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Heritabilities of morphological and agronomic traits in western wheatgrass

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Abstract

Limited research has been directed towards characterizing the phenotypic and genotypic variability of different traits in North American plant species. This study was conducted to estimate the degree of genetic control, i.e., the heritability (h^2), of several agronomic and morphological traits of ND-WWG931 western wheatgrass [*Pascopyrum smithii,* (Rydb.) Löve] and to provide insight into appropriate sample sizes needed to estimate genetic parameters. Thirty randomly selected half-sib families of ND-WWG931 western wheatgrass were evaluated over 2 years and 2 locations in seeded single-row plots. Heritabilities were determined for the following traits based on the progeny means of the 30 families: dry matter yield, tiller height, spikelets per spike, vigor, spike density, spike pubescence, and spikelet color. Spike density, dry matter yield, and vigor had relatively high heritabilities (h^2 = 79, 72, and 67%, respectively) and were estimated with the greatest precision (90% confidence interval width range: 33 to 64% as large as the point estimate). Spike pubescence, spikelets per spike, tiller height, and spikelet color demonstrated moderate to low heritabilities (h^2 = 55, 49, 33, and 0% respectively) and were estimated with the least precision as demonstrated by relatively wide confidence limits. The genetic variance components for spike density, forage yield, vigor, and spike pubescence exceeded twice their standard errors indicating that selection for these traits should be effective in ND-WWG931. Heritability estimates of fresh forage yield were essentially the same, i.e., 61.9 and 61.5%, when based on either 30 or 270 half-sib families, respectively, indicating that a sample size of 30 families was adequate to provide reliable estimates of genetic variance in ND-WWG931. These data provide general insight into the population genetics of a North American plant species and demonstrate an approach to determine the genetic variability within plant materials that are being used for rangeland revegetation.

Key Words: *Pascopyrum smithii,* perennial grass, North American plant species, germplasm preservation, genetic variation, population genetics

Western wheatgrass [*Pascopyrum smithii,* (Rydb.) Löve] is a widely adapted native perennial grass of North American rangeland ecosystems. This species occurs from British Columbia and Arizona in the west, to Texas and Ontario in the east. It is frequently dominant or codominate in the short- and mixed-grass prairies of the central and northern Great Plains, and is commonly associated with blue grama [*Bouteloua gracilis* (H.B.K.) Lag. ex Steud.] and the needlegrasses (*Stipa* spp.) (Asay and Knowles 1985). In the west it is often associated with bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Löve] and thickspike wheatgrass [*Elymus lanceolatus* (Scribn. & Smith) Gould].

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Western wheatgrass is a cross-pollinated disomic allo-octaploid ($2n=8x=56$) that resulted from intergeneric hybridization between tetraploid beardless wildrye [*Leymus triticoides* (Buckl.) Pilger] and tetraploid thickspike wheatgrass, or closely related taxa (Dewey 1975). Its rhizomes produce a uniform sod that is excellent for stabilizing erosive soils. It is adapted to a wide range of soil types and possesses good tolerance to moderately saline and alkaline soils. Western wheatgrass flowers 2 to 3 weeks later than most perennial Triticeae (Dewey 1984). Widespread use of this species for revegetation has been limited by erratic seed production.

Considerable ecotypic variation exists among western wheatgrass populations for important agronomic traits (e.g., forage yield, plant height, seed yield, water use efficiency, and digestibility) warranting continued germplasm evaluation and enhancement efforts (Frank and Karn 1988, Johnston et al. 1975, Quinones 1983). Prior to selecting and developing populations for rangeland revegetation, however, it is important to determine the heritabilities, i.e., estimates of the relative importance of genetic versus environmental effects, for important traits. This knowledge can improve the efficiency of germplasm enhancement programs by providing early information on which traits can be successfully modified.

Rangeland ecosystems in the northern Great Plains tend to exist as complex communities that are frequently dominated by grasses. Intra- and interspecific competition can be severe. Relatively few quantitative genetic studies, however, have been conducted in forage grass species grown under competitive conditions. This study was conducted to estimate the heritability (h^2), of several agronomic and morphological traits of western wheatgrass grown under competitive conditions. A second objective was to provide insight into appropriate sample sizes needed to estimate genetic parameters in this species.

