Breeding Strategies in Crested Wheatgrass

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ABSTRACT: Conventional breeding programs in crested wheatgrass [Agropyron cristatum (L.) Gaertn., A. desertorum (Fisch. ex Link) Schult., and A. fragile (Roth) Candargy] have been confined to selection and hybridizstion within the ploidy levels of the complex, particularly the diploids (Fairway) and tetraploids (Standard and Siberian). Gene flow among the three ploidy levels of the complex has been accelerated by induced polyploidy and hybridization. 'Hycrest', a cultivar developed from hybrids between induced tetraploid Fairway and natural tetraploid Standard types has shown excellent potential on semiarid range sites.

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INTRODUCTION

Since its introduction in the early 1900's (Dillman 1946), crested wheatgrass [Agropyron cristatum (L.) Gaertn., A. desertorum (Fisch. ex Link) Schult., and A. fragile (Roth) Candargy] has hsd more impact on the improvement of western rangelands than any other grass. It has been particularly valuable as a source of forage during the early spring.

The crested wheatgrass complex consists of an autoploid series of diploid (2n=2x=14), tetraploid (2n=4x=28), and hexaploid (2n=6x=42) forms. Although some structural differences are evident among the chromosomes of the crested wheatgrass species, Dewey (1974) concluded from several studies that the same basic genome occurs at all three ploidy levels. He advised grass breeders to consider the entire complex as a single gene pool from which selected characteristics could be extracted and combined at a desired ploidy level. Unfortunately, differences in ploidy levels have prevented breeders from exploiting the full range of genetic diversity within the complex. Breeding has been confined largely to selection snd hybridization within ploidy levels, primarily the diploid and tetraploid populations.

The diploids sre represented primarily by the cultivar 'Fairway' developed by Agriculture Canada at Saskatoon, Saskatchewan and released in 1932 (Elliott and Bolton 1970). Fairway, the first crested wheatgrass cultivar to be released in North America, was selected from an introduction from the U.S.S.R. (PI 19536). It is leafier and more procumbent, but less drought tolerant than the major tetraploid Standard cultivars. Fairwsy has been widely used in range reseeding programs and is still an important component of Canadian seed trade (Elliott and Bolton 1970). The diploid cultivar 'Parkway', which was selected from Fairway on the basis of improved vigor, height, and leafiness, was relessed in 1969 by Agriculture Canada at Saskatoon. It is more upright and has been more productive in terms of forage and seed thsn Fairway in Canadian trials. A relatively new cultivar, 'Ruff', was developed from Fairway-type germplasm by the U. S. Department of Agriculture-Agricultural Research Service (USDA-ARS) in cooperation with the Nebraska Agricultural Experiment Station (AES). It has a spresding (brosd-bunch) growth habit and is recommended for grazing and revegetation of problem sites in the low precipitation zones of the Great Plains (Hanson 1972, USDA Extension Service 1978).

The most commonly used tetraploids are the Standard cultivars, 'Nordan' and 'Summit', and the Siberian cultivar 'P-27'. All three cultivars were released in 1953. Nordan, which was released by the USDA-ARS Northern Great Plains Research Center at Mandan, North Dakota, in cooperation with the North Dakota AES, was derived from plant materials obtained from the cold dry plains of the U.S.S.R. It is noted for its upright growth habit, relatively large seeds, and good seedling vigor (Rogler 1954, Wolfe and Morrison 1957). Summit, released by Agriculture Canada at Saskatoon, also wss developed from germplasm obtained from the U.S.S.R. Summit is noted for its abundant forage production, but problems associated with seed processing have

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limited its popularity. The Siberian cultivar 'P-27' was released by the USDA-Soil Conservation Service (SCS). It has narrow, awnless spikes and relatively fine leaves and stems. P-27 is reported to be well adapted on light droughty soils (Hanson 1972) and it matures later and remains green longer than typical Standard types.

