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

Lei Cui [a,b,#], Yongkang Ren [a,#], Timothy D. Murray [c], Wenze Yan [a], Qing Guo [a], Yuqi Niu [a], Yu Sun [a,*], Hongjie Li [b,*]

[a] *Institute of Crop Science, Shanxi Academy of Agricultural Sciences, Taiyuan 030031, China*
[b] *The National Key Facility for Crop Gene Resources and Genetic Improvement, Institute of Crop Sciences, Chinese Academy of Agricultural Sciences, Beijing 100081, China*
[c] *Department of Plant Pathology, Washington State University, Pullman, WA 99164, USA*

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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.

* Corresponding authors.
E-mail addresses: sunyu203@126.com (Y. Sun), lihongjie@caas.cn (H. Li).
# These authors contributed equally to this work.

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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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