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Establishment of 'Hycrest' Crested and T-21076 Thickspike Wheatgrasses in Three Environments

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ABSTRACT

Introduced grass species such as standard crested wheatgrass [*Agropyron desertorum* (Fischer ex Link) Schultes] are most often used to revegetate degraded rangelands in the Intermountain region of the western USA. Use of native grass species is rising because public land management policies increasingly favor plant materials representative of native flora. Our objective was to compare the population T-21076, a promising source of germplasm of the native thickspike wheatgrass [*Elymus lanceolatus* subsp. *lanceolatus* (Scribner & Smith) Gould] [Syn-*Elytrigia dasystachya* (Hook.) A. Löve & D. Löve], with 'Hycrest' crested wheatgrass for forage yield, tiller number, and tiller weight during and after establishment. The relative importance of tiller number and tiller weight for forage yield production was compared using path coefficient analysis. Seedlings were transplanted from a greenhouse to three field environments corresponding to three moisture stress levels where six harvests were evaluated through two growing seasons. Tiller number was more affected by moisture stress than tiller weight. Forage yield production of the caespitose Hycrest was more stable under moisture stress than the rhizomatous T-21076. T-21076's forage yield depended mostly on tillering through rhizomatous spread, which was more sensitive to moisture stress than the tillering of Hycrest. Tiller weight of T-21076 was similar in all environments and was equal or lower than Hycrest's at all harvests. In contrast to T-21076, Hycrest's forage yield production relied primarily on tiller weight, a more stable trait than tiller number. Increases in Hycrest's tiller weight were able to partially compensate for reductions in its tiller number with increasing moisture stress. The advantages conferred by T-21076's rhizomatous spreading and resultant tillering are probably limited by their sensitivity to moisture stress.

Crested wheatgrass is often used to revegetate degraded rangelands in the Intermountain region (Vallentine, 1989). Hycrest crested wheatgrass has become widely seeded because it is more vigorous than older cultivars (Asay et al., 1985, 1986). Following an initial decline from maximum production a few years after seeding, crested wheatgrass maintains long-term stable levels of production (Hull and Klomp, 1966). However, an improved native grass cultivar may be preferred when plant material more representative of the pristine flora is desired and economic return is secondary (Krueger et al., 1990).

Thickspike wheatgrass is a highly rhizomatous grass that is commonly used in the Intermountain region to stabilize soil on disturbed rangelands, mine spoils, and other sites subject to erosion (Carlson, 1986). The T-21076 population, collected at The Dalles, OR, is more readily established and more productive than other germplasm of this species (J.R. Carlson, 1986, personal communication). T-21076 can also be hybridized with Snake River wheatgrass [proposed name *Elymus lanceolatus* subsp. *wawawaiensis* (Scribner & Gould) J.R. Carlson & D.R. Dewey] or slender wheatgrass [*Elymus trachycaulus* (Link) Gould ex Shinners] to develop improved native grass cultivars. These grasses are well suited to genetic improvement by hybridization since all share the S and H genome combination characteristic of *Elymus* (Barkworth and Dewey, 1985).

Studies with several temperate perennial forage grasses have shown similar seasonal patterns of tiller appearance and death (Korte, 1986). Active tillering takes place in two periods, in the spring before internodal elongation, and between anthesis and senescence. Tiller death occurs mostly during reproductive growth. Reproductive tillers have a higher growth rate than vegetative tillers (Langer, 1957), thus grasses with higher proportions of reproductive tillers may have higher growth rates at the flowering stage.

Studies of the effect of competition on tillering in a pasture situation show that the principal component of yield shifts from tiller number to tiller weight as stands mature (Nelson et al., 1977; Jones et al., 1979; Zarrough et al., 1983a,b). However, under low-plant-density conditions, several researchers cited by Zarrough et al. (1983a,b) attributed greater importance to tiller number than to tiller weight. Our objective was to evaluate and contrast Hycrest and T-21076 forage yield and yield components (tiller number and tiller weight) during and following establishment in three environments representing discrete levels of moisture stress. Interactions between environment and genotype must also be considered when comparing genotypes since their ranking may differ among environments (Eberhart and Russell, 1966). If the ease of establishment under moisture stress is similar for the two grasses, T-21076 would be a viable alternative for rangeland seeding.

