larsen, S.R.; Cattani, D.J.; Zhang, X.; Kantarski, T. Current efforts to develop perennial wheat and domesticate *Thinopyrum intermedium* as a perennial grain. In: *Perennial Crops for Food Security: Proceedings of the Food and Agriculture Organization of the United Nations [FAO] Expert Workshop*; Batello, C.; Wade, L.; Cox, S.; Pogna, N.; Bozzni, A.; Choptiany, J., Eds.; FAO: Rome, Italy, 2014; pp. 72-89.
- Denison, R.F. *Darwinian Agriculture: How Understanding Evolution Can Improve Agriculture*; 2012, Princeton University Press: Princeton, USA; pp. 97-101.
- Denison, R.F. Evolutionary tradeoffs as opportunities to improve yield potential. *Field Crops Research* 2015, 182, 3-8, <https://doi.org/10.1016/j.fcr.2015.04.004>.
- Dohleman, F.G.; Long, S.P. More productive than maize in the Midwest: how does *Miscanthus* do it? *Plant Physiology* 2009, 150, 2104-2115, <https://doi.org/10.1104/pp.109.139162>.
- Duchene, O.; Celette, F.; Barreiro, A.; Dimitrova Mårtensson, L.M.; Freschet, G.T.; David, C. Introducing perennial grain in grain crops rotation: the role of rooting pattern in soil quality management. *Agronomy*, 2020, 10, 1254, <https://doi.org/10.3390/agronomy10091254>.
- Duvick, D.N. Genetic progress in yield of United States maize (*Zea mays* L.) *Maydica* 2005, 50, 193-202.

- Emmerling, C.; Schmidt, A.; Ruf, T.; von Francken-Welz, H.; Thielen, S. Impact of newly introduced perennial bioenergy crops on soil quality parameters at three different locations in W-Germany. *Journal of Plant Nutrition and Soil Science* 2017, 180, 759-767, <https://doi.org/10.1002/jpln.201700162>.
- Glover, J. Newer roots for agriculture. *Nature Sustainability* 2022, 6, 5-6, <https://doi.org/10.1038/s41893-022-01019-y>.
- Glover, J.D.; Reganold, J.P.; Bell, L.W.; Borevitz, J.; Brummer, E.C.; Buckler, E.S.; Cox, C.M.; Cox, T.S.; Crews, T.E.; Culman, S.W.; DeHaan, L.R.; et al. Increased food and ecosystem security via perennial grains. *Science* 2010, 328, 1638-1639, <https://doi.org/10.1126/science.1188761>.
- Graham, J.B.; Nassauer, J.I.; Currie, W.S.; Ssegane, H.; Negri, M.C. Assessing wild bees in perennial bioenergy landscapes: effects of bioenergy crop composition, landscape configuration, and bioenergy crop area. *Landscape Ecology* 2017, 32, 1023-1037, <https://doi.org/10.1007/s10980-017-0506-y>.
- Hayes R.C.; Newell, M.T.; Larkin, P.J.; Bell, L.W.; Llewellyn, R.S. Prospects for perennial grains in Australian farming systems. In: *Doing More with Less. Proceedings of the 18th Australian Society of Agronomy Conference, 24-28 September 2017. Ballarat, VIC, Australia.*
- Heaton, E.A.; Dohleman, F.G.; Long, J.P.; Meeting US biofuel goals with less land: the potential of *Miscanthus*. *Global Change Biology* 2008, 14, 2000-2014, <https://doi.org/10.1111/j.1365-2486.2008.01662.x>.
- Helms IV, J.A.; Ijelu, S.E.; Wells, B.D.; Landis, D.A.; Haddad, N.M. Ant biodiversity and ecosystem services in bioenergy landscapes. *Agriculture, Ecosystems & Environment* 2020, 290, 106780, <https://doi.org/10.1016/j.agee.2019.106780>.
- Jacot, J.; Williams, A.S.; Kiniry, J.R. Biofuel benefit or bummer? A review comparing environmental effects, economics, and feasibility of North American native perennial grass and traditional annual row crops when used for biofuel. *Agronomy* 2021, 11, 1440, <https://doi.org/10.3390/agronomy11071440>.
- Jolliff, G.D.; Snapp, S.S. New crop development: Opportunity and challenges. *Journal of Production Agriculture* 1988, 1, 83-89, <https://doi.org/10.2134/jpa1988.0083>.

