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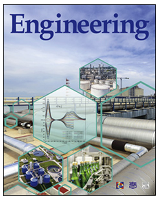

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Development of Perennial Wheat Through Hybridization Between Wheat and Wheatgrasses: A Review

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ABSTRACT

Wheatgrasses (*Thinopyrum* spp.), which are relatives of wheat (*Triticum aestivum* L.), have a perennial growth habit and offer resistance to a diversity of biotic and abiotic stresses, making them useful in wheat improvement. Many of these desirable traits from *Thinopyrum* spp. have been used to develop wheat cultivars by introgression breeding. The perennial growth habit of wheatgrasses inherits as a complex quantitative trait that is controlled by many unknown genes. Previous studies have indicated that *Thinopyrum* spp. are able to hybridize with wheat and produce viable/stable amphiploids or partial amphiploids. Meanwhile, efforts have been made to develop perennial wheat by domestication of *Thinopyrum* spp. The most promising perennial wheat–*Thinopyrum* lines can be used as grain and/or forage crops, which combine the desirable traits of both parents. The wheat–*Thinopyrum* lines can adapt to diverse agricultural systems. This paper summarizes the development of perennial wheat based on *Thinopyrum*, and the genetic aspects, breeding methods, and perspectives of wheat–*Thinopyrum* hybrids.

1. Introduction

Food security is one of the most serious global challenges due to the rapid growth of global population, climate change, and greenhouse gas emissions [1,2]. The world's population is estimated to exceed 9.8 billion by 2050 [3]. In addition, the world's marginal lands, which are defined as low or non-profit farmlands, are currently estimated to cover an area of 3.68×10^{7} h m^{2}; these lands occupy a large part of the global land mass and support over 50% of the world's population [4]. China, which feeds roughly 20% of the global population with only 9% of the global farmland, sets a "bottom line" of about 1.2×10^{8} h m^{2} of arable land for sustainable and long-term food security. Unproductive agriculture (e.g., saline-alkali soil, desertified soil, and low-rain-fed regions) is especially common in western China. The arable land in China is primarily concentrated in river valleys (e.g., the Yangtze River and Yellow River) along the southern and eastern coasts, which contain a large proportion of middle- and low-yielding farmlands [5–7]. Desertification and land degradation are serious issues in China, as well as in other countries around the world. In 2015, 25% of the world's croplands were estimated to be rapidly degrading [8].

Common annual cereal crops, such as wheat (*Triticum aestivum* L.), rice (*Oryza sativa* L.), and maize (*Zea mays* L.), are the major sources of food grains for human consumption; however, the production of annual monoculture crops exerts negative impacts on the environment, including water pollution, soil erosion, reduced carbon storage, increased greenhouse gas emissions, and large amounts of fertilizer application [9]. Annual crops are more vulnerable than perennial crops to soil erosion due to the lack of continuous ground cover [10]. Nitrogen losses due to annual crops can be 30- to 50-fold higher than those caused by perennial crops [11]. The development of perennial crops that can exist for multiple years in fields is one approach that has been taken by scientists in order to improve food security. This article summarizes the progress that has been made in the development of perennial wheat via interspecific hybridization and direct domestication, with an emphasis on wheatgrasses (*Thinopyrum* spp.). The breeding methods, potential environmental benefits, and challenges of perennial wheat are discussed.

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2. Agronomic and environmental benefits from perennial crops

A perennial plant is characterized by its ability to regrow after harvest. Such plants usually provide more ground coverage and have a longer growing season than annual crops; they also possess an extensive root system in the soil. The environmental benefits of perennial crops include reduction in soil erosion, protection of water resources, minimization of nutrient leaching, increased retention of carbon in the soil, and provision of a continuous habitat for wildlife [12,13]. The economic benefits of perennial crops include reduced expenses for seed and fertilizer (since the crop is seeded once and harvested many times), and reduced costs for weed control, tillage, and other cultural practices associated with annual crops. Perennial crops can be used not only for food and feed, but also for fuel and other nonfood bioproducts [14–17]. Potential perennial crops include perennial wheat [18,19], perennial rice (*Oryza rufipogon* Griff.) [20–22], sorghum (*Sorghum bicolor* (L.) Moench) [23], and common millet (*Panicum miliaceum* L.) [1,24].

