

Review

Breeding of the Crested Wheatgrass Complex (*Agropyron* spp.) for North American Temperate Rangeland Agriculture and Conservation

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Abstract: Species from the crested wheatgrass (*Agropyron* spp.) complex have been widely used for revegetation and grazing on North American rangelands for over 100 years. Focused crested wheatgrass breeding has been ongoing since the 1920s. These efforts resulted in the development of 18 cultivars adapted to western USA and Canadian growing conditions. These cultivars establish rapidly, persist, and provide soil stabilization and a reliable feed source for domestic livestock and wildlife. To address ecological concerns and increase rangeland agriculture efficiency, crested wheatgrass breeding requires new emphases and techniques. This review covers the history of crested wheatgrass breeding and genetics in North America and discusses emerging methods and practices for improvement in the future.

Keywords: genetic variation; genomic selection; grazing; heritability; recurrent selection

1. Introduction

Settling of the semiarid and arid Great Plains and Intermountain regions of North America began and continued through the mid to late nineteenth century. Settlers arrived based on the homestead acts in the US and Canada and began crop and domestic livestock production agriculture.

This production agriculture resulted in rangeland disturbance yet continued until the Dust Bowl era of the 1930s because of strong demand for wheat and livestock production. The collapsing commodity prices and severe drought that characterized the Dust Bowl era resulted in the abandonment of thousands of hectares of severely disturbed marginal cropland and rangeland [1–3]. In response, plant communities began to change with the loss of desirable plant material, increased soil erosion, and invasion by introduced annual weeds including Russian thistle (*Salsola kali* L.) and downy brome (*Bromus tectorum* L.) [2]. The final result was often permanent loss of ecological function arising from a cycle of loss of desirable plant materials; soil erosion; invasion of undesirable, often annual grasses, forbs, and woody species; changes to soil structure and nutrient, and water cycles; increased wildfire frequency; and in some instances, desertification [4–7].

At nearly the same time, a succession of plant introductions from Eurasia brought members of the original *Agropyron* genus to North America [8]. This included members of the crested wheatgrass complex (*Agropyron* spp.) beginning in 1898 and then a second introduction in 1906. Researchers quickly recognized the promise of crested wheatgrass because of its early spring growth and winter hardiness [9]. Many initial seeding attempts with wheatgrasses failed to produce stands or forage, although there was enough success to increase seed of the introductions and generate excitement for their use in rangeland agriculture and revegetation [8]. The Dust Bowl era triggered an increased focus on rangeland revegetation and the need for improved methods [10]. From that time, a combination of

improved equipment, seeding techniques, and plant materials enabled the widespread improvement of degraded rangeland areas [11]. Possibly the greatest advance was the recognition that crested wheatgrass was an excellent choice for revegetation efforts in more xeric regions of the northern Great Plains and big sagebrush (*Artemisia tridentata* Nuttall) rangelands of the Intermountain West [12]. This resulted in the widespread use of crested wheatgrasses (*Agropyron cristatum* (L.) Gaertn.)/*A. desertorum* (Fisch. ex Link) Schult.) for rangeland revegetation [3].

Crested wheatgrass has been instrumental in the revegetation of 6–11 M·ha in the United States and 1 M·ha in Canada [13]. Crested wheatgrass increases rangeland carrying capacity, readily establishes from seed, has excellent drought resistance and winterhardiness, provides high quality early spring and fall feed, and produces substantially more forage yield than native species [10,14]. Crested wheatgrass also suppresses invasive annual weeds and stabilizes soil from erosion on highly disturbed sites [15–18].

Despite the success of using crested wheatgrasses for site revegetation, there exist criticisms and controversy surrounding the use of crested wheatgrass in these settings. The primary criticism is that crested wheatgrass is not native to North America and that its seedings cause unwanted ecological site changes and result in monotypic stands that lack biodiversity. This criticism is unfair because the authors fail to acknowledge that the crested wheatgrass stands are frequently on sites that received heavy disturbance (i.e., grazing, fire, mechanical etc.) and soil damage from previous agricultural production [19]. Early crested wheatgrass seedings were often monocultures that were very stable and exhibited little change in components over decades [13]. Much research has focused on diversifying crested wheatgrass seedings through thinning stands and seeding native species [13,20,21]. Additionally, research has demonstrated that crested wheatgrass stands increase in species diversity over time [22].

