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# Parent-Progeny Relationships and Genotype × Environment Effects for Factors Associated with Grass Tetany and Forage Quality in Russian Wildrye

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## ABSTRACT

**Grass tetany (hypomagnesemia) has caused severe economic losses in ruminant animals grazing cool-season grasses, including Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski]. The malady has been associated with deficiencies in Mg, Ca, and carbohydrates, and high levels of K. The K/(Ca + Mg) ratio (KRAT), expressed as moles of charge, is often used to express the grass tetany potential of forage. Development and use of new cultivars with an improved balance of the associated minerals would be an economical approach to reduce the incidence of grass tetany. Objectives of this study were to characterize the genetic variability, genotype by environment interactions, and intercharacter relationships for P, K, Ca, Mg, KRAT, crude protein (CP), neutral detergent fiber (NDF), and in vitro dry matter digestibility (IVDMD), among 21 clonal lines of Russian wildrye and their polycross progenies. Evaluations were made for 2 yr at three diverse locations in the USA and Canada. The clonal lines were derived from cultivars and plant introductions. Although the clone × location interaction was usually significant, differences among the clonal lines were significant for K, Ca, Mg, and KRAT, and three forage quality estimates of CP, NDF, and true IVDMD. Although the magnitude of the genetic variability among the progenies was substantially less than that found among the clonal lines, we conclude that the grass tetany potential, CP, NDF, IVDMD, and P concentration of this breeding population can be altered through breeding. Opportunities for genetic improvement in forage quality were particularly favorable for CP. Genetic correlations among the clonal lines suggested that selection for higher levels of CP would be accompanied by increased K, Ca, Mg, and IVDMD and reduced KRAT and NDF.**

RUSSIAN WILDRYE is a caespitose, cool-season, perennial grass that is widely used in range improvement programs in western North America. Although the species has only moderate seedling vigor, established plants are resistant to drought and tolerant of grazing stress. Because of its abundant basal leaves that maintain their nutritive value at advanced stages of plant development, Russian wildrye is regarded as an excellent source of forage during the late summer and fall (Knipfel and Heinrichs, 1978; Mayland, 1988).

Grass tetany is a metabolic ailment in grazing ruminants that has been associated with low levels of Mg in the blood serum (Kemp, 1960; Sleper et al., 1989). This condition has been observed in animals grazing perennial cool-season ($C_3$) grasses including orchardgrass (*Dactylis glomerata* L.), perennial ryegrass (*Lolium perenne* L.), timothy (*Phleum pratense* L.), tall fescue (*Festuca arundinacea* Schreb.), crested wheatgrass (*Agropyron* spp.), and smooth bromegrass (*Bromus inermis* Leyss.) (Grunes et al., 1970; Sleper et al., 1989). Magnesium deficiencies may lead to reduced weight gain, milk production, and conception rate (Stuedemann et al., 1983). More severe deficiencies result in tetanic convulsions, coma, and even death. Clinical cases of grass tetany were not observed when blood serum Mg levels were greater than 9 $\mu g\ ml^{-1}$ or at Mg concentrations in the forage above 1.9 $mg\ g^{-1}$ (Kemp and t'Hart, 1957). Although differences in susceptibility to grass tetany have been observed among animal breeds (Greene et al., 1989), the condition most often occurs in early-lactating cows because of unusually high secretory losses of Mg in milk produced by these animals.

Low concentrations of Ca, carbohydrates, and dry matter, and high concentrations of K, nonprotein N, fatty acids, and organic acids also have been associated with symptoms of grass tetany (Mayland, 1988). The role of K in grass tetany is likely due to the interference

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**Abbreviations:** CP, crude protein; *H*, broad-sense heritabilities; $h^2$, narrow-sense heritabilities; HSF, half-sib families; NDF, neutral detergent fiber; IVDMD, in vitro dry matter digestibility; KRAT, K/(Ca + Mg) ratio expressed as moles of charge.

by this element with translocation of Mg from the roots to other parts of the plant (Ohno and Grunes, 1985). The KRAT is often used as an indicator of the grass tetany potential of forage. Grass tetany has been shown to be substantially reduced when the KRAT values are less than 2.2 (Butler, 1963; Kemp and t'Hart, 1957).