MATERIALS AND METHODS

Seedlings of T-21076 and Hycrest, ≈3 mo old, were transplanted from greenhouse containers to the field in April 1989. The experimental design was a split plot in three environments. Irrigated and nonirrigated environments were adjacent to each other at Greenville Farm, North Logan, UT (Millville silt loam; coarse-silty, mesic Typic Haploxeroll). The third, a nonirrigated foothill environment, was ≈1 km away, at the base of the Bear River range of the Wasatch Mountains at Logan, UT (Sterling gravely loam; loamy-skeletal, mixed, mesic Typic Calcixeroll). Despite their proximity, the foothill environment exhibited considerably more moisture stress than the Greenville environments because the FE soil was excessively well drained and on a west-facing slope.

Total precipitation from April 1989 to May 1990 was 74% of normal at the nearest official weather station, 1.3 km from the FE and 2.4 km from the IE and NIE. The precipitation in millimeters, with deviation from the normal in parentheses, was 27 (−26), 47 (+4), 22 (−17), 0 (−11),

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Abbreviations: DW, dry weight; FE, foothill environment; IE, irrigated environment; NIE, nonirrigated environment; TN, tiller number; TW, tiller weight.

8 (−17), 32 (−5), 51 (+15), 28 (−11), 8 (−33), 27 (−16), 35 (−5), 28 (−16), 43 (−9), and 41 (−3) for 14 mos in turn. A sprinkler system with two irrigation lines 30.5 m apart and sprinkler heads 6.1 m apart was used to apply 9.3 mm of water to the IE on 21 June, 17.6 on 27 June, 17.9 on 6 July, 12.3 on 21 July, 18.2 on 2 Aug., 16.3 on 18 Aug., 16.9 on 31 Aug., and 6.1 on 13 Oct. 1989. This increased total precipitation for the IE to 92% of normal for the 14-mo period.

Three replicates, consisting of six main plots (harvests), were present in each environment. Main plots were harvested once on 20 July, 20 Aug., 20 Sept., and 20 Oct. 1989, and 3 May and 4 June 1990. Exceptions to these dates for the FE are noted below. Subplots (entries) consisted of six plants of T-21076 or Hycrest spaced on 1-m centers. Plants were clipped at ground level to measure dry weight. At early harvests, tiller number was determined by counting all tillers and tiller weight was calculated as DW/TN. When it became prohibitive to count the entire sample, TN of a subsample of one-half or one-quarter of the plant's area was determined and TW was calculated from DW and TN of the subsample. To estimate total TN, the number of sampled tillers was added to the estimated number of tillers in the unsampled portion of the plant (DW of the unsampled portion/TW estimated from the sampled portion). Clippings were oven-dried at 60 °C for 48 h before weighing. To quantify rhizomatous spreading, a grid marked with 1-cm^2 gradations was used to measure plant contour area, the area within the largest polygon defined by the plant's outlying tillers. Plant basal area, the area actually occupied by live tillers (not including bare or decadent areas), was also measured with the grid. Harvest 6 reproductive-tiller percentage was calculated by dividing spike number by TN.

Because of grasshopper damage in the FE following Harvest 1, additional data collection was delayed until Harvest 6, when all remaining 15 whole plots (original 18 less 3 destroyed at Harvest 1) were measured. Least-squares means (SAS, 1990) were reported instead of ordinary means because of plant mortality resulting from grasshopper damage.

An arcsine transformation was applied to normalize reproductive-tiller percentage data. A common logarithmic transformation was applied to all other data to correct for positive correlation between mean and variance (Sokal and Rohlf, 1969). Appropriate choice of error terms for testing of hypotheses was made based on expectations of mean squares, with all effects fixed except replicates. When appropriate, the 1-df contrast between years (Harvests 1 to 4 vs. Harvests 5 to 6) was separated from the overall 5-df harvest effect. The proportion of the harvest effect explained by years was calculated as the sum of squares for years divided by the sum of squares for harvests. This procedure was also used for interactions involving harvests.

To determine whether the relative importance of yield components TN and TW on DW was consistent across harvests, environments, and entries, tests for interactions of these factors with yield components were made for the IE and NIE. Path coefficients (Li, 1975) were calculated for subsets of homogeneous data, i.e., those that exhibited no interaction with TN or TW, using the SAS CALIS procedure and its LINEQS option (SAS, 1990). Path coefficients separated the direct influences of TN and TW (independent variables) on DW (dependent variable). Confidence intervals of path coefficients were calculated assuming their distributions were normal. The LSD for confidence intervals was calculated by multiplying the path coefficient's standard error by 1.414 and the appropriate tabulated value of t.

