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Response to Selection for Reduced Grass Tetany Potential in Crested Wheatgrass

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ABSTRACT

Grass tetany (hypomagnesemia) has caused substantial economic losses in ruminant animals grazing crested wheatgrass (*Agropyron* spp.) and other cool-season (C3) grasses. This malady is most prevalent in early lactating animals grazing forage that is deficient in Mg, Ca, and carbohydrates and with high levels of K. The K/(Ca + Mg) ratio expressed as moles of charge is often used to estimate the grass tetany potential of forage samples. Previous studies have shown that heritable variation exists in crested wheatgrass populations for traits associated with grass tetany, and research was conducted to determine the genetic response to selection for these traits. Selections were made during 1985 from two crested wheatgrass breeding populations in Utah ('I-28' and 'Hycrest') based on a reduced grass tetany potential (RTP) index, which incorporates the K/(Ca + Mg) ratio along with concentrations of Ca, Mg, and K. Mean values for the K/(Ca + Mg) were reduced by 5% in I-28 and 11% in Hycrest after one cycle of selection. Narrow-sense heritability values based on actual genetic advance and parent-progeny regression ranged from 0.62 to 0.82 in analyses of data combined across two sampling dates and two years (1988 and 1989). Genetic response to selection on the basis of RTP index was closely associated with the K/(Ca + Mg) ratio and concentrations of Ca and Mg but not with levels of K. Correlations between the K/(Ca + Mg) ratio and crude protein content and digestibility suggested that selection for RTP would likely be accompanied by improved forage quality in the Hycrest breeding population.

GRASS TETANY is a malady most often found in ruminant animals grazing actively growing cool-season (C3) grasses (Moseley and Griffiths, 1984; Mayland, 1988). Crested wheatgrass may be responsible for 30% of grass tetany incidences in the USA (Mayland, 1986). Symptoms range from weight loss, reduced milk production, and conception problems to tetanic convulsions, coma, and eventual death (Mayland, 1988). Tetany is most prevalent in early lactating cows consuming forages with low concentrations of Mg, Ca, carbohydrates, and dry matter and high concentrations of K. High concentrations of K also are known to interfere with translocation of Mg from the roots to the shoots and leaves (Mayland, 1988). The K/(Ca + Mg) ratio, expressed as moles of charge, is often used as an indication of grass tetany potential in forage grasses, and a threshold value of 2.2 has been proposed as a danger level (Kemp and 'tHart, 1957).

Because Mg is stored for a relatively short time in the body tissues, it must be included in the diet on a daily basis. This can be accomplished through direct animal supplementation or development of grass cultivars with higher levels of forage Mg. Levels of Ca, Mg, and K in the forage are under genetic control in perennial ryegrass (*Lolium perenne* L.; Cooper, 1973); annual ryegrass (*Lolium multiflorum* Lam.; Hides and Thomas, 1981); *Lolium-Festuca* hybrids (Buckner et al., 1981); reed canarygrass (*Phalaris arundinacea* L.; Hovin et al., 1978); orchardgrass (*Dactylis glomerata* L.; Mika et al., 1988; Stratton and Sleper, 1979); crested wheatgrass (Mayland and Asay, 1989); tall fescue (*Festuca arundinacea* Schreber; Nguyen and Sleper, 1981); and Russian wildrye [*Psathyrostachys juncea* (Fischer) Nevski; Asay and Mayland, 1990].

Genetic progress is evident in annual ryegrass. Lactating ewes grazing the annual ryegrass population 'Bb 2067', which was bred for high Mg content, had significantly higher concentrations of serum Mg and reduced incidence of clinical hypomagnesemia compared with the control cultivar RvP (Moseley and Baker, 1991). Mayland and Sleper (1993) reduced the K/(Ca + Mg) ratio in tall fescue in two cycles of selection without affecting concentrations of P, Na, Mn, Fe, Cu, or Zn. In a preliminary study, cattle grazing the selected strain (HiMag) had higher blood plasma Mg values than those grazing four other tall fescue cultivars (Sleper et al., 1994).

