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Comparison of space-plant versus sward plot selection in thickspike wheatgrass (*Elymus lanceolatus*)

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Abstract

Thickspike wheatgrass (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould) is an important native perennial grass species used for rangeland revegetation in North America. Plant breeding efforts relying on space-plant evaluations have resulted in limited improvement in this species. The purpose of this study was to characterize the performance of thickspike wheatgrass half-sib families under space-plant and sward plot evaluations, estimate the correlation between measured traits in both evaluation settings, and determine the validity of selecting thickspike wheatgrass for rangeland revegetation in the nontarget environment space-plant plots. The study included 50 thickspike wheatgrass half-sib families and five commercial cultivars and experimental populations which were evaluated over 3 years in space-plant and sward plot evaluations at a field site in Box Elder County, Utah, USA. Collected data included stand percentage, flag leaf height, and herbage dry mass. Narrow-sense heritability estimates were low to moderate ($h^2 < 0.60$) and Spearman and genetic correlation estimates among traits were also generally low to moderate. Overall, there was little evidence to suggest the use space-plant evaluations in thickspike wheatgrass improvement programmes.

KEYWORDS

Elymus, genetic correlation, heritability, rangeland revegetation

1 | INTRODUCTION

Rangeland is the world's most extensive land cover type, is dominated by grasses and shrubs, is managed as a natural ecosystem, and often provides feed for grazing or browsing animals (Holechek, Pieper, & Herbel, 2011 and UNDDC, 2011, as cited in Briske, 2017). In the United States rangeland covers 300 M ha, primarily in the western states (Havstad, Peters, Skaggs, & Wright, 2007). Despite the size and importance of US rangelands, disturbances, such as grazing and wildfire, accompanied by drought resulted in loss of native plant materials, weed invasion, and destabilization of soil resources through erosion and changing nutrient and water cycles (Norton, Monaco, & Norton, 2007). For example, because of such disturbances approximately 2 M ha, or 10%, of the Great Basin – the largest North American desert – are now dominated by the annual grass *Bromus tectorum* L. with additional millions of hectares infested

by this and other undesirable annual species (Boyte, Wylie, Major, & Brown, 2015).

In response to these disturbances, federal and state government entities began seeding disturbed sites to revegetate and stabilize soils. These early revegetation attempts generally failed due to inadequate seed supplies of plant materials adapted to rangelands (Roundy & Call, 1988). The introduction of the crested wheatgrasses [*Agropyron cristatum* (L.) Gaertn. and *A. desertorum* (Fisch. ex Link) Schult.] provided perennial plant material adapted to establishment and persistence on the disturbed sites (reviewed in Roundy, 1999). Revegetation with crested wheatgrass proved successful and resulted in stabilized soil, competition against annual weed invasion, and increased forage production for livestock and wildlife (Asay, Horton, Jensen, & Palazzo, 2001). Despite the success of the revegetation, the frequent seeding of single species resulted in undesirable monocultures and a loss of biodiversity on extensive tracts of

rangeland (Marlette & Anderson, 1986). There is a current emphasis to rely less on introduced plant species and to proactively incorporate more native western North American plant materials in new revegetation projects. The major drawback to this approach is genotype by environment interaction. The native plant materials are maladapted to the permanently changed postdisturbance soils, site characteristics, and ecosystem functions (Asay et al., 2001; Jones, 2003; Norton et al., 2007). To overcome these limitations there is a need for focused plant breeding on native North American rangeland species to broaden their genetic base and develop improved varieties with increased establishment, persistence, and competitiveness.