This review will focus on the genetics and breeding history of crested wheatgrass for use on western North American rangelands. Specifically, it will focus on the history of cultivar development, breeding strategies, use of modern genetic tools, and future needs in this species.

2. Genomes and Genetics

The wheatgrasses belong to the Triticeae tribe of the Poaceae, or grass, family [23,24]. Triticeae grasses include both annual and perennial species, such as bread wheat (*Triticum aestivum* L.), durum wheat (*Triticum durum* Desf.), barley (*Hordeum vulgare* L.), and rye (*Secale cereal* L.) [23]. Despite the importance of the annual cereal crops, the majority of the Triticeae species are perennial and are important for forage production, site revegetation and reclamation, and as a genetic resource for the improvement of the annual cereal species [25]. These species evolved in mostly temperate arid and semiarid regions such as central Eurasia and western North America [26]. Although taxonomic revisions within the Triticeae tribe continue, the approaches of Löve [27] and Dewey [25] to base the taxonomy of this tribe on cytogenetic relationships have become the norm [28]. These treatments moved major wheatgrass species previously grouped in the *Agropyron* genus, based on having a single spikelet per node, to new genera, leaving the crested wheatgrass complex as the only members of this genus. All Triticeae species have a base chromosome number of $x = 7$. However, the genome constitution and the ploidy level and type (alloploidy or autopoloidy) differ depending on species. Hybridization barriers are not strong among members of the Triticeae tribe [28]. As a result, the perennial Triticeae grasses have been used as a gene source to develop perennial cereal grain crops [29,30]. Additionally, genetic introgression through hybridization between crested wheatgrass and wheat has resulted in increased resistance to powdery mildew (*Blumeria graminis* f. sp. *tritici*) [31] and seed weight [32].

The *Agropyron* genus, or crested wheatgrass complex, consists of 10 species, although only fairway crested wheatgrass (*A. cristatum*), standard (or desert) crested wheatgrass (*A. desertorum*), and Siberian wheatgrass (*A. fragile* (Roth.) P. Candargy) are cultivated on western North American rangelands. The most recent taxonomic treatment, which we will follow in this review, designated only two major crested wheatgrass species, and combines *A. cristatum* and *A. desertorum*, with

A. cristatum having nomenclature priority, collectively known as crested wheatgrass and *A. fragile*, known as Siberian wheatgrass [23]. The crested wheatgrass genome exceeds 6 Gbp·C⁻¹ and as a complex they are comprised of multiple copies of the P genome as diploid ($2n = 2x = 14$), tetraploid ($2n = 2x = 28$), and hexaploid ($2n = 2x = 42$) forms [33,34]. The tetraploid form is most common and has the widest distribution from Central Europe to Siberia. The diploid species have a similar distribution, but are less common, and the hexaploid species are rare and found only in Turkey and Iran [35]. The diploid and tetraploid forms are the most important in North America, and the polyploid forms are autopolyploid [36–38]. Based on chromosome pairing in interspecific hybrids, mitotic chromosome karyotypes, and hybrid fertility between ploidy levels, it has been proposed that the crested wheatgrass complex is one large gene pool [33,39–41].

Tetraploid crested wheatgrass exhibits tetrasomic inheritance [35]. Tetrasomic inheritance leads to complimentary gene action or nonallelic gene action, wherein dominant alleles suppress the expression of recessive alleles that are found in repulsion-phase linkage blocks. The rapid loss of complimentary gene action, or uncovering of the recessive alleles, under inbreeding results in severe inbreeding depression and the slow accumulation of complimentary gene action from plant breeding slows genetic progress and the resulting level of heterosis [42]. Evidence of this phenomenon is the severe inbreeding depression suffered in crested wheatgrass populations undergoing self-pollination for forage and seed yield [43–45]. Crested wheatgrass expresses a high level of self-incompatibility [46–48]. While there has been no specific research to identify the self-incompatibility loci in crested wheatgrass, the S-Z system is common to the Triticeae tribe and the probable cause of self-incompatibility in crested wheatgrass [49]. Between inbreeding depression and self-incompatibility, the use of inbreeding in crested wheatgrass for cultivar development or hybrid development is not feasible.