Based on heritability values and genetic variability detected among crested wheatgrass clonal lines for Ca, Mg, K, and the K/(Ca + Mg) ratio, Mayland and Asay (1989) concluded that breeding for reduced grass tetany would be an achievable objective in crested wheatgrass. Intercharacter correlations observed in their studies indicated, however, that genetic variation for the different mineral elements is not independent of one another. Genetic changes in Mg probably would be accompanied by increases in Ca, a positive response, and also by slight increases in K, which would increase the tetany risk. The present studies were conducted to evaluate the genetic advance through selection for reduced grass tetany potential in two breeding populations of crested wheatgrass. The associated response for plant vigor, forage quality, and other mineral elements also was of interest.

MATERIALS AND METHODS

The studies were conducted in two phases: (i) initial selection and hybridization of selected clones and (ii) evaluation of selected clones and their progenies to determine the response to selection. Both phases were completed on field sites near Logan, UT, at an altitude of 1350 m. Average annual precipitation at a weather station 2 km from the sites is ≈441 mm. Both sites were fertilized with 50 kg N ha^{-1} in mid-September annually, and no supplemental irrigation was applied during the 3-yr period.

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Abbreviations: RTP, reduced grass tetany potential; IVDMD, in vitro dry matter digestibility. **Significant at 0.01 probability level.

Initial Selection

The selection program was accomplished in the I-28 and Hycrest breeding populations of crested wheatgrass. Hycrest was derived from a hybrid between induced tetraploid fairway crested wheatgrass [*Agropyron cristatum* (L.) Gaertner] and natural tetraploid standard crested wheatgrass [*Agropyron desertorum* (Fischer ex Link) Schultes; Asay et al., 1985]. The parentage of I-28 was induced tetraploid *A. cristatum*, which had naturally outcrossed to some degree with tetraploid *A. desertorum*. Plants from the two breeding populations were established on 1-m centers on a site 2 km east of Logan, UT. Soil was classified as a Timpanogus silt loam series (fine-loamy, mixed, mesic Calcic Argixeroll). Annual precipitation at the station was 501 mm in 1985 when populations were evaluated and the selections were made and 680 mm in 1986 when the crosses were made.

Samples for mineral analyses were taken from 128 plants of the I-28 population and 183 plants of Hycrest. One-half of each plant was clipped to a 5-cm stubble height at the early boot stage on 8 May 1985. Plant samples were dried in forced-draft ovens at 60°C for 48 h and then ground to pass through a 0.4-mm (40-mesh) Wiley screen.

Subsamples of the forage were digested in 3:1 nitric/perchloric acid. This matrix was analyzed for Cu, Fe, Mn, Na, and Zn by atomic absorption. Lanthanum-spiked (1 g La L^{-1} as $LaCl_2$) solutions were analyzed for Mg and Ca by atomic absorption and K by flame emission. Phosphorous was determined colorimetrically with the vanadomolybdate procedure (Greweling, 1976).

The ratio, R = K/(Ca + Mg), was expressed as moles of charge. Selections were based on a reduced grass tetany potential (RTP) index, which was computed according to Mayland and Asay (1989) as follows:

$$\mathrm{RTP} = \left(\frac{\mathrm{Mg_i} - \mathrm{Mg_p}}{S_{\mathrm{Mg_p}}}\right) + \left(\frac{(1/R)_\mathrm{i} - (1/R)_\mathrm{p}}{S_{(1/R)_\mathrm{p}}}\right)$$

where R is the K/(Ca + Mg) ratio expressed as moles of charge, the subscript i is the value for the individual plant, the subscript p is the population mean, and S is the square root of the error mean square in the analysis of variance for a particular trait within each harvest. To avoid negative numbers in the statistical analysis, RTP values were adjusted to RTP + 10.