Two new tetraploid cultivars, 'Ephraim' and 'Hycrest', were released in 1983 and 1984, respectively. Ephraim was selected from collections made near Ankara, Turkey and released by the USDA-Forest Service (FS), USDA-SCS, Utah Division of Wildlife Resources, and several state experiment Stations. It is reported to be a persistent and drought resistant cultivar; however, it is noted primarily for its sod-forming characteristics. Rhizomes are usually present by the second or third year under semiarid conditions. The cultivar is slightly shorter, but similar to Fairway in biomass production. Hycrest was released in 1984 by the USDA-ARS in cooperation with the Utah AES. It was developed from hybrids between induced tetraploid Fairway and natural tetraploid Standard types (Asay et al. 1985). Hycrest, the first interspecific hybrid of crested wheatgrass to be released, tends to be more productive and vigorous than either of the parental species, particularly during the seedling establishment phase. This cultivar is discussed in more detail under Interploidy Breeding.

BREEDING PROGRAMS

The USDA at Utah State University is actively involved in a research program to develop improved germplasm and cultivars of range grasses, including crested wheatgrass. Breeding populations for this program are obtained from both intra and interploidy hybridization and selection procedures. Even without the added time required to introgress genetic diversity into breeding populations through interploidy crosses, the development of improved, stable cultivars involves a series of time consuming procedures (Fig. 1). Clonal lines selected from genetically broad based source nurseries are often progeny tested in field and laboratory trials. Selection criteria during this phase vary according to the objectives of the breeding program and available resources. They include improved seed and forage yield, better seasonal distribution of growth, leafiness, forage quality, seedling vigor, resistance to plant pests, and resistance to environmental stress.

The grass improvement program at Logan has emphasized evaluation and selection of clonal and progeny lines under range conditions in the field. Laboratory screening procedures are also being refined to evaluate breeding lines for characteristics associated with seedling vigor under environmental stress, and for resistance to insects and diseases. It is encouraging that significant heritable genetic variation has been found among progeny lines in both the field and laboratory. This indicates that selection will result in genuine genetic progress. Superior clones have been selected and isolated in crossing blocks to produce breeders seed of experimental strains, which are evaluated over a range of field environments for possible release as new cultivars.

Interploidy Breeding

The amount of genetic diversity available from a given taxon is limited. Thus, it would be helpful for breeders to investigate the potential benefits of genetic introgression among related taxa. Combining the genetic resources of the three ploidy levels in the crested wheatgrass complex would substantially expand the genetic diversity available at any one level. Barriers, which have restricted crosses among taxa in the complex, have been largely removed by induced polyploidy (Dewey and Pendse 1968). All combinations of crosses have now been made among the diploid, tetraploid, and hexaploid levels (Knowles 1955; Dewey 1969, 1973).

Interploidy breeding at diploid level--Transfer of genes from hexaploid (6x) or tetraploid (4x) crested wheatgrass to diploid forms through (4x-2x) or (6x-2x) X 2x crosses has been difficult to achieve. The necessary crosses and backcrosses are hard to make and the triploids (3x) needed to bridge the transfer are sterile (Asay and Dewey 1979; Dewey 1971). In addition, the triploid hybrids produce a preponderance of functional unreduced (3x) eggs, which results in a one-way gene flow from the diploid to higher ploidy levels. Restriction of genetic transfer to the lower ploidy levels has also been observed in orchardgrass, *Dactylis glomerata* L. (Jones and Borrill 1962, Zohary and Nur 1959).