Another complication for crested wheatgrass breeding is its perennial growth habit. Perenniality requires that a plant survives across multiple environments (i.e., years, locations, etc.) while maintaining acceptable agronomic production. To adequately evaluate the potential of crested wheatgrass genotypes in a breeding program requires three to five years per selection cycle: One year for establishment, two to three years for phenotypic evaluation, and one to two years for hybridization and seed production from selected genotypes [50]. Among other possibilities, this increased cycle length is a primary reason for the near non-existent genetic gains in perennial forage grasses, including crested wheatgrass [51]. The requirement for multi-year evaluations in crested wheatgrass results in substantially lower annual genetic gains than in annual row crops that often complete multiple selection cycles in a single year [52].

3. Breeding, and Cultivar Development

Beginning in Canada, initial cultivars of crested wheatgrass resulted from the evaluation of plant introductions and collections from around the world for the identification of superior plant introductions and subsequent seed increase. As crested wheatgrass breeding increased after the Dust Bowl era, Canadian programs expanded and additional programs began in the United States at several locations in the Great Plains and Intermountain Regions [37]. These research programs have released 18 cultivars over the past 90 years.

In Canada, the University of Saskatchewan and Agriculture and Agri-Food Canada in Saskatoon, SK have worked together to release five cultivars. The first North American cultivar was the diploid cultivar Fairway, which resulted from several cycles of mass selection within PI 19536 from Siberia for fine leafy plants [53]. Subsequent cultivars were Summit (1953), Parkway (1969), Kirk (1987), and Goliath (2006). The tetraploid cultivar Summit is the result of selection for uniformity out of an introduction from Siberia, but this cultivar has floundered in the seed market because of seed production issues [37,54]. The diploid cultivar Parkway is a 16-clone synthetic selected following several cycles of recurrent selection for leafy, tall, and vigorous plants followed by polycross progeny tests [54]. The development of the tetraploid cultivar Kirk consisted of the open pollination of an introduction from Finland with nine local Canadian strains and four European introductions, followed by two cycles of phenotypic selection for vigor, fertility and reduced seed shatter and awn development [55].

The tetraploid cultivar Goliath possesses increased seed size and fertility due to selection from one genotype of Kirk, chromosome doubled genotypes of the diploid Parkway, and genotypes from the cross of Kirk and the Parkway chromosome doubled populations. Several additional cycles of selection for plant vigor, height, regrowth, seed size and fertility resulted in the 22-clone synthetic that became Goliath [56].