Metabolic disorders including scouring, frequent urination, and reduced weight gains have been observed in beef animals grazing Russian wildrye during the spring or early summer, when grass tetany is most prevalent (Rogler and Lorenz, 1970). Although the malady was not conclusively attributed to grass tetany, the KRAT ratios of the forage were higher than the 2.2 threshold value (Kemp and t'Hart, 1957). The KRAT values in Russian wildrye forage have also been reported to be well above that of other cool season grasses (Lawrence et al., 1982; Asay and Mayland, 1990; Karn et al., 1983).

The use of specific fertilization regimes, mineral supplementation, and other management practices have been proposed to reduce the risk of grass tetany (Robinson et al., 1989). Although these approaches offer promise, they are unduly expensive on vast rangeland areas. Magnesium supplements also are unpalatable. Magnesium supplements often are mixed with salt or protein carriers to improve their poor palatability; however, this alternative adds to the expense.

Breeding cool-season grasses with reduced grass tetany potential is a promising alternative to supplementation. The range in genetic variability and magnitude of heritability values for factors related to grass tetany indicate that substantial genetic progress can be made through breeding in several grasses (Asay et al., 1996; Mayland and Asay, 1989; Sleper et al., 1989, 1994; Moseley and Baker, 1991; Vogel et al., 1989). Selection for reduced grass tetany potential in tall fescue has been particularly effective (Mayland and Sleper, 1993). Forage from 'HiMag', which was derived through selection for high Mg concentration, contained 22% more Mg and 18% more Ca than the three other tall fescue cultivars evaluated (Crawford et al., 1998). Heritablity values reported for mineral elements in Russian wildrye (Asay and Mayland, 1990) support the premise that breeding would be effective in this species; however, the potential of lowering KRAT below 2.2 appeared to be limited by the range in available genetic variation. To correct this deficiency, research has been initiated to assemble and evaluate the tetany potential of a wide range of Russian wildrye germplasm (Jefferson et al., 2001).

Breeding for improved forage quality has received considerable attention in forage grasses (Casler et al., 1996; Marten, 1989; Vogel and Sleper, 1994). Casler and Vogel (1999) reviewed the progress and impact of breeding for improved forage quality in forages, including cool-season grasses. They concluded that from 8 to 45 g $kg^{-1}$ $cycle^{-1}$ had been achieved through breeding for improved IVDMD in forages, which, on a percentage basis, is comparable to genetic advances in grain yield achieved through breeding in many cereal crops. Moreover, genetic advances in IVDMD were generally found to be repeatable over a range of environments and management systems.

Little information is available in the literature regarding parent-progeny relationships for factors associated with grass tetany and forage quality in Russian wildrye, particularly when considered across diverse locations. The objectives of this study were to characterize the genetic variability, genotype by environment interactions, and intercharacter relationships for P, K, Ca, Mg, KRAT, CP, NDF, and IVDMD among 21 clonal lines of Russian wildrye and their polycross progenies.

## MATERIALS AND METHODS

Twenty-one clonal lines of Russian wildrye and their polycross progenies were included in the studies. The clonal lines were originally derived from named cultivars and plant introductions, and represent the parentage of a breeding population presently included in the USDA-ARS breeding program at Logan, UT. Although the population had been previously subjected to selection for characters associated with forage and seed yield, seedling vigor, and resistance to biotic and abiotic stress, no selection pressure had been applied for mineral concentration and forage quality. The experiments were conducted at three locations: Logan, UT (41° 46′ N latitude, 107° 50′ W longitude); Mandan, ND (46°48′ N latitude, 100°46′ W longitude); and Swift Current, SK, Canada (50° 17′ N latitude, 107° 50′ W longitude). These locations were selected to represent three diverse environments within the area of adaptation for Russian wildrye in North America. Soil types were a fine, mixed, mesic, semiactive Aquic Argiustolls (silty clay loam) at the Logan site; a fine-silty, mixed superactive, frigid, Pachic Haplustolls at Mandan; and a fine, mixed, mesic, Aridic Haploborolls (sandy loam) at Swift Current.