Thickspike wheatgrass, also known as northern or streambank wheatgrass, (*Elymus lanceolatus* [Scribn. & J.G. Sm.] Gould) is a perennial grass native to the Intermountain and northern Great Plains regions of the United States and Canada. It is an allotetraploid species with a genetic constitution that combines the *Pseudoroegneria* and *Hordeum* genomes (StStHH). Thickspike wheatgrass exhibits relatively poor seed production and stand establishment, yet, its rhizomatous growth habit enables established plants to thrive and persist in semiarid to arid conditions (Asay & Jensen, 1996) and makes it an important revegetation species for disturbed rangeland and dryland sites. It produces the majority of its forage production in late spring and early summer. Thickspike wheatgrass germplasm contains ample genetic variation for gains in seed production, stand establishment, and other agronomic traits (Robins & Jensen, 2008, 2010).

Typical plant breeding and selection methods in this species, as in other perennial, cross-pollinated grass species, rely on phenotypic selection of widely spaced individual plants. While the selection strategy often incorporates among- and within-family selection, the selected entity remains the individual space plant (Vogel & Pedersen, 1993). Based on genetic correlation between space and sward plant evaluations, recent selection studies in other perennial grass species suggest that this methodology may be ineffective (Casler & Ramstein, 2018; Waldron, Robins, Peel, & Jensen, 2008). In contrast, arguments for space-plant selection in rangeland settings suggest that space-plant evaluation more realistically mimics rangeland plant communities which are not dense such as typical pasture settings, but are widely spaced due to competition among plants for limited soil water and nutrient resources.

In this study, we characterized the performance of a set of thickspike wheatgrass half-sib families under space-plant and sward plot evaluations. The objectives were to determine the correlation among traits evaluated in both environments and to determine the validity of selecting thickspike wheatgrass for rangeland revegetation in the nontarget environment space-plant plots.

2 | MATERIALS AND METHODS

During the winter and spring of 2004, we clonally propagated 30 ramets from each of 50 thickspike wheatgrass genotypes in the greenhouse at Logan, Utah, USA. The 50 genotypes came from the thickspike wheatgrass cultivars “Bannock” (33 genotypes) and

“Schwendimar” (17 genotypes). “Bannock” is a more productive cultivar and was developed from a composite of six collections from the states of Idaho, Oregon, and Washington in the USA (Ogle, St. John, Holzworth, Winslow, & Jones, 2013). “Schwendimar” is a cultivar that establishes rapidly on coarse textured soils and was developed from a single collection from the state of Oregon, USA (Ogle et al., 2013).

In May 2004, we transplanted the clonal ramets of a polycross nursery at the Utah State University Blue Creek Experimental Farm in Box Elder County, Utah, USA (41.9336°N, 112.4386°W). The Blue Creek experimental farm is 1,565 m asl, receives 253 mm mean annual precipitation, and is comprised of a Timpanogos silt loam soil. We harvested and bulked seed from each ramet based on the maternal clone. From this seed we created 50 half-sib thickspike wheatgrass families. The population development included only a single cycle of random mating. We also included the four cultivars “Bannock”, “Critana”, “Schwendimar”, and “Sodar”; and the experimental population “UTEL0401” for comparison. In November 2008, we seeded the sward plot evaluation at the Blue Creek experimental farm. We used a cone seeder to plant seeds at a depth of 1.3 cm and a rate of one pure live seed linear/cm (500 pure live seed/m²). Plots consisted of five rows, each 2 m long and spaced at 25 cm between rows. The sward experimental design was a randomized complete block with four replications.

In January 2009, we started seedlings of each half-sib family and cultivar in individual containers in a greenhouse at Logan, Utah, USA. We allowed the seedlings to grow for approximately 3 months and then in April transplanted them to a space-plant evaluation at the Blue Creek experimental farm. Space-plant plots consisted of ten plants each placed on 1 m centers. The space-plant experimental design was a randomized complete block with four replications.