Nine plants of I-28 and ten plants of Hycrest were initially selected on the basis of RTP for generation advance. Polycrosses among the selected plants from each of the two separate populations were made in the field by first enclosing five spikes in each of three parchment bags per plant just prior to anthesis. On three consecutive days at anthesis, each selected plant was pollinated with a pollen mix from the remaining plants in the appropriate population (I-28 or Hycrest). Seed from the three bags on each plant were then bulked to form the polycross seedlots. Due to insufficient numbers of spikes and poor seed set, enough polycross seed for the next phase of the study was obtained from only five selected plants of I-28 and eight selected plants of Hycrest.

Evaluation of Response to Selection

The base population, selected parental clones, and progenies of selected clones from the two breeding populations were established ≈2 km south of Logan at the Utah State Univ. Evans Research Farm at an altitude of 1350 m. Soil on this site is a Nibley silty clay loam series (fine, mixed, mesic Aquic Argiustoll). Annual precipitation at a weather station 2 km from the experimental site was 438 mm during the year of establishment (1987) and 319 and 368 mm during each of the two subsequent years, respectively.

The I-28 and Hycrest populations were established as spaced plants on 1-m centers in adjacent experiments arranged as modified split-plot designs. Plots of the selected clonal lines and progenies from selected clonal lines were randomized in blocks (whole plots) within each of the four replicates. The base populations, which were derived from seed used to establish the two initial breeding nurseries, were established in 40-plant plots in each replicate. Thus, each replicate consisted of a clonal block, a progeny block, and a 40-plant plot of the base population. Plots of selected clones consisted of four plants, and plots of the progenies from selected clones consisted of nine plants for the five I-28 entries and five plants for the eight Hycrest entries. Plots of one I-28 progeny line was restricted to three plants. Plot size for the progenies was dictated by the availability of polycross seed.

All plants were started in the greenhouse prior to transplanting in the field. Progeny plants were derived from seed, and the clonal lines from vegetative tillers. Field plantings were made during mid-April 1987, and 1 yr was allowed for establishment.

One-half of the forage from each plant in the two nurseries was sampled for analyses on 2 May at the vegetative stage of plant development (Harvest 1), and the remaining half of the plant was clipped on 16 and 17 May at the boot stage (Harvest 2) in 1988 and 1989. Samples were dried, ground, and analyzed as described above. In vitro dry matter digestibility (IVDMD) and crude protein were determined for the Hycrest samples by near-infrared-reflectance spectroscopy according to procedures described by Marten et al. (1989). Data were expressed on a dry matter basis. Plots were rated for vegetative vigor on a 1 to 9 scale, with 9 being the most vigorous, prior to the first harvest.

Data were analyzed within and across harvests and years with a general linear model (SAS Institute, 1990). Clonal and progeny entries were nested within groups (clones or progenies). Because the plot randomization of these perennial grasses was not changed each harvest and year, F tests for mean squares involving harvests and years and interactions involving these effects were tested with their respective interactions with replicates.

Single degree of freedom contrasts were used to evaluate the responses to selection by comparing clonal and progeny means with their respective base population. Parent–progeny correlations and regression analyses were computed on entry-group and harvest × entry-group means pooled across populations and years (n = 13). Heritability estimates based on actual genetic advance and regression of progeny on parental means were interpreted with populations as a fixed effect. Intercharacter correlations were computed to determine if selection for grass tetany potential could be accomplished independent of vegetative vigor and other mineral elements evaluated in the study.

RESULTS AND DISCUSSION

Selection on the basis of the RTP index effectively increased the levels of Ca and Mg in forage of the selected clonal lines when grown in a different environment as well as in their polycross progenies. Differences among groups (base population, selected clones, and polycross progenies) were significant ($P < 0.05$) for Ca, Mg, K, and K/(Ca + Mg) in most analyses of the I-28 and

Table 1. Mean squares from the analysis of variance of elemental traits in the I-28 crested wheatgrass population within each of two years and combined across years.