In addition to perennial wheat, weeping grass (*Microlaena stipoides* (Labill.) R. Br.), a large-seeded native grass in Australia, was used to develop perennial grain crops [25]. Some herbaceous native legumes were shown to have potential as perennial grain crops after domestication in Australia [26,27]. The commercial grasses *Microlaena stipoides* and *Distichlis palmeri* (Vasey) Fassett ex I. M. Johnst. were domesticated as perennial grain crops [28,29]; however, these crops achieved limited success [30].

3. Utilization of wheatgrasses in the development of perennial wheat

The major strategies used to develop new perennial crops are domestication of wild perennial species and interspecific hybridization between annual crops and perennial relative species. Interspecific hybridization is preferred over direct domestication because it combines the perennial growth habit with grain quality, and reduces the time needed to develop perennial crops. The majority of species in the tribe Triticeae are perennial, such as *Aegilops tauschii* Coss., *Agropyron cristatum* Gaertn, *Psathyrostachys huashanica* Keng, *Pseudoroegneria spicata* Pursh, *Elymus scaber* R. Br., and *Thinopyrum* spp., and many of these species are able to hybridize with common wheat [31,32]. Other grass species, such as *Australopyrum* (Tzvekev) Á. Löve, are also regarded as potential donor species of perennial growth habit [27]. *Thinopyrum* spp. are attractive as perennial donors because of their genetic affinity with *Triticum* spp. and their long history of study [32–34].

The genus *Thinopyrum* consists of about 11 species with a wide range of genomic composition from diploids to autoallodecaploids; examples include *Th. elongatum* D. R. Dewey ($2n = 2x = 14$), *Th. bessarabicum* (Savul & Rayss) Á. Löve ($2n = 2x = 14$), *Th. junceiforme* Á. Löve ($2n = 4x = 28$ or $2n = 6x = 42$), *Th. intermedium* Barkworth & D. R. Dewey ($2n = 6x = 42$), and *Th. ponticum* Beauv. ($2n = 10x = 70$). These species have long been considered important genetic resources for wheat improvement because species in the genus collectively contain numerous genes for resistance to biotic (i.e., diseases and pests) and abiotic (i.e., salinity, drought, and extreme temperatures) stresses [19,33,35–37]. Compared with other perennial grass species, *Thinopyrum* spp. has desirable agronomic traits including a large seed size (5.3 g per 1000 grain weight) and nutritious grain [38–41]. *Thinopyrum* spp. produces more biomass than annual wheat and is regarded as the most productive forage species in the western United States [42,43]. *Thinopyrum* spp. also has extensive root systems that are able to capture fertilizer and significantly reduce nitrate leaching [19]. The grain quality of *Th. intermedium* was reported to be similar to that of wheat, with a high protein content and flour that performs well in baked products [44,45]. Larkin et al. [46] reported that wheat–*Th. elongatum* and wheat–*Th. intermedium* derivatives were able to persist in the field and produce grains for more than four years; however, the yield tended to decline with time. The Rodale Institute (Kutztown, PA, USA) began to develop perennial grain in 1983 by domesticating *Th. intermedium* after evaluating about 100 species of perennial grasses [13,38,46,47].