RESULTS AND DISCUSSION

Irrigated and Nonirrigated Environments at Greenville Farm

Dry weight demonstrated marked environment × harvest × entry interaction (Table 1). Further inspection revealed that this was primarily a result of a difference between Year 1 and Year 2 harvests, where growth was primarily vegetative and reproductive, respectively (Fig. 1). This constituent environment × year × entry interaction (1 df) accounted for 56% of the overall environment × harvest × entry interaction. While the entries were similar across environments in Year 1, at both Year 2 harvests, T-21076 outperformed Hycrest in the IE while the reverse was true in the NIE. As the experiment progressed, T-21076 was able to take greater advantage of the IE's supplemental water.

While TN of Hycrest stabilized after Harvest 3 in both environments, TN of T-21076 continued to increase through the remainder of Year 1 and into Year 2 (Fig. 1). This resulted in a harvest × entry interaction (Table 1), 90% of which was accounted for by the constituent year × entry (1 df) interaction. In Year 2, TN of T-21076 was much greater than Hycrest, but the difference was much greater in the IE than the NIE, again indicating the greater ability of T-21076 to exploit the supplemental water.

Moisture stress influenced TW less than TN (Fig. 1). Consequently, the environment main effect and its interactions with harvest and entry were nonsignificant for TW ($P > 0.10$) (Table 1). Hycrest exhibited higher TW in Year 2, when growth was reproductive, but the two entries were similar in Year 1. The constituent year × entry interaction (1 df) accounted for 86% of the overall harvest × entry interaction. Year 2 TW was similar between environments for T-21076 but higher in the NIE than the IE for Hycrest. This resulted in a significant ($P < 0.10$) environment × harvest × entry interaction, of which 89% was explained by the constituent environment × year × entry interaction (1 df).

T-21076's increase in DW over harvests was explained by the concomitant increase in TN, especially in Year 1. In contrast, Hycrest showed no significant increase in tillering after Harvest 3. After this time, Hycrest increased its DW solely by increasing TW. T-21076 TW was never significantly higher than Hycrest TW and did not increase from Year 1 to Year 2 as much as Hycrest. Lack of irrigation did not decrease Hycrest DW in Year 2 as much as T-21076 DW because of Hycrest's greater ability to maintain TN under stress and a compensatory increase in TW (Table 2).

By Harvest 2, plant contour area of T-21076, with its rhizomatous growth habit, significantly exceeded that of Hycrest (Fig. 1). This difference was enhanced by supplemental irrigation resulting in an environment × entry interaction. Tillering of T-21076 was closely related to plant contour area (Fig. 1), implying T-21076 increased its TN primarily through rhizomatous spreading.

Plant basal areas of Hycrest and T-21076 were more similar to one another than their plant contour areas

Table 1. Mean squares for wheatgrass dry weight, tiller number, tiller weight, plant contour area, and plant basal area in the irrigated and nonirrigated environments at Greenville Farm (North Logan, UT).

		Mean sqaures				
Source	df	Dry weight	Tiller number	Tiller weight	Plant contour area	Plant basal area
Environment	1	5.48**	6.72**	0.06 NS	18.97*	7.92**
Replication (Environment)	4	0.03	0.15	0.09	0.97	0.27
Harvest	5	31.84**	11.92**	7.25**	24.07**	15.67**
Environment × Harvest	5	0.29 NS	0.23*	0.05 NS	0.51 NS	0.21†
Error *a*	20	0.15	0.03	0.06	0.24	0.09
Entry	1	2.14*	0.61**	0.46**	58.91**	0.90**
Environment × Entry	1	0.24 NS	0.37**	0.01 NS	4.30**	0.25 NS
Harvest × Entry	5	0.21†	1.46**	0.71**	2.10**	0.16 NS
Environment × Harvest × Entry	5	0.29*	0.18*	0.07†	0.41 NS	0.16 NS
Error *b*	24	0.09	0.06	0.03	0.33	0.09

†,*,** Significant at $P < 0.10$, 0.05, and 0.01, respectively.