Materials and Methods

The germplasm used in this study was derived from ND-WWG931 western wheatgrass (Barker et al. 1993). ND-WWG931 originated from 5,140 genotypes that were vegetatively collected from 1,028 sites in western North and South Dakota (Barker et al. 1983). ND-WWG931 was produced from 2 cycles of phenotypic recurrent selection for plant vigor, rhizomatous spread, density of foliage cover, and seed yield. Each cycle was generated by intermating approximately 400 parents and forming a balanced composite of seed from each plant.

Maternal half-sib families were synthesized by harvesting open-pollinated seed from 270 genotypes that were randomly selected from among 2,000 space plants of ND-WWG931 western wheatgrass. Half-sib families were established at 2 locations using a blocks in replicates experimental design. Families were randomly assigned to 9 blocks of 30 families. Two cultivars, Rodan and

Walsh were included in each block. Families were represented by single 1.5-m rows that were seeded at a rate of 0.6 g plot^{-1} (i.e., approximately 100 seed m^{-1}). Plots were spaced 1.2 m apart and were separated by a single border row of tetraploid crested wheatgrass (experimental population M-3478). Three and 2 replicates of the experiment were established near Mandan, N.D., on 29 May 1990 (Location 1) and 1 June 1990 (Location 2). The 2 sites are located approximately 5 km apart. The soil at Location 1 is a Wilton silt loam (fine-silty, mixed Pachic Haploborolls), while the soil at Location 2 is a Parshall fine sandy loam (coarse-loamy, mixed Pachic Haploborolls). Nitrogen was not applied to either nursery during this study because soil fertility tests in September 1990 indicated approximately 130 and 120 kg ha^{-1} N at location 1 and 2, respectively. The nurseries were not cultivated and received only natural precipitation, which totaled 340 mm, 414 mm, and 363 mm, in 1990, 1991, and 1992, respectively. Single applications of Lasso[1] (2-Chloro-2'-6'-diethyl-N-[methoxymethyl]-acetanilide; Monsanto Agricultural Co., St. Louis, Mo.) were applied at a rate of 3.36 kg a.i. ha^{-1} in May 1991 and 1992 to control warm-season annual species.

Heritabilities on a progeny mean basis were determined from estimates of variance components for 30 half-sib families (i.e., 1 block) that were randomly selected from among the 270 entries of ND-WWG931. The following traits were evaluated at both locations: dry matter yield, tiller height, vigor, spike density, spikelets per spike, and spikelet color. Spike pubescence was measured at Location 1 only. Fresh forage yield was also measured for all 270 families at Location 1 only. Data were collected the second week of July, (i.e., 2 weeks post anthesis) in 1991 and 1992 and were expressed on a plot mean basis. Forage yield (g plot^{-1}), was determined by clipping each plot at a uniform height with a sickle bar harvester. Forage samples of all 270 families were immediately weighed to determine fresh forage yield and the samples from the selected 30 families were then placed in a cloth bag, dried at 60° C for 48 hours, and reweighed to determine dry matter yield. Tiller height (cm) was determined by measuring the tallest spike (i.e., inflorescence) from each of 3 random subsamples containing 10 spikes. Spike density and forage vigor, a visual estimate of forage yield and degree of rhizomatous spread, were evaluated relative to Rodan using a scale of 1 to 5 where: 1 = 0 to 20%, 2 = 21 to 40%, 3 = 41 to 60%, 4 = 61 to 80%, and 5 = 81 to 100% of the spike density or vigor of Rodan. Spikelets per spike, spike pubescence, and spikelet color were determined from 3 spikes that were randomly selected from each plot. Spike pubescence was evaluated on a scale of 1 to 4 where 1 = glabrous and 4 = dense pubescence. Spikelet color was evaluated on a scale of 1 to 5 where 1 = no anthocyanin pigment (i.e., green) and 5 = darkly pigmented.