Source	df	Ca	Mg	K	K/(Ca + Mg)	RTP†
				1988		
Groups (G)‡	2	13.51*	0.35	145.57*	4.32**	26.61*
Entry/G (E/G)	8	10.71**	0.29	138.21**	2.91**	17.16**
Harvests (H)	1	0.56	0.68	921.37*	7.80	0.70
G × H	2	0.81	0.03	22.27	0.64	1.97
H × E/G	8	0.22	0.02	8.43	0.13	1.36
				1989		
Groups (G)	2	22.66**	0.36**	192.59	2.12§	49.88**
Entry/G (E/G)	8	41.26**	1.18**	217.02**	5.52**	84.94**
Harvests (H)	1	2.92	0.96*	2.70	0.57	10.15
G × H	2	5.03**	0.57**	74.47*	0.89**	24.50**
H × E/G	8	0.39	0.03	14.66**	0.04	1.25
				Combined across years		
Groups (G)	2	32.71**	0.54*	281.84	5.39*	64.67**
Entry/G (E/G)	8	46.21**	1.28**	342.82**	8.08**	85.74**
Harvests (H)	1	0.47	1.63*	408.29*	6.27**	8.14
G × H	2	4.85**	0.42*	16.38*	1.26*	19.30**
H × E/G	8	0.51	0.03	14.14*	0.14*	1.58
Years (Y)	1	209.57**	22.77**	3248.26**	3.50	1.22
G × Y	2	3.48	0.16*	57.30	1.05*	11.95*
Y × E/G	8	5.79**	0.21**	13.40	0.34	11.39**
H × Y	1	3.03	0.01	508.10*	2.04	2.80
G × H × Y	2	1.01	0.17	80.93**	0.27	7.25
H × Y × E/G	8	0.09	0.02	8.95	0.04	1.03

*, ** Significant at $P < 0.05$ and 0.01 levels of probability, respectively.
† RTP = reduced grass tetany potential, see Materials and Methods.
‡ Groups = base population, selected clones, and progenies from selected clones.

Table 2. Mean squares from the analysis of variance of elemental traits in the Hycrest crested wheatgrass population within each of two years and combined across years.

Source	df	Ca	Mg	K	K/(Ca + Mg)	RTP†
				1988		
Groups (G)‡	2	23.85*	1.71§	0.99	12.54**	130.26**
Entry/G (E/G)	14	3.31**	0.43**	32.23**	0.57**	18.12**
Harvests (H)	1	62.49**	4.30**	985.08**	60.19**	1.27
G × H	2	0.91	0.03	24.13	1.83*	12.14§
H × E/G	14	0.43**	0.05**	14.84**	0.13	1.46
				1989		
Groups (G)	2	18.35**	1.83**	24.46	5.73**	125.15**
Entry/G (E/G)	14	3.08**	0.25**	58.17**	0.44**	9.76**
Harvests (H)	1	0.13	0.01	1307.00**	7.51**	1.12
G × H	2	0.91	0.27	18.37	0.03	7.86
H × E/G	14	0.30	0.05**	20.87**	0.04	0.94
				Combined across years		
Groups (G)	2	42.01**	3.50*	15.11	17.60**	254.90**
Entry/G (E/G)	14	6.04**	0.63**	69.95**	0.83**	25.00**
Harvests (H)	1	28.36**	2.05**	11.93	12.50**	2.39
G × H	2	1.62	0.07	10.44	1.14	19.72
H × E/G	14	0.30	0.05**	24.91**	0.08	0.92
Years (Y)	1	299.90**	18.21**	2597.82**	23.48**	0.01
G × Y	2	0.18	0.05	10.44	0.66	0.48
Y × E/G	14	0.36	0.05	20.46**	0.18*	2.85
H × Y	1	34.04**	2.24*	2281.27**	55.02**	0.01
G × H × Y	2	0.20	0.22*	31.99	0.72	0.27
H × Y × E/G	14	0.42**	0.05**	10.70**	0.08*	1.48*

*, ** Significant at $P < 0.05$ and 0.01 levels of probability, respectively.
† RTP = reduced grass tetany potential, see Materials and Methods.
‡ Groups = base population, selected clones, and progenies from selected clones.

Hycrest data combined across harvests (Tables 1 and 2). Mean squares for groups were significant ($P < 0.05$) for the RTP index for each year and when the data were combined across years in both populations.