We collected data from 2009 to 2011 in the sward evaluation and from 2010 to 2012 in the space plant evaluation. We collected stand percentage (%), flag leaf height (mm), and dry herbage mass (g/plot) from both evaluations. We did not collect flag leaf height from the space plants in 2011 or sward plots in 2010 and dry herbage mass from the space plants in 2012. We estimated stand percentage annually following spring green-up by counting the number of live plants in each plot of the space-plant evaluation and by using the grid method (Vogel & Masters, 2001) in the sward evaluation. We measured flag leaf height by determining the length from ground level to the base of the flag leaf of three plants from each plot of the space-plant evaluation and from three random locations in each plot of the sward evaluation. We measured dry herbage mass by harvesting the entire plot of each evaluation to a height of 100 mm using either a flail or sickle-bar harvester. We determined the fresh weight of each plot and then dried samples in a forced-air drier at 60°C for 3–5 days to determine dry weights. We then adjusted the fresh weights using the percent moisture from the dried herbage to determine dry herbage mass. We collected annual precipitation and mean temperature values for the duration of the study (Table 1) from the PRISM Climate Group (prism.oregonstate.edu).

We analysed the resulting data using mixed model methods with the ASReml-R package (Butler, 2009) of R (R Core Team, 2017).

Specifically, we analysed the data within evaluation (sward or space-plant) and across the 3 years of data collection, using the `rcov` command to account for the repeated measures on each plot and the spatial variation within the field. In the statistical models, we coded year as a fixed effect and half-sib family/cultivar (population), complete block, and all other interactions as random effects. The results were best linear unbiased predictors (BLUPs) of random effects and best linear unbiased estimators (BLUEs) of fixed effects. To calculate narrow-sense heritability (Nguyen & Sleper, 1983) and genetic correlations, we removed the cultivars from the dataset and re-ran the analysis on the modified dataset. We estimate genetic correlation using the `sommer` package of R (Covarrubias-Pazaran, 2016).

3 | RESULTS

The population variance differed from zero for all three traits in both evaluations (Table 2). The year-by-population interaction effect variance differed from zero only for sward herbage dry mass. Due to the limited significance of the year-by-population interaction variance and the perennial nature of thickspike all further discussion of results will be across the three years of the study in the space-plant and sward evaluations, respectively.

Phenotypic (r) and Spearman (ρ) correlation estimates were low to moderate (<0.60) among traits within the same evaluation and between evaluations for the same trait (Table 3). The highest correlation estimates were between herbage dry mass and flag leaf height ($r = 0.73$ and $\rho = 0.61$, $p < 0.001$) in the sward evaluation. None of

TABLE 1 Annual precipitation and mean temperature values for the years 2008 to 2012 at the Blue Creek (Cache County, Utah, USA) farm

Year	Precipitation (mm)	Mean temperature (°C)
2008	349	7.1
2009	436	7.2
2010	424	7.5
2011	470	7.1
2012	290	9.3
30 Year Mean	436	7.6

TABLE 2 Variance components (with standard errors) for stand percentage (SP), herbage dry mass (HDM), and flag leaf height (FLH) measured on 55 thickspike wheatgrass half-sib families and cultivars over 3 years and under space plant and sward plot evaluations

Source	SP	HDM	FLH
Space			
Population	2.8 ± 1.0	46,820 ± 13,560	1,020 ± 340
Year-by-Population	0	0	280 ± 250
Sward			
Population	1.6 ± 0.5	4,450 ± 1,660	660 ± 220
Year-by-Population	0	1,970 ± 660	0

the other correlation estimates was greater than 0.60. This level of correlation indicated there was little relationship among traits. In particular, there was little relationship among the rankings of the populations across the space-plant and sward evaluations. Because of the importance of rank changes among the evaluated populations all further discussion will be based on results across the three years of the study in both evaluations.