4. Current status of breeding perennial wheat

Early attempts to hybridize wheat and wheatgrasses can be dated back to the 1920s and 1930s, when scientists in the former Union of Soviet Socialist Republics (USSR), the United States, Germany, and Canada made crosses between wheat and wheatgrasses [12,48–52]. The first wheat–*Thinopyrum* cross was made by Tsitsin [51], who was aiming to develop perennial wheat; however, his attempt failed. Nevertheless, those studies demonstrated that it might be possible to directly introgress the genes conferring the perennial growth habit into wheat through recombination or chromosomal translocation. Early efforts to develop perennial wheat were unsuccessful until the commercial release of the first perennial wheat cultivar, Montana-2 (MT-2), in 1987 [53,54]. MT-2 was developed by crossing durum wheat (*Triticum turgidum* L. var. *durum*) and *Th. intermedium* at Montana State University in Bozeman, MT, USA. Lammer et al. [55] reported that an additional pair of chromosome 4E from *Th. elongatum* in Chinese Spring wheat was associated with the ability to regrow after harvest; but the regrowth was not as vigorous as that of the perennial amphiploid progenitor. The perennial growth habit was reported to be a polygenic trait controlled by multiple genes, which would be not easy to introgress from the perennial parents to an annual wheat cultivar [12,13,27,56]. This is one of the difficulties in using *Thinopyrum* spp. as the donor species for the development of perennial wheat through interspecific hybridization. It is probably easier to transfer the simply inherited domestication traits from wheat into existing perennial species so that wild traits such as seed- and head-shattering traits, indeterminate flowering, and larger kernels can be improved [57]. This will make it possible to adapt the wild perennial species to modern agricultural production. Significant progress has been made in the direct domestication of several perennial species including *Th. intermedium* at the Land Institute (Salina, KS, USA). Twenty promising perennial wheat lines developed from a cross between wheat or durum wheat and *Th. intermedium* were grown and evaluated in nine countries around the world [19,34]. In Australia, over 150 wheat × wheatgrass derivatives originating from the wheat collections of Australia, the United States, and China were evaluated for the ability to regrow after harvest and produce grain yield over multiple years. Several perennial lines were able to produce grain over three successive years and some lines were able to produce both forage and grain [26,27,46,58]. Some perennial lines had dehydration tolerance and were able to survive under severe water deficit in Australia [46]. Perennial wheat was believed to have the potential to contribute to the next substantial advance in wheat production in Australia [27].

5. Hybridization between wheat and wheatgrasses in China

The wheatgrasses *Th. intermedium* and *Th. ponticum* have been used for wheat improvement in China since the early 1950s [59]. Hybridization between wheat and *Th. intermedium* was initiated by Shancheng Sun at Northeast Agricultural University in 1953 [60]. In subsequent studies, a large number of perennial wheat lines were selected from the progeny of backcrosses between the octoploid and hexaploid wheat–wheatgrass hybrids and wheat.

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Hybrids derived from crosses of the diploid *Th. elongatum* ($2n = 14$) with common wheat exhibited weak regrowth in the dry and cold conditions of Shanxi Province; consequently, the hexaploid *Th. intermedium* ($2n = 42$) or octoploid wheat–*Th. intermedium* lines ($2n = 56$) were preferred as the donors of perennial growth habit. F_1 plants from the crosses between octoploid wheat–*Th. intermedium* hybrids and durum wheat–*Th. intermedium* hybrids usually exhibited vigorous regrowth and were able to survive for at least three years in the field, with some being able to survive for seven years; however, the F_1 generation had low seed-setting rates of 24.0% on average. The F_2 to F_4 generation progeny was segregated into three types based on morphological characteristics: common wheat types, intermediate (*Tritielytrigia*) types, and forage/wheatgrass (resembling the *Th. intermedium* parent) types (Fig. 1). The seed-setting rates of the hybrids improved in advanced generations, and reached 65.4% and 64.7% for the F_2 and F_3 generations, respectively [61]. Genomic *in situ* hybridization (GISH) analysis demonstrated that the perennial wheat–*Th. intermedium* lines 12–480, 12–787, 12–1150, and 12–1269 had 50–56 chromosomes that were composed of 8–14 *Th. intermedium* chromosomes, and were able to survive in the field for more than two years (unpublished data from Yu Sun). These lines were also tall (115–146 cm) and tolerant to cold (−20 °C), and they had multiple spikelets (20–61) along with a high protein and nutrient composition (Figs. 2 and 3). These lines are promising genetic resources for the development of forage perennial wheat. In addition, several perennial wheat lines were resistant to the cereal cyst nematodes *Heterodera avenae* Wollenweber and *H. filipjevi* (Madzhidov) Stelter, and to the fungal pathogens *Puccinia striiformis* Westend f. sp. *tritici* and *Blumeria graminis* (DC) E.O. Speer f. sp. *tritici* emend. É. J. Marchal (the causal agents of wheat stripe rust and powdery mildew, respectively), and were thus valuable resources for improving resistance in wheat to these diseases. In addition to perennial performance, wheat–*Th. intermedium* partial amphiploids, such as the “Zhong” series, possess multiple resistances to other pests and pathogens including *wheat streak mosaic virus* and its vector, the wheat curl mite (*Aceria tosichella* Keifer), barley yellow dwarf virus, eyespot (caused by *Oculimacula yallundae* (Wallwork & Spooner) Crous & W. Gams and *Oculimacula acuformis* (Boerema, R. Pieters & Hamers), and the cereal cyst nematode (*Heterodera* spp.) [32,36,62]. Zhao et al. [56] developed perennial wheat lines from the cross octoploid *Trititrigia* × *Th. intermedium*, which exhibited vigorous regrowth and was well-adapted to the cold environment of Heilongjiang Province. Crosses between wheat and tall wheatgrass, *Th. ponticum*, were made in 1956 and used mainly for com-