(Table 2; Fig. 1). Although T-21076 colonized a greater surface area above ground, tillering was sparse and most of the surface area was not covered by live tillers. Plant basal area of Hycrest was actually 23% greater than T-21076 in the NIE, though they did not differ in the IE. Though rhizomatous spreading may improve soil conservation, increased forage yield may not be an advantage of this growth habit. Bunchgrasses are more prominent in semiarid environments (Caldwell et al., 1983), and many suspect that they are better competitors in such environments. For example, bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] populations in drier environments are strictly caespitose, while those in more mesic environments may have short rhizomes (Evans and Tisdale, 1972).

The percentage of vernalized tillers (Harvest 4 TN/Harvest 5 TN) closely corresponded to Harvest 6 reproductive-tiller percentage. Percentages of vernalized tillers (and corresponding reproductive-tiller percentages) were 92 (86), 92 (91), 44 (48), and 35 (38) for Hycrest IE, Hycrest NIE, T-21076 IE, and T-21076 NIE, respectively. Most Hycrest tillers present at the end of the experiment were present at the end of Year 1, while this as not true for T-21076, especially in the NIE. The higher proportion of ver-

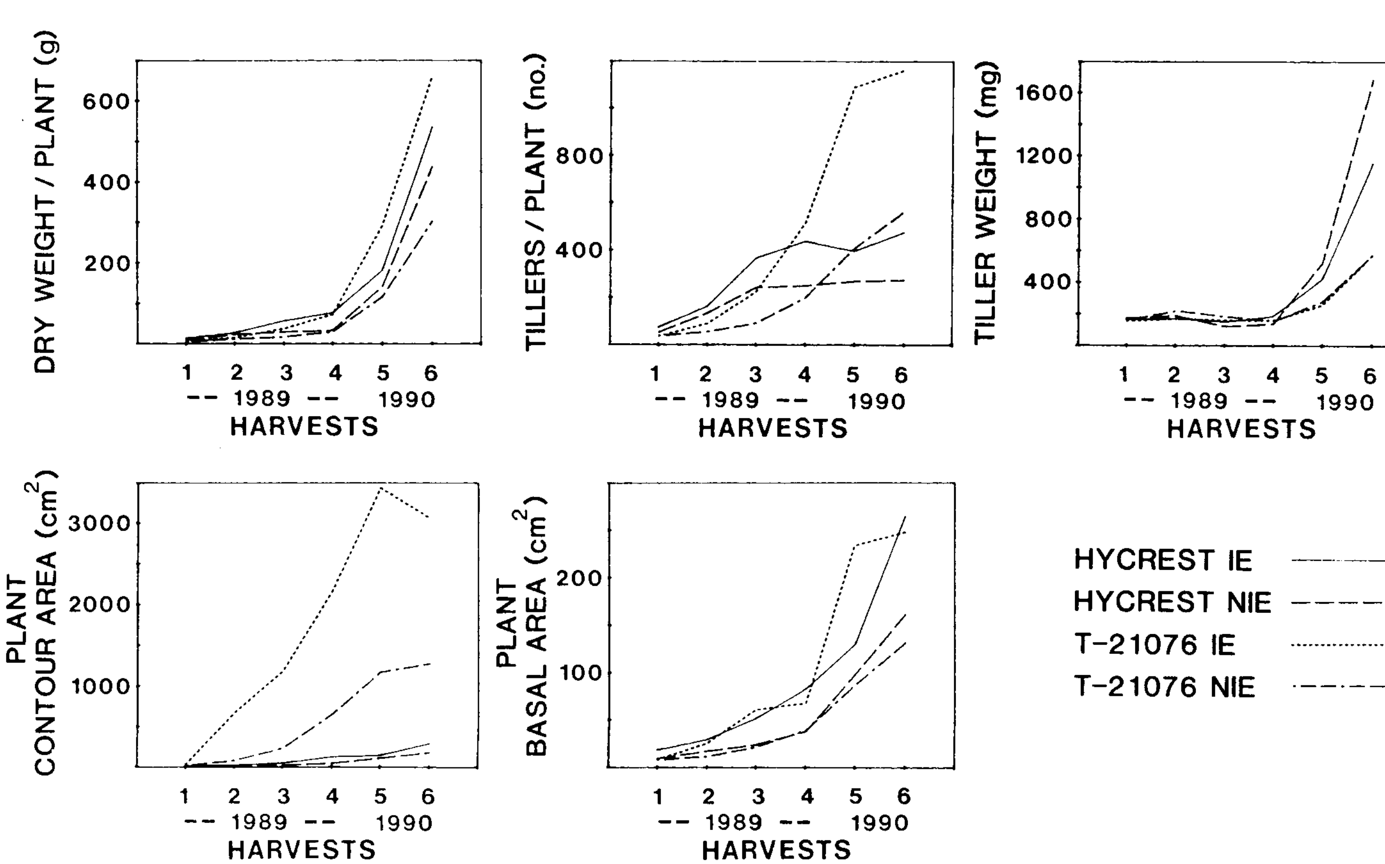

Fig. 1. Dry weight per plant, tillers per plant, tiller weight, plant contour area, and plant basal area of Hycrest crested and T-21076 thickspike wheatgrasses at six harvests in the irrigated (IE) and nonirrigated (NIE) environments at Greenville Farm, North Logan, UT. Error measurement not given, because data were transformed before analysis. See Tables 2 and 3 for statistically significant differences.

nalized tillers for T-21076 in the IE is a result of irrigation in Year 1. Tillering in Year 2 (nonvernalized tillers) in the IE would not be expected to be greater than in the NIE because water was not applied to the IE in Year 2.

Since all interactions between yield components and entry, environment, and harvest factors (independent variables) were significant for DW (dependent variable), path coefficients from each of the 24 combinations of entry, environment, and harvest were calculated independently to allow analysis of homogeneous subsets of data. Tabulation of the number of instances where each yield component's coefficient was significantly higher indicted that TN was usually more important than TW for T-21076 (7 vs. 1 comparisons, with 4 not significantly different) and usually less important than TW for Hycrest (2 vs. 9 comparisons, with 1 not significantly different) (Table 3).

Comparison of the Foothill Environment with the Greenville Environments