Years (Y), locations (L), families (F), and replicates (R) were considered random. For traits that were evaluated on a scale of 1 to 4 or 1 to 5, the data were rank transformed across years, locations, and replicates/locations prior to applying analysis of variance procedures (Conover and Iman 1976). Analyses of variance were computed as a split-plot in time and the mean squares of the interaction effects having replicates as a factor were pooled as an experimental error term. Tests of significance were conducted based on the expected mean squares (EMS). Calculation of approximate F tests was not necessary, because the mean square of most family by environment interaction effects were less than the error mean square.

Genetic and phenotypic variances and their standard errors were calculated based on the EMS using conventional procedures (Anderson and Bancroft 1952). Negative variance component estimates were considered to be equal to 0. Heritability on a progeny mean basis was expressed as the ratio of the genetic variance component to the phenotypic variance (Knapp et al. 1985);

$$h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_{gy}/y + \sigma^2_{gl}/l + \sigma^2_{gyl}/yl + \sigma^2_e/ylr) \quad (1)$$

where σ^2_g, σ^2_{gl}, σ^2_{gy}, σ^2_{gyl}, and σ^2_e are the genetic variance component and the variance components due to genotype by year, genotype by location, genotype by year by location, and experimental error, respectively. Two-sided 90% confidence intervals were also computed to determine the precision of heritability estimates. The lower 90% confidence limit for h^2 was defined as

$$1 - [F_{\alpha/2:df1,df2}/F] \quad (2)$$

and the upper 90% confidence limit was defined as

$$1 - [F_{\alpha/2:df1,df2}(F)]^{-1} \quad (3)$$

where $F = (1 - h^2)^{-1}$ (Knapp et al. 1987).

Results and Discussion

Intra- and interspecific competition for available soil water were likely severe because crested and western wheatgrass initiate spring growth at approximately the same time. Furthermore, crested wheatgrass completes its development 2 to 3 weeks earlier and produces significantly more forage than western wheatgrass (Frank et al. 1985). Competition for soil water was probably greatest prior to the third week of June in 1992 when total precipitation was 54% below normal (based on a 78-year average).

In 1991 all plots of western wheatgrass were clearly distinguishable as single rows with some degree of rhizome production. The basal area of each plot increased significantly from 1991 to 1992 as

[1]Mention of a trademark, proprietary product, or vendor does not constitute endorsement by the USDA and does not imply approval to the exclusion of other products or vendors that may also be suitable.

Table 1. Yearly means and ranges (in parentheses) of agronomic and morphological traits of 30 half-sib families of ND-WWG931 western wheatgrass and the cultivars, Rodan and Walsh.

	Trait						
Year	Dry matter yield	Tiller height	Spikelets per spike	Vigor	Spike density	Spike pubescence	Spikelet color
	(g plot^{-1})	(cm)	(no. spike^{-1})	(visual score[†])			
1991	180.0	84.3	11.9	3.3	3.2	1.4	1.7
	(44.4 - 286.5)	(77.3 - 92.9)	(9.6 - 14.2)	(1.5 - 4.6)	(1.4 - 4.2)	(1.0 - 2.8)	(1.0 - 3.0)
1992	189.2	53.6	10.2	3.9	4.2	1.5	2.3
	(83.0 - 238.8)	(45.6 - 63.1)	(8.7 - 12.1)	(2.2 - 4.9)	(2.3 - 5.0)	(1.0 - 3.1)	(1.7 - 3.1)
$\bar{X}$	184.6	68.2	11.1	3.5	3.6	1.4	2.0
Rodan	284.6	76.2	11.6	5.0	5.0	1.2	1.8
Waslh	135.9	69.8	10.3	2.9	4.5	1.6	1.6
LSD (0.05)	51.9	4.9	1.2	0.7	0.7	0.5	0.5

[†]Evaluated on a scale of 1 to 4 or 1 to 5 (see Materials and Methods for definition of scale).

Table 2. Significance of mean squares from analysis of variance for various morphological and agronomic traits of 30 half-sib families of ND-WWG931 western wheatgrass.