Forty-five and 47 populations exhibited high (did not statistically differ from the numerically highest value) stand percentage in the space plant and sward plot evaluations, respectively (Figure 1). Thirty-eight populations exhibited high stand percentage values in both evaluations, including 36 half-sib families and the cultivars “Critana” and “UTEL0401”. Fourteen and eight populations exhibited high herbage dry mass in the space plant and sward plot evaluations, respectively (Figure 2). Only three half-sib families exhibited high herbage dry mass in both evaluations. Thirteen and 42 populations exhibited high flag leaf height in the space plant and sward plot evaluations, respectively (Figure 3). Eleven populations, including “UTEL0401”, exhibited high flag leaf height in both evaluations. Two populations exhibited low stand percentage in both evaluations. The cultivars “Critana”, “Schwendimar”, and “Sodar” exhibited low flag leaf heights in both evaluations and “Critana” and “Sodar” exhibited low herbage dry mass in both evaluations.

In contrast, the cultivars “Schwendimar” and “Sodar” exhibited high space-plant stand percentage but low sward stand percentage and 12 half-sib families exhibited low space-plant stand percentage but high sward stand percentage. Two half-sib families exhibited low space-plant flag leaf height but high sward flag leaf height.

Narrow-sense heritability estimates (Table 4), calculated without the check cultivar data, for the three traits in the two evaluations were low to moderate in magnitude ($h^2 = 0.28$ – 0.59). With the exception of the sward flag leaf height ($h^2 = 0.28 \pm 0.18$), the heritabilities provided evidence of genetic control of the phenotypes in both evaluations. Based on this result, selection to improve the measured traits should be successful using either evaluation method, but

TABLE 3 Phenotypic (r) and Spearman (ρ) correlation estimates among predictors for stand percentage (SP, %), flag leaf height (FLH, mm), and herbage dry mass (HDM, g/plot) under space-plant and sward evaluation conditions

	r	ρ
Space-plant SP/Space-plant FLH	−0.31*	−0.23
Space-plant SP/Space-plant HDM	0.01	−0.01
Space-plant FLH/Space-plant HDM	0.55***	0.44***
Sward SP/Sward FLH	0.43***	0.38**
Sward SP/Sward HDM	0.56***	0.55***
Sward FLH/Sward HDM	0.73***	0.61***
Space-plant SP/Sward SP	−0.06	−0.16
Space-plant FLH/Sward FLH	0.57***	0.40**
Space-plant HDM/Sward HDM	0.48***	0.30*

Correlation estimates are significant at the *5%, **1%, and ***0.1% levels, respectively.