- Jordan, N.; Boody, G.; Broussard, W.; Glover, J.D.; Keeney, D.; McCown, B.H.; McIsaac, G.; Muller, M.; Murray, H.; Neal, J.; Pansing, C. Sustainable development of the agricultural bio-economy. *Science* 2007, 316, 1570-1571, <https://doi.org/10.1126/science.1141700>.
- Jungers, J.M.; DeHaan, L.H.; Mulla, D.J.; Sheaffer, C.C.; Wyse, D.L. Reduced nitrate leaching in a perennial grain crop compared to maize in the Upper Midwest, USA. *Agriculture, Ecosystems & Environment* 2019, 272, 63-73, <https://doi.org/10.1016/j.agee.2018.11.007>.
- Kim, K.; Daly, E.J.; Hernandez-Ramirez, G.H. Perennial grain cropping enhances the soil methane sink in temperate agroecosystems. *Geoderma* 2021, 388, 114931, <https://doi.org/10.1016/j.geoderma.2021.114931>.
- Knowles, R.P. Recurrent mass selection for improved seed yields in intermediate wheatgrass. *Crop Science* 1977, 17, 51-54, <https://doi.org/10.2135/cropsci.1977.0011183X001700010015x>.
- Knudsen, S.; Wendt, T.; Dockter, C.; Thomsen, H.C.; Rasmussen, M.; Egevang Jørgensen, M.; Lu, Q.; Voss, C.; Murozuka, E.; Østerberg, J.T.; Harholt, C. et al. FIND-IT: Accelerated trait development for a green evolution. *Science Advances* 2022, 8, <https://doi.org/10.1126/sciadv.abq2266>.
- Kritee, K.; Drishya, N.; Zavala-Araiza, D.; Proville, J.; Rudek, J.; Adhya, T.K.; Loecke, T.; Esteves, T.; Balireddygari, S.; Dava, O.; Ram, K.; Anilash, S.R.; Madasamy, M.; Dokka, R.V.; Anandaraj, D.; Athiyaman, D.; Reddy, M.; Ahuja, R.; Hamburg, S.P. High nitrous oxide fluxes from rice indicate the need to manage water for both long- and short-term climate impacts. *Proc. Natl Acad. Sci. USA*, 2018, 115, 9720–9725 <http://doi.org/10.1073/pnas.1809276115>.
- Kuzon, W.; Urbanchek, M.; McCabe, S. The seven deadly sins of statistical analysis. *Annals of Plastic Surgery* 1996, 37, 265-272, <https://doi.org/10.1097/00000637-199609000-00006>.
- Lemmon, Z.H.; Reem, N.T.; Dalrymple, J.; Soyk, S.; Swartwood, K.E.; Rodriguez-Leal, D.; Van Eck, J.; Lippman, Z.B. Rapid improvement of domestication traits in an orphan crop by genome editing. *Nature Plants* 2018. 4, 766-770, <https://doi.org/10.1038/s41477-018-0259-x>.
- Li, T.; Yang, X.; Yu, Y.; Si, X.; Zhai, X.; Zhang, H.; Dong, W.; Gao, C.; Xu, C. Domestication of wild tomato is accelerated by genome editing. *Nature Biotechnology* 2018. 36, 1160-1163, <https://doi.org/10.1038/nbt.4273>.

- Li, Z.; Lathe, R.S.; Li, J.; He, H; Bhalerao, R.P. Towards understanding the biological foundations of perenniality. *Trends in Plant Science* 2022, 27, 56-68, <https://doi.org/10.1016/j.tplants.2021.08.007>.
- Loomis, R.S. Perils of production with perennial polycultures. *Outlook on Agriculture* 2022, 51, 22-31, <https://doi.org/10.1177/003072702110639>.
- McClure, K.A.; Sawler, J.; Gardner, K.M.; Money, D.; Myles, S. Genomics: a potential panacea for the perennial problem. *American Journal of Botany* 2014, 101, 1780-1790, <https://doi.org/10.3732/ajb.1400143>.
- McGowan, A.R.; Nicoloso, R.S.; Diop, H.E.; Roozeboom, K.L.; Rice, C.W. Soil organic carbon, aggregation, and microbial community structure in annual and perennial biofuel crops. *Agronomy Journal* 2019, 111, 128-142, <https://doi.org/10.2134/agronj2018.04.0284>.
- McKenna, T.P.; Crews, T.E.; Kemp, L.; Sikes, B.A. Community structure of soil fungi in a novel perennial crop monoculture, annual agriculture, and native prairie reconstruction. *PLoS One* 2020, 15:e0228202, <https://doi.org/10.1371/journal.pone.0228202>.
- Means, M.; Crews, T.; Souza, L. Annual and perennial crop composition impacts on soil carbon and nitrogen dynamics at two different depths. *Renewable Agriculture and Food Systems* 2022, 37, 437-444, <https://doi.org/10.1017/S174270522000084>.
- Moore, K.J.; Anex, R.P.; Elobeid, A.E.; Fei, S.; Flora, C.B.; Goggi, A.S.; Jacobs, K.L.; Jha, P.; Kaleita, A.L.; Karlen, D.L.; Laird, D.A. Regenerating agricultural landscapes with perennial groundcover for intensive crop production. *Agronomy*, 2019, 9, 458, <https://doi.org/10.3390/agronomy9080458>.
- Newell, M.T.; Hayes, R.C. An initial investigation of forage production and feed quality of perennial wheat derivatives. *Crop and Pasture Science* 2017, 68, 1141-1148, <https://doi.org/10.1071/CP16405>
- Peterson, C.J. Similarities among test sites based on cultivar performance in the hard red winter wheat region. *Crop Science* 1992, 32, 907-912, <https://doi.org/10.2135/cropsci1992.0011183X003200040014x>.
- Price, J.H.; Brandvain, Y.; Smith, K.P. Measurements of lethal and nonlethal inbreeding depression inform the de novo domestication of *Silphium integrifolium*. *American Journal of Botany* 2021, 108, 980-992, <https://doi.org/10.1002/csc2.20748>.