Source of Variation	Dry matter yield	Tiller height	Spikelets per spike	Vigor	Spike density	Spike pubescence	Spikelet color
	(g plot^{-1})	(cm)	(no. spike^{-1})	(visual score†)			
Half-sib							
Families (F)	**	NS	*	**	**	*	NS
F × Year (Y)	NS	NS	NS	NS	NS	NS	NS
F × Location (L)	NS	NS	NS	NS	NS	—‡	NS
F × Y × L	NS	*	NS	NS	NS	—	**
CV, %	23.1	7.9	12.6	31.0	31.7	42.9	46.1

†Evaluated on a scale of 1 to 4 or 1 to 5 (see Materials and Methods for definition of scale). Data were rank transformed prior to analysis.
‡Data not available because trait was measured at only 1 location.
*,**Significant at $P \leq 0.05$ and 0.01, respectively.
NSNot significant, $P > 0.05$.

a result of rhizome production, and most 1992 plots consisted of a uniform sod contained within the crested wheatgrass border rows. Biomass production, however, did not increase significantly over years due to limited precipitation during April through June of 1992 (Table 1). Drought reduced tiller height significantly, and the population distribution for this trait showed no overlap between years. Spike size, as estimated by the number of spikelets per spike, also decreased in response to drought. Rhizome production increased the basal area of each plot and resulted in an increase in vigor scores over years. Spike density increased from 1991 to 1992. This may be attributed, in part, to favorable moisture conditions that occurred in the fall of 1991 during reproductive tiller initiation. Spike pubescence was relatively unaffected over years. Spikelet color was more intense in 1992 than in 1991, most likely as a result of cool, cloudy weather that occurred prior to scoring in 1992.

Variation among families was significant across years and locations for dry matter yield, spikelets per spike, vigor, and spike density; and across years for fresh forage yield (data not shown) and spike pubescence (Table 2). Variation among families was not significant ($P \geq 0.10$) for either tiller height or spikelet color. Fresh forage yield and dry matter yield were highly correlated ($r = 0.99$, $P < 0.01$). The correlation coefficients of vigor with fresh forage yield and dry matter yield were 0.88 and 0.85 ($P < 0.01$), respectively, indicating that vigor can be used reasonably well to predict forage yield. Significant genotype by environment interactions were detected only for the family by year by location (F × Y × L) interaction of tiller height and spikelet color. In alfalfa (Teuber et al. 1991) and crested wheatgrass (Lamb et al. 1984), significant genotype by year interactions were not detected for forage yield; however, genotype by location interactions were significant ($P \leq 0.01$) for this trait. In intermediate wheatgrass significant genotype by year ($P \leq 0.05$) and genotype by location ($P \leq 0.01$) interactions were detected (Vogel et al. 1986). For each of these studies, however, the variance components for the genotype by environment interactions were small relative to the genetic variance. Although the soil textures between the 2 locations used in our study were very different, the close proximity of the sites may account for the lack of significant genotype by location interactions.

Barker et al. (1989) reported a broad-sense heritability estimate of 95% for dry matter yield in western wheatgrass using 12 clonally replicated genotypes. Heritability estimates using variance components from half-sib family means (approaching narrow-sense heritability) ranged from 0 to 79% (Table 3). Precision among estimates varied as demonstrated by differences in the confidence interval widths. In general, traits evaluated based on whole-plot measurements were estimated most precisely. Dry matter yield, vigor, and spike density had relatively high heritabilities, ranging from 67 to 79%, with confidence interval widths ranging from 33 to 64% as large as the point estimate. Traits that were determined by subsampling within each plot were estimated with the least precision. Tiller height, spikelets per spike, spike pubescence, and spikelet color demonstrated moderate to low heritabilities (range 0 to 56%) and had relatively wide confidence intervals. Subsample sizes may have been inadequate to accurately measure these traits.

Table 3. Heritability estimates with 90% confidence limits for morphological and agronomic traits of 30 half-sib families from ND-WWG931 western wheatgrass.

Trait	Heritability (%)	Lower limit	Upper limit	Width‡
Dry matter yield (g plot^{-1})	72.3	58.1	82.1	33.1
Tiller height (cm)	33.3	0.0	64.2	192.8
Spikelets per spike (no. spike^{-1})	49.2	5.5	72.7	136.6
Vigor†	67.3	39.2	82.4	64.2
Spike density†	78.5	60.0	88.4	36.2
Spike pubescence†	55.6	17.4	76.1	105.6
Spikelet color†	0.0	0.0	46.2	—

†Evaluated on a scale of 1 to 4 or 1 to 5 (see Materials and Methods for explanation of scale). Data were rank transformed prior to analysis.
‡Expressed as the ratio (%) of the confidence interval width relative to the heritability point estimate.