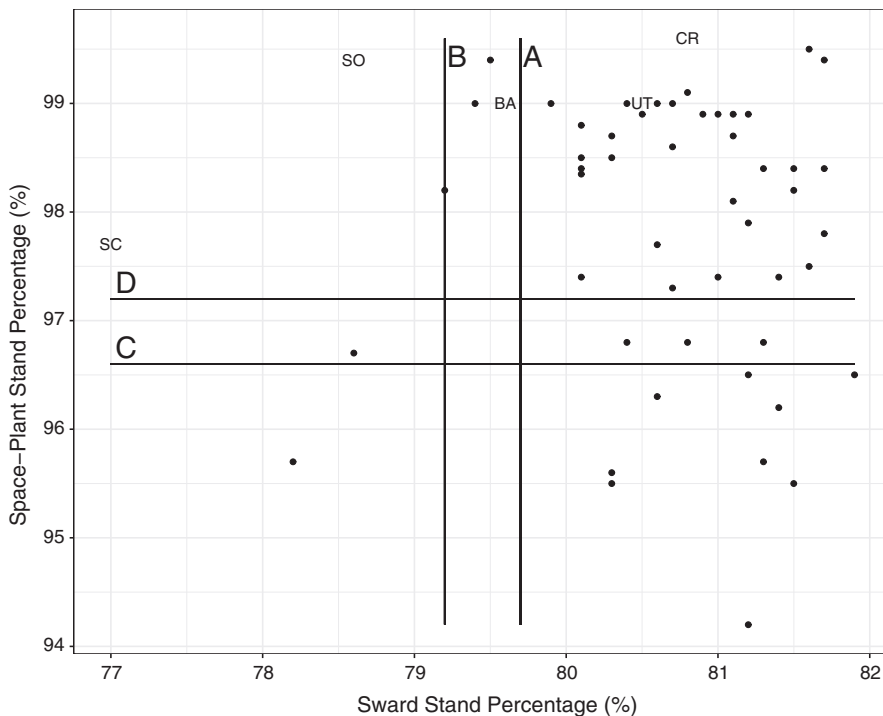


FIGURE 1 Best linear unbiased predictors of stand percentage of 55 thickspike wheatgrass half-sib families and cultivars under space-plant and sward plot evaluations across 3 years at a Box Elder County, UT, USA field site. Half-sib families are designated by dots and cultivars are designated by letters (BA – Bannock, CR – Critana, SC – Schwendimar, SO – Sodar, UT – UTELO401). The vertical lines designated A and B delineate families/cultivars that do not significantly differ from the numerically highest (A) or lowest (B) values in the sward evaluation. The horizontal lines C and D delineate families/cultivars that do not significantly differ from the numerically highest (C) or lowest (D) values in the space-plant evaluation

correlations between the methods were low. The greatest heritabilities corresponded to stand percentage in both evaluations. The flag leaf height and herbage dry mass heritabilities were lesser. Additionally, excepting flag leaf height, the sward heritabilities were greater than the space-plant heritabilities. Genetic correlations estimates were -0.06 , 0.76 , and 0.30 between space-plant and sward stand percentage, flag leaf height, and herbage dry mass, respectively. Only the genetic correlation estimate for flag leaf height significantly differed from zero (0.76 ± 0.31).

4 | DISCUSSION

Because of continuing rangeland disturbances and the resulting infestation of annual weed species, breeding of perennial plants for rangeland revegetation is an ongoing pursuit. In addition to traditionally used introduced Eurasian species, there is now a growing demand for native plant materials for these projects. Unfortunately, many, if not most, of the native perennial plant materials are the result of limited selection and almost no testing. For example, of the four cultivars of thickspike wheatgrass included as checks in this study, only “Bannock” (six collection sites) derived from seed from more than one collection site (Ogle et al., 2013). Selection of these cultivars consisted of selection among collections followed, in some instances, by mass selection and elimination of off-types within the chosen collection(s).

This approach to plant breeding, while not ideal, is necessitated by the resources available to the developing entity. In most cases the entities developing rangeland revegetation plant materials have limited resources and are attempting to improve many unrelated plant species simultaneously. Additionally, the inefficiency of space

plant evaluation has only been shown in the recent past (Casler & Ramstein, 2018; Robins & Jensen, 2017; Waldron et al., 2008), is more important for some traits than others (Sykes, Allen, DeSantis, Saxton, & Benelli, 2017), and is not absolute (Bhandari, Fasoula, & Bouton, 2013).

The primary finding of this study was that the concordance between the space-plant and sward evaluations depended on the trait evaluated. This lack of concordance was further exacerbated by the presence of populations that exhibited high performance in one evaluation and low performance in the other evaluation. Because of this the populations (parents) selected in the space plant conditions are not necessarily the same plants selected in sward conditions.

The target environment for thickspike wheatgrass is establishment and persistence under a seeded (sward) condition in revegetation settings. Thus, the use of space-plant evaluations is a case of indirect selection (Ceccarelli, 2015). Nontarget selection environments are only useful if the heritability of the trait in the nontarget environment is higher than the heritability of the trait in the target environment and the genetic correlation between environments is high. For the case of thickspike wheatgrass this criterion is only feasible for flag leaf height because there was limited to no genetic correlation for stand percentage and herbage dry mass between the evaluations.