Entries within groups were significant for most traits associated with grass tetany in analyses within years and combined across years, suggesting that genetic differences remained in the selected populations for additional selection. The group × harvest interaction was significant ($P < 0.05$) for all traits associated with grass tetany in 1989 and in the analyses combined across years for I-28; however, this interaction for Hycrest was nonsignificant in each year or when combined across years. In contrast, differences among entries within groups were more consistent across harvests in the I-28 population than in Hycrest as indicated by the magnitude of the harvest × entry-group interactions. This interaction was nonsignificant in both populations for the K/(Ca + Mg) ratio, however.

The group × year interaction was significant ($P <$

Table 3. Means, phenotypic standard deviations (SD), and probability levels for single degree of freedom contrasts comparing the base population (base) with the five selected clonal lines (clones) and the five polycross progenies for elemental traits associated with grass tetany in I-28 crested wheatgrass, data combined across two years.

Trait	Harvest 1			Harvest 2			Harvests combined		
	Base	Clones	Progeny	Base	Clones	Progeny	Base	Clones	Progeny
	mg g^{-1}								
Ca									
Mean	3.97	4.62**	4.46**	4.17	4.45*	4.43*	4.07	4.53**	4.45**
SD	0.85	1.28	1.09	0.86	1.22	0.95	0.86	1.25	1.02
Mg									
Mean	1.40	1.48**	1.52**	1.40	1.37	1.44	1.40	1.43	1.48*
SD	0.28	0.30	0.27	0.30	0.28	0.28	0.29	0.29	0.28
K									
Mean	26.01	24.59	26.82	27.10	26.19	27.62	26.56	25.39	27.22
SD	4.09	3.95	4.46	3.73	3.87	3.39	3.95	3.99	3.98
K/(Ca + Mg)									
Mean	2.17	1.86**	2.02	2.20	2.09*	2.14	2.19	1.97*	2.08
SD	0.38	0.44	0.38	0.38	0.51	0.42	0.38	0.49	0.41
RTP† index									
Mean	9.52	10.65**	10.22**	9.83	10.16*	10.12	9.68	10.40**	10.17**
SD	1.38	1.81	1.44	1.26	1.55	1.46	1.33	1.70	1.45

*, ** Difference between base population and selected clones or between base population and progenies from selected clones significant at 0.05 and 0.01 probability levels, respectively, as determined by single degree of freedom contrasts.
† RTP = reduced grass tetany potential.

Table 4. Means, phenotypic standard deviations (SD), and probability levels for single degree of freedom contrasts comparing the base population (base) with the clonal lines (clones) and the polycross progenies for elemental traits associated with grass tetany in Hycrest crested wheatgrass, data combined across two years.

Trait	Harvest 1			Harvest 2			Harvests combined		
	Base	Clones	Progeny	Base	Clones	Progeny	Base	Clones	Progeny
	mg g^{-1}								
Ca									
Mean	3.77	4.19*	4.08	3.38	3.92**	3.88**	3.57	4.05**	3.98**
SD	0.78	0.61	0.74	0.95	0.80	0.92	0.89	0.72	0.84
Mg									
Mean	1.26	1.39*	1.34	1.16	1.32**	1.29**	1.21	1.36**	1.31*
SD	0.22	0.23	0.20	0.23	0.25	0.25	0.23	0.24	0.23
K									
Mean	25.13	24.88	24.85	24.78	24.99	24.49	24.95	24.94	24.67
SD	4.29	3.91	3.40	2.67	2.33	2.79	3.58	3.22	3.11
K/(Ca + Mg) Ratio									
Mean	2.24	1.98**	2.05*	2.52	2.16**	2.17**	2.38	2.07**	2.11**
SD	0.37	0.29	0.31	0.59	0.39	0.44	0.51	0.35	0.39
RTP† index									
Mean	9.51	10.52*	10.15	9.17	10.57**	10.49**	9.34	10.54**	10.32**
SD	2.33	1.36	1.33	1.57	1.32	1.62	1.99	1.34	1.49

*, ** Difference between base population and selected clones and between base population and progenies from selected clones significant at 0.05 and 0.01 probability levels, respectively, as determined by single degree of freedom contrasts.
† RTP = reduced grass tetany potential.