Comparison of the FE with the Greenville environments was based on Harvest 6. Hycrest DW was nearly twice that of T-21076 in the FE (Table 2). Hycrest DW was considerably greater in the NIE and FE relative to the IE than T-21076, indicating Hycrest's DW was more stable under moisture stress. Tiller number of T-21076 did not exceed that of Hycrest in the FE as it did in the IE and NIE. T-21076 TW was stable across the three environments but never exceeded Hycrest's TW. In contrast to T-21076, Hycrest's TW varied among environments, being greater in the NIE than either the IE or the FE. Rhizomatous spreading of T-21076 was greatly restricted by moisture stress such that plant contour area in the FE was only 6% that in the IE. In the FE, Hycrest plant basal area was 36% higher than T-21076. Plant basal area of Hycrest increased relative to T-21076 with increasing moisture stress.

While reproductive-tiller percentage of Hycrest for the FE (87) was similar to the IE (86) and NIE (91), T-21076's reproductive-tiller percentage was considerably higher; 73 (FE) vs. 48 (IE) and 38 (NIE). Although the proportion of vernalized tillers was not measured in the FE, its close association with reproductive-tiller percentage in the IE and NIE suggests that a far greater percentage of the total number of T-21076 tillers was produced during Year 1 at the FE relative to the IE and NIE. The relative paucity of tillering of T-21076 in Year 2 in the FE is probably associated with the smaller amount of rhizomatous spreading in this environment.

Table 2. Dry weight per plant, tillers per plant, tiller weight, plant contour area, plant basal area, and reproductive-tiller percentage of Hycrest crested and T-21076 thickspike wheatgrasses at Harvest 6 in the irrigated and nonirrigated environment at Greenville Farm (North Logan, UT) and the foothill environments (Logan, UT).

	Irrigated (IE)		Nonirrigated (NIE)		Foothill (FE)	
			Dry weight plant^{-1}			
			g (% of irrigated)			
Hycrest	534	(100)	436	(82)	118	(22)
T-21076	659NS	(100)	303*	(46)	62**	(9)
			Tillers plant^{-1}			
			no. (% of irrigated)			
Hycrest	475	(100)	273	(58)	129	(27)
T-21076	1162**	(100)	561**	(48)	147NS	(13)
			Tiller weight			
			mg (% of irrigated)			
Hycrest	1151	(100)	1683	(146)	890	(77)
T-21076	572**	(100)	571**	(100)	598NS	(105)
			Plant contour area			
			cm^2 (% of irrigated)			
Hycrest	290	(100)	177	(61)	63	(22)
T-21076	3062*	(100)	1273**	(42)	186**	(6)
			Plant basal area			
			cm^2 (% of irrigated)			
Hycrest	264	(100)	161	(61)	57	(22)
T-21076	248NS	(100)	131*	(53)	42*	(17)
			Reproductive-tiller percentage			
			% (% of irrigated)			
Hycrest	86	(100)	91	(105)	87	(101)
T-21076	48**	(100)	38**	(78)	73**	(153)

*,** Significant at $P < 0.05$ and 0.01, respectively.