A further limitation of the space plant evaluation method is that it does not allow for the evaluation of stand establishment following seeding. For the most part, traits such as flag leaf height and herbage dry mass are less important to rangeland revegetation than stand establishment and persistence (Robins, Jensen, Jones, & Cary, 2013). Potential wildlife and livestock feed sources are worthless if the plant material fails to establish and persist. While forage sources are important for wildlife and livestock, they are of much lower

FIGURE 2 Best linear unbiased predictors of herbage dry mass of 55 thickspike wheatgrass half-sib families and cultivars under space-plant and sward plot evaluations across 3 years at a Box Elder County, UT, USA field site. Half-sib families are designated by dots and cultivars are designated by letters (BA – Bannock, CR – Critana, SC – Schwendimar, SO – Sodar, UT – UTEL0401). The vertical lines designated A and B delineate families/cultivars that do not significantly differ from the numerically highest (A) or lowest (B) values in the sward evaluation. The horizontal lines C and D delineate families/cultivars that do not significantly differ from the numerically highest (C) or lowest (D) values in the space-plant evaluation

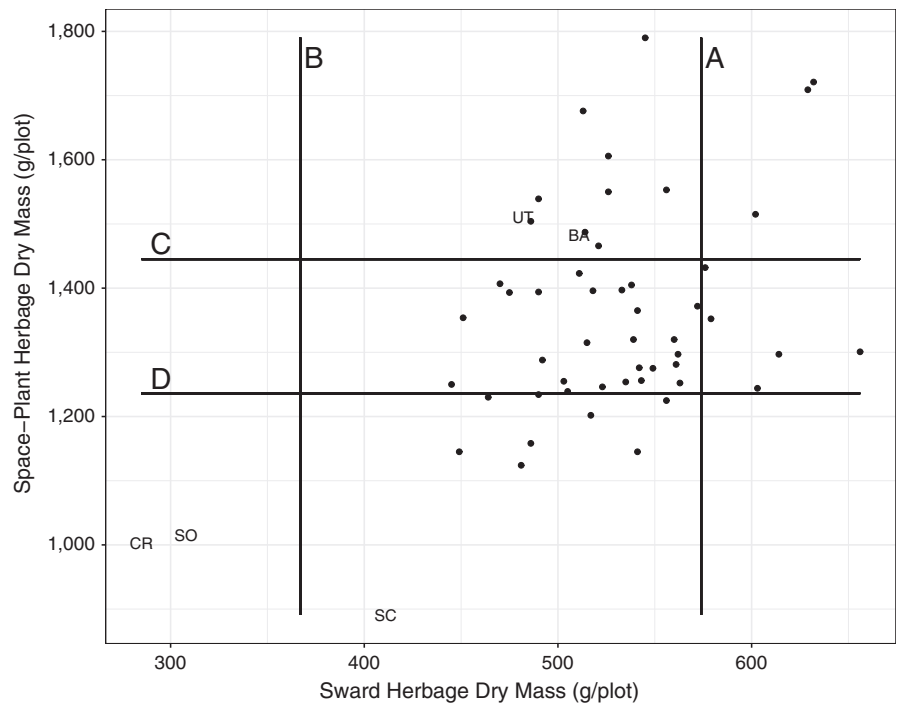
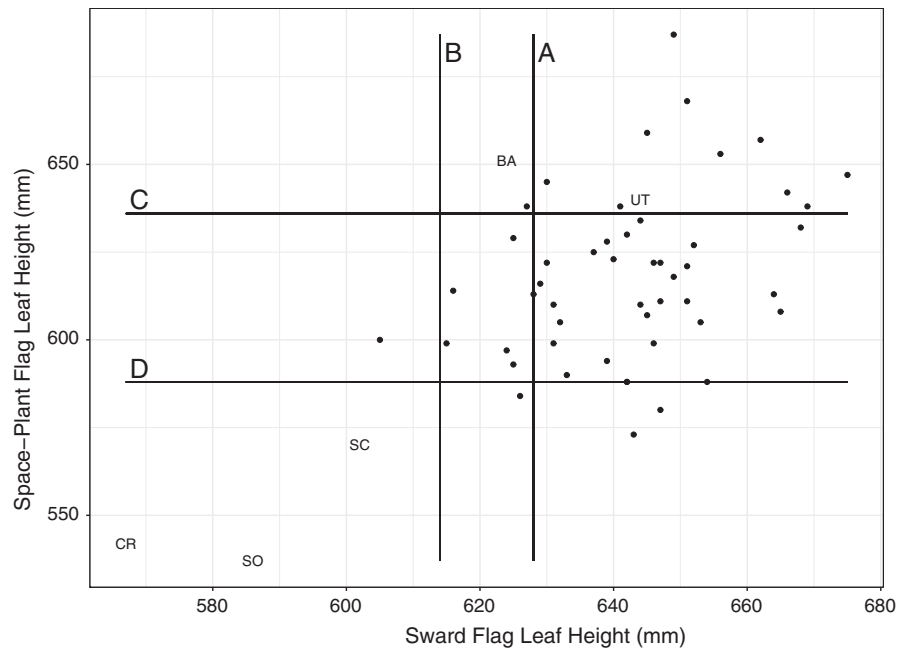