0.05) for Mg and the K/(Ca + Mg in the I-28 population but was nonsignificant for all characters associated with grass tetany in Hycrest. The entry-group × year interaction was significant ($P < 0.01$) for Ca, Mg, and the RTP index in I-28. This interaction was significant for K ($P < 0.01$) and K/(Ca + Mg) ($P < 0.05$) in the Hycrest population.

Differences between the base population and the selected clonal lines were significant ($P < 0.05$ or 0.01) in most instances and in all analyses involving K/(Ca + Mg) and the RTP index (Tables 3 and 4). Although the differences between the means of the base population and the progenies were often significant, the magnitude of these differences were consistently less than those found between the base population and the clonal lines. This is an expected response because advantages associated with nonadditive genetic effects in the selected clones would not be recovered in their progenies. For example, in the I-28 population, differences between the base population and the selected clones for the RTP index were significant ($P < 0.05$ or 0.01) at each harvest and in the combined analysis; however, corresponding differences involving the progenies were significant only in the combined analysis. Similar trends were evident in the Hycrest population.

To provide insight into possible genotype × environment interactions, analyses also were made within harvests and years for each population (data not shown). The response to selection was particularly consistent in the Hycrest breeding population. For example, differences between the Hycrest base population and the selected clones and between the base population and the progenies were significant in all but one analysis for the K/(Ca + Mg) ratio. The response to selection was not as consistent in I-28. Although differences between the I-28 base population and the selected clones were significant ($P < 0.01$) in all four analyses, the difference between the base population and the progenies was significant ($P < 0.05$) only at Harvest 1 in 1988.

Realized heritability can be estimated as the ratio of

Table 5. Parent-progeny correlation coefficients (r), regression coefficients (b), and standard errors of regression coefficient (s_b) based on Hycrest and I-28 entry means combined across two years (n = 13).

Trait	Harvest 1			Harvest 2			Harvests combined		
	r	b	s_b	r	b	s_b	r	b	s_b
Ca	0.83**	0.42**	0.09	0.84**	0.50**	0.10	0.84**	0.46**	0.09
Mg	0.69**	0.44**	0.14	0.66*	0.44*	0.15	0.69**	0.44**	0.14
K	0.48	0.26	0.14	0.58*	0.47*	0.20	0.51	0.36	0.18
K/(Ca + Mg)	0.84**	0.33**	0.06	0.81**	0.36**	0.08	0.82**	0.34**	0.07
RTP† Index	0.78**	0.28**	0.07	0.78**	0.37**	0.09	0.79**	0.31**	0.07
Cu	0.22	0.30	0.41	0.21	0.89	1.26	0.39	0.71	0.50
Fe	0.41	0.54	0.36	0.20	0.06	0.09	0.45	0.20	0.12
Mn	0.74**	0.62**	0.17	0.76**	0.59**	0.15	0.75**	0.62**	0.16
Na	0.93**	0.85**	0.10	0.88**	0.71**	0.11	0.92**	0.79**	0.10
P	0.70**	0.49**	0.15	0.61*	0.54*	0.21	0.68**	0.56**	0.18
Zn	0.33	0.43	0.37	0.26	0.98	1.08	0.33	0.40	0.34
Protein‡	0.78*	0.28*	0.09	0.97**	0.23**	0.02	0.88**	0.26**	0.06
IVDMD‡	0.82*	0.35*	0.10	0.72*	0.30*	0.12	0.78*	0.32*	0.11

*, ** r value significant and b value significantly different than zero at 0.05 and 0.01 probability levels, respectively.
† RTP = reduced grass tetany potential.
‡ Values for protein and in vitro dry matter digestibility (IVDMD) are from Hycrest data only (n = 8).

Table 6. Correlations (*r*) among mineral elements and K/(Ca + Mg) ratio for Hycrest and I-28 entry means combined across years (*n* = 52).