This study also provides information pertaining to the adequacy of population sample sizes for determining heritability estimates in western wheatgrass. For ND-WWG931, heritability estimates of forage yield over 2 years and 1 location were essentially the same, i.e., 61.9 and 61.5%, when based on either 30 or 270 half-sib families, respectively. Relative confidence interval widths for this trait were 26% ($F_{0.05:29,116} = 1.56$; upper limit = 75.6, lower limit = 59.5), and 21% ($F_{0.05:261,1044} = 1.18$; upper limit = 67.4, lower limit = 54.6) as large as the point estimate when based on either 30 or 270 families, respectively. These data indicate that a random sample of 30 families from a population should provide a precise estimate of genetic variance. Relative to larger populations, however, some loss of precision will likely occur as a result of fewer degrees of freedom in the F tests.

Heritability is estimated from the degree of resemblance among relatives (Falconer 1989). In germplasm enhancement programs half-sib, full-sib, and S_1 progeny are commonly used. Full-sib or S_1 progeny, however, may provide inflated heritability estimates because the additive genetic variance is confounded with dominance genetic variance, additive by dominance, and dominance forms of epistatic variance. Half-sib families, therefore, provide more precise estimates of additive genetic variance. In ND-WWG931 western wheatgrass, the genetic variance components for dry matter yield, vigor, spike density, and spike pubescence

Table 4. Variance component estimates with standard errors over years and locations for various morphological and agronomic traits of 30 half-sib families from ND-WWG931 western wheatgrass.

Component	Variance ± SE						
	Dry matter yield	Tiller height	Spikelets per spike	Vigor	Spike density	Spike pubescence	Spikelet color
	(g plot^{-1})	(cm)	(no. spike^{-1})	(visual score‡)			
σ^2_g†	930 ± 328	3.9 ± 2.8	0.28 ± 0.16	924 ± 367	1528 ± 506	533 ± 266	0 ± 252
σ^2_{gy}	0 ± 166	1.0 ± 4.0	0.07 ± 0.15	0 ± 177	253 ± 222	288 ± 228	0 ± 484
σ^2_{gl}	0 ± 150	0.0 ± 3.3	0.00 ± 0.10	111 ± 244	0 ± 156	—	0 ± 414
σ^2_{gyl}	0 ± 255	8.4 ± 5.6	0.00 ± 0.20	0 ± 232	0 ± 224	—	1402 ± 781
σ^2_e	3512 ± 377	31.0 ± 3.6	2.42 ± 0.279	3938 ± 424	2924 ± 318	1408 ± 118	3743 ± 305

†*g* = genetic; *gy* = genotype by year; *gl* = genotype by location; *gyl* = genotype by year by location; and *e* = experimental error.
‡Evaluated on a scale of 1 to 4 or 1 to 5 (see Material and Methods for explanation of scale). Data were rank transformed prior to analysis.

exceeded twice their standard errors (Table 4). These traits also had moderate to high heritability estimates, providing evidence that there is additive genetic variation for these traits in ND-WWG931 and that selection for these traits should be effective. Genetic variance components for tiller height, spikelets per spike, and spikelet color were not significantly different from zero, indicating that selection for these traits may not be effective in ND-WWG931. Variance component estimates of the family by environment interactions (i.e., years and locations) were never significantly different from zero.

These data help provide general insight into the population size needed to provide reliable estimates of genetic parameters in western wheatgrass. This study also demonstrates that relatively unselected populations offer tremendous potential for genetic modification and improvement. The calculated heritabilities, however, are applicable only to ND-WWG931 because allele frequencies differ among species, populations within species, and cycles of selection within populations.

In other cross-pollinated genera, where phenotypic variability and estimates of genetic parameters have not been characterized, collection of open-pollinated seed from individual plants, i.e., half-sib progeny, could be subjected to similar research as described in this study. Such research would provide valuable information pertaining to the genetic variability within plant materials that are being used for rangeland revegetation.

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