In the United States, separately and jointly, various state Agricultural Experiment Stations (AES), the USDA Agricultural Research Service (ARS), Soil Conservation Service (SCS), and Forest Service (FS), among other state agencies, have released 13 crested wheatgrass cultivars. The first U.S.-developed crested wheatgrass cultivar was the tetraploid Nordan, released by the North Dakota AES. Nordan traced to selections from a remnant seeding, followed by two cycles of open-pollinated selection under spaced plants for vigorous, leafy, and erect plants that produced large, awnless seeds. Bulk seed from the seven most promising plants from the best line was increased, tested, and then released as Nordan [57]. The SCS and Idaho AES released the tetraploid, Siberian-type cultivar P-27, derived from an original introduction from Kazakhstan. Selection for P-27 was from clones selected from remnant field nurseries. P-27 possesses narrow, awnless heads, leafy plants, and is preferred on light, sandy soils [54]. The ARS and the Nebraska AES released the diploid cultivar Ruff and the tetraploid cultivar NU-ARS AC2. Ruff came from the selection of seven lots of diploid germplasm followed by three generations of selection. The cultivar is leafy, fine, and short [54]. A spaced plant evaluation of tetraploid and diploid accessions, from which the four most promising accessions were selected for forage yield and digestibility, was the basis of the cultivar NU-ARS AC2. From these four accessions, spaced plants were visually selected and hybridized [58]. The FS, SCS, Utah Division of Wildlife Resources, and the Arizona, Idaho, and Utah AESs cooperated to release the tetraploid cultivar Ephraim. Ephraim derived from the increase and selection from an original introduction from near Ankara, Turkey. Ephraim is the first crested wheatgrass cultivar to possess rhizomes, which is a useful trait for soil stabilization and turfgrass settings [59]. The ARS at Logan, UT, in conjunction with the Utah AES, and sometimes the SCS, has released nine crested wheatgrass cultivars. The first were the tetraploid cultivars Hycrest and the Siberian-type Vavilov, and the hexaploid Douglas. Hycrest originated from hybridization between an induced tetraploid (fairway type) and a standard tetraploid. Development included two cycles of selection for seed and forage yield, among other traits, followed by the isolation and crossing of 18 clones to develop the breeders seed. Hycrest possessed substantially improved seedling establishment, forage, and seed yield than the cultivars Nordan and Fairway [60]. Vavilov was derived from the hybridization of P-27, with Russian and Turkish collections, followed by three cycles of selection for seedling and vegetative vigor, drought tolerance, seed yield, and disease and insect resistance, and then bulked seed from the open-pollinated progeny of 14 selected lines formed the breeder seed [61]. Douglas is the product of hybridization between hexaploid Russian, Turkish, and Iranian collections, followed by two cycles of selection for broad leaves, vegetative vigor, seed yield, and resistance to drought and pests [62]. Ongoing crested wheatgrass breeding by this group resulted in the tetraploid cultivars CD-II, RoadCrest, Hycrest II, Vavilov II, Stabilizer, and RangeCrest. CD-II originated from a 40,000-plant nursery of Hycrest followed by four cycles of selection for seedling vigor and vegetative vigor, leafiness, disease and insect tolerance, and leafiness [63]. RoadCrest is a rhizomatous crested wheatgrass derived from two Turkish introductions that went through two cycles of selection for rhizomatous growth habit, fine leaves, short stature, and seedling vigor [64]. Hycrest II was derived from five cycles of phenotypic selection within the induced tetraploid parent of the cultivar Hycrest based on seedling vigor, vegetative vigor, and seed yield [65]. Vavilov II was derived from selections from the original Vavilov and multiple introductions from Kazakhstan for seedling establishment, vegetative vigor, and seed yield [66]. Stabilizer is a Siberian-type crested wheatgrass selected from six introductions originating from Kazakhstan over two cycles of selection for seedling vigor, persistence, seed yield, pubescence, and reduced forage yield [67]. RangeCrest was derived from the cross of Hycrest and a hexaploid introduction, followed by a backcross to Hycrest.

Five cycles of selection followed this backcross for vegetative vigor, leafiness, color retention, seedling vigor, seed yield, and seed mass [68].

4. Genetic Variation

This collection of crested wheatgrass cultivars represents a substantial breeding effort and provides material adapted to most semiarid and arid regions of western North America. A strong focus of these breeding efforts was seedling establishment, seed yield, and size. This is because, in many instances, ground cover and stand establishment are more important than total forage production, or in other words, land managers and livestock producers may value a consistent stand of grass for soil stabilization and feed over a high forage yield [69,70]. The identification of substantial genetic control of these traits also drove this early breeding focus on seedling vigor and seed yield. Heritability for seed yield is moderate to high, with single plant values ranging from 0.66 to 0.87 and replicated plot values ranging from 0.96 to 1.00 [71]. Further, substantial genetic variation exists in crested wheatgrass populations for seedling characteristics including emergence height, dry weight, and fall stand [72]. These high levels of genetic control make these traits obvious targets for rapid genetic gain through plant breeding. Seed size is also a target because increased seed size leads to increased seedling emergence, although gains in this trait are complicated because it is inversely related to seed yield [72–75].