Fig. 1. Morphology of spikes from the F_2 plants of a wheat × *Th. intermedium* cross. A is *Th. intermedium*, B–J are different progeny spikes of the hybrid, and K is wheat cultivar Jinmai 47.

Fig. 2. Perennial wheat derived from the wheat × *Th. intermedium* cross in plots, Dongyang, Shanxi Province, China.

Fig. 3. A hill of the perennial wheat line derived from the wheat × *Th. intermedium* cross in Dongyang, Shanxi Province, China.

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mon wheat improvement, resulting in the release of a series of wheat cultivars that included Xiaoyan 6 [63].

6. Breeding methods of perennial wheat

Domestication of wild *Triticum* relatives is one approach to develop a perennial wheat, and several orthologous genes that contribute to domestication traits and the improvement of annual crops have been identified in this process [13,24,64,65]. For example, grain weight is controlled by the same gene *GW2* in rice, wheat, and maize [66,67]; flowering time is controlled by the *VRN1* gene in wheat, barley (*Hordeum vulgare* L.), and ryegrass (*Lolium perenne* L.) [68]; and glutinous grain is controlled by *GBSSI* or *Waxy* genes in wheat, barley, maize, and sorghum [13]. Selection and introduction of these genes may speed the development of perennial wheat using marker-assisted selection (MAS) or gene transfer during long-term selection. Scientists at the Rodale Institute (Kutztown, PA, USA) and Land Institute (Salina, KS, USA) have been working on the domestication of the perennial grass *Th. intermedium* since 1983 [12,34,38]. They have developed several accessions with an increased harvest index and reduced plant spread compared with the donor, *Th. intermedium*.

The domestication or development of perennial wheat is time-consuming and includes the following steps: ① evaluating wild relative species and determining which have the greatest potential; ② creating the initial population by crossing candidate perennial donors to desirable commercial wheat resources with promising agronomic performance; ③ selecting desired lines until the genes or loci for domestication and agronomic traits are fixed; and ④ testing materials extensively over several years, followed by the release of potential lines [13,65]. During this process, agronomically desirable plants can be used as parents for hybridization.

Wild relatives often perform poorly for agronomic traits due to the genetic complexity of some traits and the linkage of desirable and undesirable traits such as late flowering, small seed size, and seed shattering. *Thinopyrum* spp. and other perennial species in the tribe Triticeae can be hybridized with commercial wheat cultivars to combine the perennial growth habit with the productivity of wheat [69]. Breeding methods, such as pedigree selection, backcrossing, and recurrent selection, can be applied to remove the deleterious traits while maintaining the perennial trait [13,45]. Early generation selection (F_2 to F_4) should emphasize traits such as seed size, plant height, self-fertility, and chromosome constitution. Stable chromosome counts should also be prioritized [13,24]. The selection in later generations should focus on traits such as grain yield and quality, disease resistance, and robust post-harvest regrowth [70–72]. In addition to several generations of trait selection, emphasis should be placed on the genetic changes in the newly developed alloploid lines in order to ensure accommodation between the alien genomes and the wheat genomes [30]. Fertility and stability must be considered during the process of developing perennial wheat. Beyond considerations of ploidy and genetic compatibility, perennial wheat lines might not exhibit a regrowth ability in environments other than the one in which they were selected due to differences in climate (precipitation and temperature), soil, and pathogens that affect the fitness of individual lines [13,30].