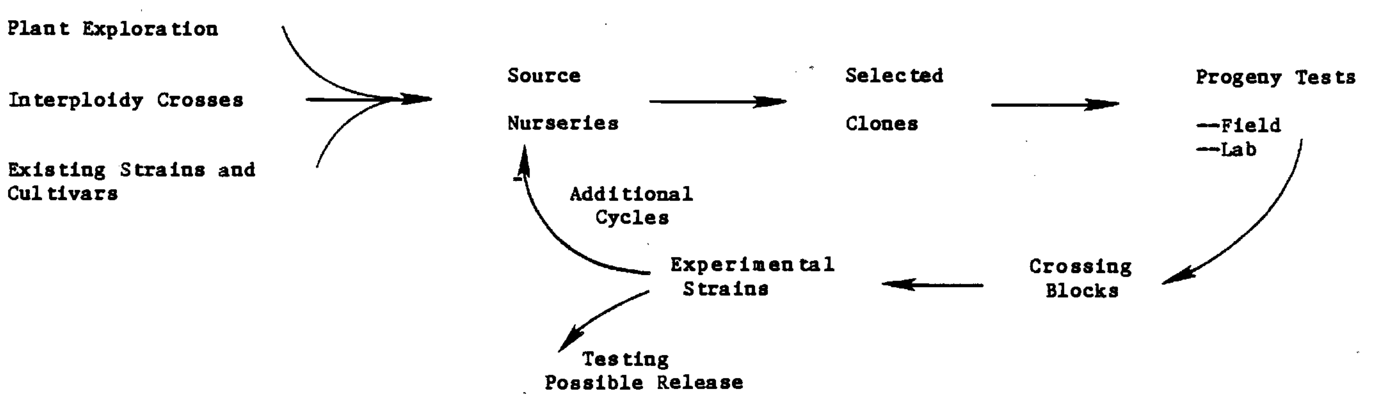

Figure 1.—Sequence of events in crested wheatgrass breeding program.

An infusion of genetic traits from the hexaploids and tetraploids to the diploid level would be particularly valuable to the crested wheatgrass breeder. Although diploid Fairway is leafier and of better forage quality than the Standard forms, it has smaller seeds and tends to be less productive and drought hardy. Moreover, the genetic variability available for selection has been especially limited in the diploid breeding population.

Dewey (1971) found that triploids with a colchicine-induced tetraploid (C4x) in their parentage produced an increased proportion of functional reduced gamètes. This made these triploids potentially more useful as a genetic bridge from the natural tetraploid (N4x) to the diploid level. Using triploids from (N4x-C4x) X 2x crosses in a backcrossing sequence, he successfully transferred genes from the tetraploid to the diploid level. This procedure should be extremely useful to breeders working with diploid crested wheatgrass.

Fairway type germplasm has been the only known diploid crested wheatgrass of economic importance. Additional diploid types have recently been reported (Dewey and Asay 1982), and others may yet be found through plant exploration. These diploids may be valuable in the development of improved diploid or tetraploid cultivars or as a source of genetic traits to infuse into Fairway breeding populations. Some proposed schemes for utilizing these diploids are shown in Figure 2. Schemes 1, 2, and 3 illustrate how new tetraploid types could be developed through hybridization and induced polyploidy. Alternative 4 is suggested as a means of combining traits of exotic diploids with Fairway.

Interploidy breeding at tetraploid level--Several procedures could be effectively used to combine germplasm from the three ploidy levels at the tetraploid level (Fig. 3). Fertile tetraploid (C4x) plants have been obtained by treating Fairway diploids with colchicine (Tai and Dewey 1966). Subsequently, Dewey and Pendse (1968) reported that C4x clones crossed readily with N4x selections and

1. C_1C_1 X $C_2C_2 \longrightarrow C_1C_2 \xrightarrow[\text{Treatment}]{\text{Colchicine}} C_1C_1C_2C_2$

2. C_1C_1 Colchicine Treatment $C_1C_1C_1C_1$

X $\longrightarrow C_1C_1C_2C_2$

C_2C_2 Colchicine Treatment $C_2C_2C_2C_2$

3. $C_1C_1C_2C_2$ / $C_1C_1C_1C_1$ X Existing Tetraploids $\longrightarrow$ New Tetraploids

4. Transfer of genetic diversity from diploid taxa to Fairway

C_1C_1 X Fairway (C_3C_3) $\longrightarrow C_1C_3$

C_3C_3 X $C_1C_3 \longrightarrow C_3, C_3,$

Figure 2.--Breeding schemes to combine the genetic resources of diploid taxa of crested wheatgrass. Cn represents a genome of 7 chromosomes and CnCn or CnCnCnCn diploid or tetraploid taxa, respectively.