Following the successful development of cultivars with increased seedling establishment and plant persistence across a wide range of geographical and climatic conditions, there is now greater opportunity to focus on additional agronomic and ecological traits. While vegetative plant vigor has been a common trait used in selection of current commercial cultivars, there has been little focused effort to measure this trait quantitatively. This is despite the ample variation that exists within crested wheatgrass germplasm for this trait. A series of studies on different populations, including diploid and tetraploid germplasm, and competition levels found high levels of genetic variation and moderate to high heritability (0.53 to 0.86) for fresh and dry forage yield, tiller height, flag leaf width, first-cut vigor, and regrowth vigor [76,77]. Additional research with other populations and locations found genetic variation for forage yield with and without competition from other species, such as alfalfa (*Medicago sativa* L.), and the lack of correlation between first-cut vigor and regrowth vigor suggests that these traits may be improved simultaneously [77–79]. Unfortunately, and despite underlying genetic variation, genetic forage yield improvement is complicated in perennial forages due to several factors including the lack of an appropriate harvest index, ineffective selection methods for this trait, and inconsistent heritability values at different within species competition levels [50,80,81]. The widely varying environmental conditions associated with semiarid and arid rangelands in western North America further complicates improvements for forage yield. Annual precipitation, temperatures, and other environmental stresses are inconsistent year-to-year and the effect of genotype-by-environment interaction on this trait is large when compared to genotypic effects [69,70,78,82]. Another important factor for this trait is the general lack of ongoing recurrent selection within any single crested wheatgrass population for any trait. Successful and ongoing forage yield improvements will require consistent recurrent selection with optimized selection methods for perennial forage crops [51].

Research has identified genetic variation and/or moderate to high levels of heritability for several other quantitative traits in crested wheatgrass. These include the morphological and phenological traits of spikelets per spike, flag leaf pubescence, and rhizomatous growth habit; seedling and mature plant salt tolerance; nutritive value, including various measures of in vitro digestibility, protein content, and cell wall components; carbon isotope discrimination, which is a surrogate for water-use efficiency; flowering time, or maturity, for which a delayed maturity would increase the grazing season and increase livestock performance by prolonging the length of time that the plants are palatable; and mineral content for decreased risk of tetany [76,77,83–96]. Work on nutritive value in crested wheatgrass has been limited because other traits are considered more important. Nevertheless, relatively high levels of heritability were identified for digestibility, protein, and cell wall structure [92]. Additionally,

quality traits are not affected by $G \times E$ [78]. Thus, with concerted effort and resources, there is ample genetic variation to yield genetic gains in several traits that would have positive impacts on livestock production and/or rangeland revegetation.

5. Molecular Breeding and Genomics

Crested wheatgrass has been an orphan crop with little to no available resources for molecular biological investigations [97]. To this end, efforts to understand the crested wheatgrass genome and genes have relied on its close relationship with important cereal grain crops such as wheat [34]. Nevertheless, several studies laid the groundwork for further research and current studies are beginning to focus on the genomics and gene identification within this species.

Early spring growth and its correlation with a lack of anthocyanin has been the focus of various biochemical and genetic studies in crested wheatgrass. The first marker in crested wheatgrass was a seedling marker for a lack of anthocyanin pigment [98]. Further research using anonymous amplified fragment length polymorphism (AFLP) markers identified the genomic regions associated with reduced anthocyanin content and increased early spring growth [99]. Associated biochemical research found that crested wheatgrass possesses higher levels of non-structural carbohydrates in early spring and maintains these levels better than other grasses across the growing season. This early spring concentration of non-structural carbohydrates facilitates the early spring growth characteristic of crested wheatgrass and is a probable mechanism for its ability to compete with winter annual weeds such as downy brome (*Bromus tectorum* L.) [100,101]. Other biochemical analyses identified mechanisms for varying responses of different crested wheatgrass germplasm to osmotic stress. Those with greater resistance to osmotic stress maintain higher levels of proline and total nonstructural carbohydrates but lower levels of malondialdehyde and hydrogen peroxide [102].