CONCLUSIONS

Many researchers cited by Zarrough et al. (1983a,b) found TN influenced forage yield more than TW under spaced-plant conditions, a common situation for establishing seedlings. Under mesic conditions, a closed sward eventually develops and TW becomes more important. However, a closed sward is less likely to develop under range conditions. Our study was conducted at a 1-m plant spacing. Higher plant densities would be expected to increase the superiority of Hycrest over T-21076 because of greater interplant competition in the rhizomatous grass.

By year 2, the contrasting tillering strategies of the

Table 3. Path coefficients of tiller number (TN) and tiller weight (TW) on dry weight of Hycrest crested and T-21076 thickspike wheatgrasses at six harvests in the irrigated and nonirrigated environments at Greenville Farm (North Logan, UT).

	T-21076			Hycrest		
Harvest	TN	TW	SE†	TN	TW	SE†
			Irrigated environment (IE)			
1	0.767	0.646	0.077	0.380	0.695	0.065*
2	0.815	0.493	0.041*	0.541	0.827	0.056*
3	0.782	0.355	0.041*	0.571	0.655	0.043
4	0.780	0.711	0.108	0.669	0.963	0.091*
5	0.664	0.597	0.038	0.368	0.748	0.059*
6	0.900	0.465	0.051*	0.782	0.911	0.059*
			Nonirrigated environment (NIE)			
1	0.982	0.704	0.083*	0.473	0.836	0.064*
2	0.650	0.786	0.059*	0.486	0.940	0.085*
3	0.886	0.367	0.044*	0.874	0.440	0.144*
4	0.932	0.347	0.052*	0.604	0.917	0.052*
5	0.618	0.666	0.067	0.483	0.849	0.041*
6	0.925	0.450	0.081*	1.032	0.787	0.055*

* Difference between coefficients significant at $P < 0.05$.
† Standard error of coefficients.

two grasses were clearly apparent. New tiller production of T-21076 continued simultaneously with reproductive development, while Hycrest's tillering slowed dramatically (Fig. 1). This was coupled with Hycrest Year 2 tiller weights more than double those of T-21076 despite similar Year 1 tiller weights. T-21076 devoted a higher proportion of its fixed C to vegetative propagation, while Hycrest devoted more to seed production. This is reflected by higher reproductive-tiller percentages for Hycrest (86 IE, 91 NIE, 87 FE) than for T-21076 (48 IE, 38 NIE, 73 FE). High TW of Hycrest during stem elongation and flowering was critical to DW production since this grass stopped tillering by Harvest 3. Hycrest did not make use of ground area through rhizomatous spreading as did T-21076, and its TN did not decrease as much with moisture stress.

At low plant densities, the greater tillering of T-21076 might confer an advantage over Hycrest. However, T-21076 TN was heavily dependent on rhizomatous spreading, which in turn was quite sensitive to moisture stress. Rangelands generally exhibit moisture-stress conditions closer to those in the FE, thus T-21076 DW is likely to be restricted by limited rhizomatous spreading and resultant tillering.

Stability can be defined as the maintenance of yield under stressful environmental conditions. Hycrest's more important yield component, TW, was more stable under moisture stress relative to TN, explaining its higher DW stability during and following establishment. In contrast, T-21076's greater dependence on TN resulted in lower DW stability because TN was severely limited by moisture stress.

T-21076 was used in this study because of its exceptional establishment ability relative to other native cool-season grasses, which generally perform poorly relative to commonly seeded introduced species such as crested wheatgrass, intermediate wheatgrass [*Thinopyrum intermedium* (Host) Barkw. & D.R. Dewey], and smooth bromegrass (*Bromus inermis* Leysser.). Despite the preeminence of T-21076 among native wheatgrasses, its performance could not compare with Hycrest's in the stressful FE. However, response to selection for establishment ability in T-21076 has been encouraging and should continue to improve.

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