Induced Tetraploid (C4x) X Natural Tetraploid (N4x) $\longrightarrow$ 4x

(N4x - 2x) X N4x $\longrightarrow$ 4x

Hexaploid - Diploid Crosses (6x-2x) $\longrightarrow$ 4x

(6x-2x) X N4x $\longrightarrow$ 4x

[(6x - 2x) X C4x] X N4x $\longrightarrow$ 4x

(6x - 4x) $\longrightarrow$ 5x $\longrightarrow$ 4x

(6x-4x) $\longrightarrow$ 5x X 4x $\longrightarrow$ 4x

Figure 3.--Interploidy breeding schemes to transfer germplasm to tetraploid (4x) level in crested wheatgrass.

that the fertility of the derived C4x-N4x hybrids compared favorably with that of the parents. Their results also indicated that fertility of the hybrid could be further improved through selection. Furthermore, many of the hybrid plants were substantially more vigorous than the parental species.

The USDA-ARS at Utah State University has included the C4x-N4x hybrid in an intense breeding program. Eighteen clones were selected from an original population of 8,000 hybrid plants on the basis of evaluation in a source nursery and progeny tests on range sites. Selection for vigor of seedlings and mature plants, seed and forage yield, resistance to environmental stress, and resistance to plant pests was stressed. The 18 parental clones were isolated in a crossing block to produce an experimental strain that was evaluated and released as the cultivar, 'Hycrest'. The hybrid has been evaluated on several representative range sites in the Intermountain West. Forage yield data during and immediately after stand establishment at five locations are presented in Table 1. In each of these trials, Hycrest was easier to establish and produced significantly more forage than Nordan or Fairway. The superiority of the hybrid is particularly noteworthy under environmental stress where stands are usually difficult to obtain. This was demonstrated at Location D (Lakeside, UT), where drought, soil salinity, and infestations of cheatgrass and halogeton seriously impeded the establishment of other cultivars (Table 1). Long-term productivity and persistence of Hycrest are being evaluated. Additional crosses are now being made among clones of the parental species to improve the general performance level and broaden the genetic base of the C4x-N4x hybrid breeding population.

Other hybridization schemes offer promise in the interploidy transfer of genetic traits to the tetraploid level (Fig. 3). Although N4x-2x triploids are plagued with sterility problems, Dewey (1971) concluded that fertile 4x plants could be derived from (N4x-2x) X 4x crosses. This would provide an alternative method of transferring germplasm from the diploid to the tetraploid level. Dewey (1969, 1974) also found that stable 4x populations could be derived from 6x-4x crosses. Many of the pentaploid (5x) plants from this cross were more vigorous than either parent and their fertility approached that of natural tetraploids. Dewey proposed that stable 4x populations could be

Table 1.--Forage yield of three crested wheatgrass cultivars on five range sites during stand establishment (Yr-1) and subsequent seasons (Yr-2 and Yr-3).

Cultivar	Location A	B	C	D		E	
	Yr-1	Yr-1	Yr-2	Yr-2	Yr-3	Yr-2	Yr-3
	lbs/A						
Hycrest	3652	1199	2239	2333	1827	3522	2381
Nordan	3387	431	1556	1380	1338	2174	1743
Fairway	3239	565	----	858	1263	2835	----
$LSD_{(0.05)}$	495	107	449	346	222	743	418

Location A = Decker, MT coal surface mine, 12.5 in average annual precipitation (AP); B = NW Utah, 14.4 in AP; C = near Sublette, ID, 12.8 in AP; D = Lakeside, UT, 6.1 in AP; and E = Thiokol, Wasatch Div., 14.1 in AP.

selected from 5x populations and from progenies of 5x-4x crosses. Crosses between hexaploids and diploids have been proposed as a breeding tool to combine germplasm from all three ploidy levels at the tetraploid level (Asay and Dewey 1979). Although the 6x-2x tetraploids are difficult to obtain and have limited agronomic merit in their own right, they may be crossed with other natural and induced tetraploids to produce genetically diverse breeding populations.