- Reilly, E.C.; Gutknecht, J.L.; Sheaffer, C.C.; Jungers, J.M. Reductions in soil water nitrate beneath a perennial grain crop compared to an annual crop rotation on sandy soil. *Frontiers in Sustainable Food Systems* 2022, 6, 996586, <https://doi.org/10.3389/fsufs.2022.996586>.
- Rife, T.W.; Graybosch, R.A.; Poland, J.A. A field-based analysis of genetic improvement for grain yield in winter wheat cultivars developed in the US Central Plains from 1992 to 2014. *Crop Science* 2019, 59, 905-910, <https://doi.org/10.2135/cropsci2018.01.0073>.
- Robertson, B.A.; Doran, P.J.; Loomis, L.R.; Robertson, J.R.; Schemske, D.W. Perennial biomass feedstocks enhance avian diversity. *GCB Bioenergy* 2011, 3, 235-246, <https://doi.org/10.1111/j.1757-1707.2010.01080.x>.
- Runck, B.C.; Kantar, M.B.; Jordan, N.R.; Anderson, J.A.; Wyse, D.L.; Eckberg, J.O.; Barnes, R.J.; Lehman, C.L.; DeHaan, L.R.; Stupar, R.M.; Sheaffer, C.C. The reflective plant breeding paradigm: A robust system of germplasm development to support strategic diversification of agroecosystems. *Crop Science* 2014, 54, 1939-1948, <https://doi.org/10.2135/cropsci2014.03.0195>.
- Ryan, M.R.; Crews, T.E.; Culman, S.W.; DeHaan, L.R.; Hayes, R.C.; Jungers, J.M.; Bakker, M.G. Managing for multifunctionality in perennial grain crops. *BioScience* 2018, 68, 294-304, <https://doi.org/10.1093/biosci/biy014>.
- Sanford, G.R.; Jackson, R.D.; Booth, E.G.; Hedtcke, J.L.; Picasso, V. Perenniality and diversity drive output stability and resilience in a 26-year cropping systems experiment. *Field Crops Research* 2021, 263, 108071, <https://doi.org/10.1016/j.fcr.2021.108071>.
- Seyum, E.G.; Bille, N.H.; Abiew, W.G.; Munyengwa, N.; Bell, J.M.; Cros, D. Genomic selection in tropical perennial crops and plantation trees: a review. *Molecular Breeding*, 2022, 42, 58, <https://doi.org/10.1007/s11032-022-01326-4>.
- Smaje, C. The strong perennial vision: A critical review. *Agroecology and Sustainable Food Systems* 2015, 39, 471-499, <https://doi.org/10.1080/21683565.2015.1007200>.
- Soto-Gómez, D.; Pérez-Rodríguez, P. Sustainable agriculture through perennial grains: Wheat, rice, maize, and other species. A review. *Agriculture, Ecosystems & Environment* 2022, 325, <https://doi.org/10.1016/j.agee.2021.107747>.