FIGURE 3 Best linear unbiased predictors of flag leaf height of 55 thickspike wheatgrass half-sib families and cultivars under space-plant and sward plot evaluations across 3 years at a Box Elder County, UT, USA field site. Half-sib families are designated by dots and cultivars are designated by letters (BA – Bannock, CR – Critana, SC – Schwendimar, SO – Sodar, UT – UTEL0401). The vertical lines designated A and B delineate families/cultivars that do not significantly differ from the numerically highest (A) or lowest (B) values in the sward evaluation. The horizontal lines C and D delineate families/cultivars that do not significantly differ from the numerically highest (C) or lowest (D) values in the space-plant evaluation



importance than stands of desirable plant materials. Healthy stands of perennial plant materials maintain healthy soils and serve as a guard against annual weed infestation and soil erosion. For this reason, stand establishment is possibly the single most important characteristic for rangeland revegetation plant materials (Robins et al., 2013). The space plant evaluation method decreases the ability to identify families that establish well on two fronts. First, because the seedling establishment of the space plants occurs in controlled greenhouse environments the selection for seedling vigour is limited to identifying those seeds that germinate and emerge from the soil most rapidly. It is not an adequate replacement for evaluation of

TABLE 4 Narrow-sense heritability estimates for stand percentage (%), herbage dry mass (g/plot), and flag leaf height (mm) measured on 50 half-sib families under space plant and sward plot evaluation across three production years

Evaluation	Stand percentage	Flag leaf height	Herbage dry mass
Space-plant	0.52 ± 0.20	0.40 ± 0.21	0.31 ± 0.12
Sward	0.59 ± 0.27	0.28 ± 0.18	0.44 ± 0.13

seedling establishment in an actual rangeland environment where water, and other resources, are limited and under competition; and environmental conditions are less than ideal for establishment,

including extreme cold or heat during germination. Second, once transplanted the space plant plots are at nearly 100% stands, which then have almost no problems persisting through the study – the lowest entry mean was 92%. This is in contrast with the seeded sward plots which slowly increase their stand percentage over years and must compete for resources from a much less developed beginning. The seeded species must establish rapidly under limited water resources. If the seeding fails, the soil resource is left unprotected from erosion and expansion of annual weedy species, which once established cause permanent changes to soil characteristics and are difficult to remove.

Successful plant breeding requires adequate measurement of the desired traits for improvement in the target environment. The non-target space-plant evaluations exhibited limited rank concordance and genetic correlation with the target sward environment. This finding brings into question the validity of space-plant evaluations for improvement of thickspike wheatgrass for rangeland revegetation, particularly when space-plant evaluations do not measure the ability of the thickspike wheatgrass to establish in the target environment.

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CONFLICT OF INTEREST

The authors have no conflict of interest.

AUTHORS CONTRIBUTION

JGR designed the experiment, conducted all analyses, and wrote the manuscript. KBJ developed the thickspike wheatgrass half-sib families and wrote the manuscript.

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