Interploidy breeding at hexaploid level--Selection and hybridization of crested wheatgrass at the hexaploid level is possible but probably is not a productive alternative. Although only a limited number of hexaploid ecotypes have been observed under range conditions in the U.S. and Canada, they appear to be relatively coarse textured and of limited agronomic merit. In addition, the complex inheritance patterns in the hexaploids make them more difficult to manipulate in a breeding program than are the tetraploids or diploids. The rarity of hexaploids under natural range conditions suggests that 2n=42 is above the optimum ploidy level for crested wheatgrass.

Nonetheless, genetic transfer from diploids and tetraploids to the hexaploid level has been achieved (Dewey 1974). Fully fertile 6x plants have been selected from progenies of first generation backcrosses of 6x-C4x or N4x hybrids with the 6x parent. Dewey also produced reasonably fertile 6x plants from crosses among 5x hybrids.

PLANT EXPLORATION

Because crested wheatgrass is indigenous to Asia, plant exploration in this area is essential to provide plant breeders with wider genetic diversity. Most of the early reseeding on western rangeland was done with a relatively few introductions made in the early 1900s, the majority of which were from the U.S.S.R. Plant breeding improved the general performance level of the available plant materials, but the parentage of most cultivars has a relatively narrow genetic base. As the value of crested wheatgrass became more generally accepted, plant exploration efforts were expanded. Introductions from U.S.S.R., Iran, China, and other countries have contributed to the current storehouse of genetic diversity.

Plant materials recently collected from Iran are particularly noteworthy. Significant differences have been found among these accessions for characters such as maturity date, plant height, seed size, seed yield, plant texture, and rhizome development. More than one-half of the plants are rhizomatous (Dewey and Asay 1975). Other accessions recently introduced from Turkey also are rhizomatous. A breeding program is in progress to incorporate selections from these accessions into new rhizomatous cultivars or to transfer the character to existing cultivars. These plant materials will probably be of most utility in special use situations where soil stabilization is a major concern. A low-growing, sod-forming type with a longer green period would be particularly useful for dryland lawns in suburban and rural areas. Newly acquired introductions from the U.S.S.R. and China are also being evaluated. Some of these accessions have shown promise, particularly in terms of aftermath production after clipping or grazing.

SUMMARY

Although crested wheatgrass in its present form has been a valuable source of plant materials for improving western rangelands, it is evident that its potential can be substantially improved through the development of improved cultivars. Plant breeding to date has been restricted largely to selection and hybridization within populations with similar chromosome numbers, primarily diploids (2n = 14) and tetraploids (2n = 28). The noteworthy cultivars released from these intraploidy breeding programs are Fairway, Parkway, Ruff, Nordan, Summit, P-27, and Ephraim.

Several schemes have been devised and tested to transfer genetic traits among the different ploidy levels of crested wheatgrass. The USDA-ARS at Utah State University has successfully combined the germplasm of the diploids and tetraploids by crossing induced tetraploid Fairway with natural tetraploid Standard types. The cultivar 'Hycrest', released in 1984 from this research program, was developed from this hybrid. Hycrest has been significantly more productive than the most commonly used cultivars, Nordan and Fairway, particularly in terms of stand establishment on harsh range sites. Results from research indicate that additional crosses involving more select parentage will yield even more genetic progress. New diploid populations and rhizomatous forms, obtained from plant collections recently made in Asia, also have made significant contributions to the genetic resources available to geneticists working to improve crested wheatgrass.

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