7. Genetic research on perennial wheat

Thus far, the genes that confer the perennial growth habit have not been identified. Studies have shown that some of the attributes of the perennial growth habit are present when extra chromosomes from perennial donors are added to wheat [55,73–76]. Potentially perennial wheat lines that show vigorous regrowth usually contain a group of chromosomes from their perennial parents, and those that survived for multiple years under field conditions required at least one genome from *Th. intermedium* [18,58]. Our results are consistent with previous studies that indicate that some perennial wheat lines had 54–56 chromosomes, with 12–14 chromosomes originating from *Th. intermedium* (unpublished data from Yu Sun). With an increase in wheatgrass chromosomes and decrease in wheat chromosomes, the hybrids may exhibit a vigorous perennial habit; however, there is no evidence as to what percentage of chromosomes from wheatgrass species will ensure a strong perennial growth habit. Progeny lines with fewer wheat chromosomes often exhibit severe genetic instability and are more like the grass parent in their growth habit. Assessment of the effects of complete genomes using advanced generations is not possible because of chromosome elimination. Scientists at the Land Institute (Salina, KS, USA) are trying to understand how many wheat and *Th. intermedium* genomes will improve the performance of the perennial growth habit by developing a series of full amphiploids with different genomic constitutions by crossing diploid, tetraploid, and hexaploid *Triticum* species with *Thinopyrum* spp. [13,24,34,58]. The alien chromosomes in the partial amphiploids usually consist of chromosomes from different genomes [35]. This mixture of chromosomes or synthetic genome in the partial amphiploids may cause poor fertility and loss of the perennial donor chromosomes. Chromosomes from different genomes of *Thinopyrum* spp. can be discriminated by GISH analysis using the S (or St) genomic DNA from *Pseudoroegneria stipifolia* (Czern. ex Nevski) Á. Löve or *Pseudoroegneria strigosa* (M. Bieb) Á. Löve based on different banding patterns [35,54]. For example, the perennial wheat cultivar MT-2 consists of A, B, D, E, and St genomes, and variation in chromosome composition was detected within and among the MT-2 lines. This perennial cultivar was composed of a mean chromosome content of 26.2 wheat + 9.4 St + 18.8 E + 1.5 St/E translocation [54]. Chen et al. [77] reported that the genome of MT-2 included 10 chromosomes from the St genome, eight from the J^s genome, and 13 from the J genome. Some researchers advocated the use of the diploid wheatgrass species (e.g., *Th. elongatum*) as the perennial donor, resulting in an amphiploid hybrid with AABBEE (similar to hexaploid triticale, AABBRR) or AABBDDEE (analogous to octoploid triticale, AABBDDRR) when using tetraploid wheat or hexaploid wheat as parents, respectively [13,46,58]. The recovery of full fertility, high yields, and promising regrowth may require multiple generations of selection.

Determining the role of cytoplasm in developing perennial wheat by interspecific hybridization is necessary because many studies have indicated an interaction between the nucleus and cytoplasm during wide hybridization [76,78,79]. Since it is incompatible with wheat cytoplasm, the gene (or genes) conferring the perennial growth habit from *Thinopyrum* spp. may be eliminated or silenced [34].