- Sprunger, C.D.; Culman, S.W.; Peralta, L.A.; DuPont, S.T.; Lennon, J.T.; Snapp, S.S. Perennial grain crop roots and nitrogen management shape soil food webs and soil carbon dynamics. *Soil Biology and Biochemistry* 2019, 107573, <https://doi.org/10.1016/j.soilbio.2019.107573>.
- Street, D.J. Fisher's contributions to agricultural statistics. *Biometrics*, 1990, 46, 937-945, <https://doi.org/10.2307/2532439>.
- Tork, D.G.; Anderson, N.O.; Wyse, D.L.; Betts, K.J. Ideotype selection of perennial flax (*Linum spp.*) for herbaceous plant habit traits. *Agronomy* 2022, 12, 3127, <https://doi.org/10.3390/agronomy12123127>.
- Tyl, C.; DeHaan, L.; Frels, K.; Bajgain, P.; Marks, M.D.; Anderson, J. Emerging crops with enhanced ecosystem services: progress in breeding and processing for food use. *Cereal Foods World* 2020, 65, <https://doi.org/10.1094/CFW-65-2-0016>.
- van der Pol, L.K.; Nester, B.; Schlautman, B.; Crews, T.E.; Conrath, M.F. Perennial grain Kernza® fields have higher particulate organic carbon at depth than annual grain fields. *Canadian Journal of Soil Science* 2022, 102, 1005-1009, <https://doi.org/10.1139/cjss-2022-0026>.
- Van Tassel, D.L.; DeHaan, L.R.; Cox, T.S. Missing domesticated plant forms: can artificial selection fill the gap? *Evolutionary Applications* 2010, 3, 434-452, <https://doi.org/10.1111/j.1752-4571.2010.00132.x>.
- Vico, G.; Manzoni, S.; Nkurunziza, T.; Murphy, K.; Weih, M. Trade-offs between seed output and life span—a quantitative comparison of traits between annual and perennial congeneric species. *New Phytologist* 2016, 209, 104-114, <https://doi.org/10.1111/nph.13574>.
- Wagoner, P. Perennial grain development: past efforts and potential for the future. *Critical Reviews in Plant Sciences* 1990, 9, 381-408, <https://doi.org/10.1080/07352689009382298>.
- Yu, H.; Li, J. Breeding future crops to feed the world through de novo domestication. *Nature Communications* 2022, 13, 1171, <https://doi.org/10.1038/s41467-022-28732-8>.
- Zhang, S.; Huang, G.; Zhang, Y.; Lv, X.; Wan, K.; Liang, J.; Feng, Y.; Dao, J.; Wu, S.; Zhang, L.; Yang, X. Sustained productivity and agronomic potential of perennial rice. *Nature Sustainability* 2023, 6, 28-38, <https://doi.org/10.1038/s41893-022-00997-3>.

Zhu, X.G.; Zhu, J.K. Precision genome editing heralds rapid de novo domestication for new crops. *Cell* 2021, 184, 1133-1134, <https://doi.org/10.1016/j.cell.2021.02.004>.

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:

Although this work received no direct financial support, the ideas presented in this Discussion are supportive of sustained funding of research directions currently engaged in by the authors.

Author Contributions

Lee R. DeHaan: Writing- Original Draft, Reviewing and Editing, **James A. Anderson:** Writing – Reviewing and Editing, **Prabin Bajgain:** Writing – Reviewing and Editing, **Andrea Basche:** Writing – Reviewing and Editing, **Douglas J. Cattani:** Writing – Reviewing and Editing, **Jared Crain:** Writing – Reviewing and Editing, **Timothy E. Crews:** Writing – Reviewing and Editing, **Christophe David:** Writing – Reviewing and Editing, **Olivier Duchene:** Writing – Reviewing and Editing, **Jessica Gutknecht:** Writing – Reviewing and Editing, **Richard C. Hayes:** Writing – Reviewing and Editing, **Fengyi Hu:** Writing – Reviewing and Editing, **Jacob M. Jungers:** Writing – Reviewing and Editing, **Søren Knudsen:** Writing – Reviewing and Editing, **Wenqian Kong:** Writing – Reviewing and Editing, **Steve Larson:** Writing – Reviewing and Editing, **Per-Olof Lundquist:** Writing – Reviewing and Editing, **Guangbin Luo:** Writing – Reviewing and Editing, **Allison J. Miller:** Writing – Reviewing and Editing, **Pheonah Nabukalu:** Writing – Reviewing and Editing, **Matthew T. Newell:** Writing – Reviewing and Editing, **Lennart Olsson:** Writing – Reviewing and Editing, **Michael Palmgren:** Writing – Reviewing and Editing, **Andrew H. Paterson:** Writing – Reviewing and Editing, **Valentin D. Picasso:** Writing – Reviewing and Editing, **Jesse A. Poland:** Writing – Reviewing and Editing, **Frik J. Sacks:** Writing – Reviewing and Editing, **Shuwen Wang:** Writing – Reviewing and Editing, and **Anna Westerhagen:** Writing – Reviewing and Editing

Graphical abstract

Journal Pre-proof