	Mg	K	Ratio	RTP†	Vigor‡	Protein	IVDMD§	Fe	Mn	Na	P
Ca	0.68**	0.11	−0.80**	0.71**	−0.23	0.51**	0.19	0.20	0.36**	0.30*	0.25
Mg		0.45**	−0.45**	0.62**	0.11	0.73**	0.24	0.30*	0.66**	0.38**	0.56**
K			0.44**	−0.20	0.35	0.25	−0.34	0.28*	0.66**	0.45**	0.79**
Ratio				−0.76**	0.37	−0.64**	−0.65**	0.03	−0.01	−0.01	0.18
RTP					−0.14	0.37*	−0.03	0.20	0.06	−0.23	0.06
Vigor						−0.02	−0.46	−0.30	0.26	−0.04	0.26
Protein							0.70**	0.16	0.48**	−0.09	0.30
IVDMD								0.09	−0.03	0.13	−0.34
Fe									0.10	0.24	0.16
Mn										0.59**	0.70**
Na											0.43**

*, ** Significant at 0.05 and 0.01 probability levels, respectively.
† RTP = reduced grass tetany potential.
‡ Correlations involving vigor are for Harvest 1 only, and those involving crude protein and IVDMD are for Hycrest only.
§ IVDMD = in vitro dry matter digestibility.

the actual genetic gain (base population mean − mean of progenies) to the selection differential (base population mean − mean of selected clones). Realized heritability for the RTP index in the I-28 population was 0.68 for the analysis combined across years and harvests. The corresponding value for Hycrest was 0.82. The genetic advance for the K/(Ca + Mg) ratio in the I-28 population, based on selection for RTP, was 7% of the base population mean for Harvest 1, 3% for Harvest 2, and 5% in the analysis combined across both harvests and years. Corresponding values for Hycrest were 8% at Harvest 1, 14% at Harvest 2, and 11% in the combined analysis.

In a typical breeding situation, a much larger breeding population would be used, which would permit greater selection pressure or a larger selection differential. Assuming that heritability for the traits involved remained relatively stable, more rapid genetic advance would be achieved.

The magnitude of parent–progeny correlation and regression coefficients computed from the data combined across the two populations provided additional support to the premise that selection for RTP would be feasible in these crested wheatgrass populations (Table 5). Correlation coefficients (*r*) between parent and progeny means were significant ($P < 0.01$) and ranged from 0.78 to 0.84 for K/(Ca + Mg) and RTP index. In cross-pollinated forages where only one parent is known, narrow-sense heritability (h^2) can be estimated as 2(*b*), where *b* is the regression coefficient of progeny on parental means (Asay et al., 1968). In the analyses of the data combined across years and harvests, h^2 estimated in this manner was 0.62 for the RTP index and 0.68 for K/(Ca + Mg). These values are similar to the realized heritability estimates computed for these traits.

Intercharacter correlations (Table 6) indicated that, of the traits related to grass tetany, the RTP index was significantly associated with the K/(Ca + Mg) ratio (r = 0.76**), Ca (r = 0.71**), and Mg (r = 0.62**) but not with K ($r = -0.20$). The K/(Ca + Mg) ratio was most closely associated with Ca (r = −0.80**) and to a lesser degree with Mg (r = −0.45**) and K (r = 0.44**). Vigor was not significantly correlated with any trait evaluated, suggesting that selecting on the basis of vigor may not increase the risk of grass tetany. Crude protein was positively correlated with Ca and Mg (r = 0.51** and 0.73**, respectively) and negatively correlated with K/(Ca + Mg) ratio (r = 0.64**). These correlations, along with the negative correlation between the K/(Ca + Mg) ratio and IVDMD, indicated that selecting for traits associated with RTP [Ca, Mg, and the K/(Ca + Mg) ratio] would probably be accompanied by improved forage quality.

Although the results indicated that selection for RTP would be a worthy breeding objective in crested wheatgrass, genotype × environment interactions were found. Care should be taken to adequately sample environmental variation associated with years and locations when selecting for characters associated with this malady.

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