8. Challenges and opportunities

The rapid development of next-generation sequencing (NGS) techniques enables the production of high-quality reference genomic sequences for many crops and plant species, which may provide useful information for accelerating the breeding of perennial wheat. It is possible to deal with large and complex genomes (both diploid and polyploid) by taking advantage of NGS. *Th. intermedium* is an allohexaploid species ($2n = 6x = 42$, $StStJ^sJ^sJJ$) with a genome size of 12.6 Gb, the majority of which (ca. 80%–90%) contains repetitive sequences [13]. Recently, Zhang et al. [80] optimized the genotyping-by-sequencing (GBS) technology for *Th. intermedium* and identified many genome-wide markers across the genome of *Th. intermedium* without a reference genomic sequence. Kantarski et al. [81] developed the first integrated genetic map of *Th. intermedium* with 21 linkage groups, including 10 029 GBS markers

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and covering 5061 centimorgans (cM) using seven populations. This consensus map displayed high collinearity with the barley genome and would be useful for a better understanding of the genetic control of the perennial growth habit in *Th. intermedium* and increase the efficiency of genomic selection on the improvement and domestication of *Th. intermedium*. High-throughput phenotyping platforms based on field performances provide precise phenotypic data for dissecting the genetic controls of perennial traits, as well as those of agronomic traits, which increases the effectiveness of domestication and development of perennial crops [13,82].

Further research is needed to identify the underlying mechanism of the perennial growth habit and to integrate the genes responsible for better agronomic performance. In Australia, a well-adapted perennial cultivar is expected to be released by 2030 [46]. By crossing wheat with the partial amphiploids of perennial wheat–*Th. intermedium* hybrids, we have developed many lines with promising perennial performance, large biomass, and good seed fertility that have potential as forage cultivars. These perennial wheat lines are adapted to different areas in the Xinjiang Uygur and Ningxia Hui Autonomous Regions of China; however, the adaptability of some perennial wheat lines needs to be improved since many of them flowered late, produced few seeds, and yielded poorly. Perennial grains will need to be profitable if they are to be adopted widely in agriculture [83]. The availability of perennial wheat with robust regrowth, cold-hardiness, and drought tolerance that meets the needs of and benefits farmers is limited. Like other newly emerged crops, perennial wheat should be cultivated first in marginal fields at the edge of agricultural areas before it becomes a more productive, mainstream crop. The end-use purpose of perennial wheat must be considered to be to act as a breeding target during the development and improvement of this new crop [84]. Additional concerns about perennial crops include their potential to become serious weeds and the possibility that they may serve as a "green bridge" for certain pathogens, thus increasing the risk of disease epidemics [85].

The advance of modern genomic approaches that are being used in common wheat, as well as in other well-adapted annual crops, will benefit the development of perennial wheat. Integrative techniques that combine genome-wide markers, powerful statistical tools, and phenotypic assessment platforms have revolutionized the cultivated crop breeding and domestication of perennial wheatgrasses. In view of the complex inheritance and time-consuming selection for perennial growth habit, high-throughput genotyping based on genomic approaches and phenotyping techniques will increase the efficiency of selection accuracy [86–89]. Genomics-based speed-breeding techniques that allow multiple generations of crop production per year [90] will reduce the breeding-cycle time and accelerate the improvement of existing perennial lines and the domestication of perennial wheatgrasses.

9. Concluding remarks

Given the increasing concern about food security in the face of an increasing global population, increased risks from climate change, and losses in arable land due to development and soil degradation, perennial wheat offers a promising new approach to increase food production and diversify agroecosystems. The development of perennial wheat cultivars that can be planted once and harvested many times would provide new options, especially for marginal and low-productivity situations. Perennial wheat that produces a high biomass yield with low input would benefit farmers by allowing them to cultivate marginal lands using perennial wheat as forage or bioenergy feedstock. Perennial crops may serve different purposes in different situations. Continued research toward the development of adapted perennial wheat cultivars is necessary to ensure success. Wheat–*Th. intermedium* amphiploids and/or partial amphiploids have demonstrated good perennial performance in multiple environments. Modern high-throughput genotyping and phenotyping technologies, in combination with speed-breeding techniques, should accelerate the development of perennial wheat cultivars.

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Compliance with ethics guidelines

Lei Cui, Yongkang Ren, Timothy D. Murray, Wenze Yan, Qing Guo, Yuqi Niu, Yu Sun, and Hongjie Li declare that they have no conflict of interest or financial conflicts to disclose.

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