Work with molecular markers provides insights into the crested wheatgrass genome and its relationship with other Triticeae species. The advent of anonymous markers such as AFLP and random amplified polymorphic DNA (RAPD) markers, the development of simple sequence repeat (SSR) markers from synteny with other Triticeae, and next-generation sequencing and genotyping-by-sequencing (GBS) techniques, has enabled genomic work to progress without a crested wheatgrass genome sequence. Analysis of crested wheatgrass germplasm with AFLP and SSR markers identified high levels of within population (>85%) genetic diversity rather than between populations [38,103]. Research with single nucleotide polymorphisms (SNP) and diversity array technology (DArT) markers or GBS have characterized genetic diversity and separated crested wheatgrass populations [104,105].

The first crested wheatgrass genetic linkage map created with AFLP and RAPD markers laid the groundwork for continuing genomic efforts and identified substantial levels of segregation distortion within the genome, which is consistent with other outcrossing, perennial species [106,107]. Ongoing linkage mapping has led to the identification of quantitative trait loci (QTL), including major QTL for ear stem length, second internode length, spike length, plant height, leaf number, fresh weight, dry weight, leaf length, tiller number, panicle length, leaf width, panicle width, stem diameter, and stem to leaf ratio [108–110]. RNA-Seq studies have identified differentially expressed genes controlling floral transition and development, including the identification of homologues to *TIMING OF CAB*, *CRY1*, *GI*, *FT*, and *CONSTANS* [111,112]. These genes provide a way to dissect pathways controlling these traits and potential marker-assisted selection for trait improvement.

Due to the perennial nature of crested wheatgrass that requires long cycle times, inefficient breeding strategies, and the strong effect of genotype-by-environment interaction on many traits, the use of molecular breeding strategies has the potential to greatly increase the efficiency of crested wheatgrass breeding. Crested wheatgrass is also a good candidate for molecular breeding approaches because of its outcrossing nature. While the rapid decay of linkage disequilibrium in outcrossing species requires a larger number of molecular markers to assess the genome, the remaining linkage disequilibrium is persistent and lends itself quite well to genomic selection approaches [52,113]. Current genomic

selection in the closely related intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkworth & D.R. Dewey) will provide a framework for genomic selection in crested wheatgrass [114]. Unfortunately, the use of molecular approaches in crested wheatgrass has been limited up to now, its status as an orphan crop and the limited resources available to breeding programs being the primary constraints.

6. Future Implications

Crested wheatgrass has been and will continue to be a key species for rangeland agriculture and revegetation. Despite the controversy surrounding its use on western North American rangelands [19], there is continued need for a perennial grass species that establishes rapidly and persists under harsh conditions to provide soil stabilization and feed for domestic livestock and wildlife. Unfortunately, there are only two active crested wheatgrass breeding and genetic programs in North America, which are led by the University of Saskatchewan, Saskatoon, and the USDA ARS Forage and Range Research Laboratory, Logan, UT. The two programs are responsible for developing crested wheatgrass cultivars with broad adaptations across the entire production region, while simultaneously working on additional species [69]. This requires obvious tradeoffs for trait development and resource allocation.

Despite this, breeding and genetic efforts are ripe for improvement. Updated selection methods can increase efficiency by utilizing family structure and simulating actual production, rather than spaced plant conditions, and incorporating genomic selection to decrease selection cycle times [50,114–116]. Additional steps could include attempts to develop hybrids or population hybrids for production settings [117,118]. The strong combining ability in crested wheatgrass germplasm and outperformance of hybrids over synthetic crested wheatgrass increases the feasibility of this approach, although the commercial seed production of crested wheatgrass population hybrids will require changes to the seed industry [106,119,120].

Efforts can also be made to develop cultivars better suited for mixed rangeland seedings. Research has shown that native plant materials establish and persist better when seeded with crested wheatgrass [121]. The days of monoculture crested wheatgrass seedings are over. From a breeding and genetics standpoint, efforts may focus on developing cultivars specifically for mixed seedings, perhaps by using ecological combining ability, wherein plants are selected in the presence of genotypes from other species [79,122]. Future crested wheatgrass breeding and genetics requires improved breeding and molecular breeding methods in conjunction with ecological, rather than agronomic approaches to revegetation. This focus will result in novel cultivars that meet environmental and agricultural sustainability measures.

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