The polycross progenies and parental clones were transplanted from the greenhouse to the field on 1-m centers during mid-April 1991 at Logan, and early May 1991 at Mandan and Swift Current. The progenies, initially started as seedlings, were established in single-row plots consisting of eight plants each. The parental clones were derived from vegetative sprigs and transplanted into two-plant plots. Fewer plants were used for the parents because plants within a plot were genetically identical. The progeny and parental plots were arranged in separate randomized complete blocks with four replications. Data were collected for 2 yr following the year of establishment.

In the progenies, one-half of each of three plants per plot was sampled at the V4 stage of plant development, and the remaining half of the plants at the E2 stages of plant development, as described by Moore et al. (1991). The V4 stage is classified as vegetative when the fourth leaf is collared, and the E2 stage is during the stem elongation phase (prior to the boot stage), when the second node is palpable or visible. One plant per plot of the parental clones was sampled at the same stages of plant development. Samples were analyzed for K, Ca, Mg, P, NDF, CP, and true IVDMD.

Samples for mineral analyses were dried in a forced-draft oven at 60°C and then ground to pass through a 40-mesh screen. Subsamples of forage were digested in 3:1 nitric:perchloric acid and diluted with 1 g $L^{-1}$ La as $LaCl_2$. Determinations of Mg and Ca concentrations were made by atomic absorption, and K by flame emission. Analysis for P was made colorimetrically using the Vanadomolybdate procedure (Greweling, 1976). An alfalfa sample of known mineral concentration was analyzed with the grasses to monitor analytical precision. Results from the analyses of this sample were 3.4 ± 0.3 mg

$g^{-1}$ Mg, 14.5 ± 0.8 mg $g^{-1}$ Ca, and 23.5 ± 1.0 mg $g^{-1}$ K. Data from the mineral analyses were expressed on a dry matter basis as g $kg^{-1}$, and KRAT was computed on a mole equivalent basis.

Samples for determinations of forage quality were dried at 60°C, double ground through a 1 mm screen, and scanned with a model 6250 (Pacific Scientific, Silver Spring, MD) near infrared spectroscopy instrument. Using NIRSystems software, representative samples from each year and location were selected as a calibration data set for wet lab analysis. The calibration data set consisted of 395 samples, which included 46 and 104 from Logan, 41 and 57 from Swift Current, and 95 and 52 from Mandan for the two sampling years, respectively. Calibration samples were analyzed for N using a Carlo Erba Model NA 1500 Series 2 N/C/S analyzer (CE Elantech, Lakewood, NJ). Neutral detergent fiber and true IVDMD were determined according to procedures described by Goering and Van Soest (1970). Neutral detergent fiber in the forage samples and in the residue following a 48-hr in vitro fermentation was determined with an ANKOM fiber analyzer (Cherney et al., 1997). After wet lab analyses were completed on calibration samples, equations were developed to predict N, NDF, and IVDMD on all samples.

Data were analyzed within and across years, locations, and dates (maturity stage) using linear regression models (SAS Institute, 1999). Years, entries (clonal or progeny lines), and replications were considered as random effects, and locations and dates as fixed. Statistical interactions involving dates were generally nonsignificant, so subsequent analyses were made from individual plot data averaged across dates. Variance components for main effects and interactions involving random effects were computed using the method of moments procedure in PROC MIXED Method=Type 3, where it is assumed that the sum of interactions between random and fixed effects does not equal zero (Searle, 1971). Pseudo F tests, computed on the basis of expected mean squares, were used to evaluate the significance of main effects and interactions.

Additive genetic variances ($\sigma^2_A$), and narrow-sense heritabilities ($h^2_F$) were estimated assuming the variance among half-sib families (HSF) was equivalent to $1/4\sigma^2_A$. Estimates were calculated for each individual location and across locations. Narrow-sense heritabilities were calculated based upon HSF means as

$$h^2_F = \sigma^2_F/(\sigma^2_F + \sigma^2_{FL}/l + \sigma^2_{FY}/y + \sigma^2_{FLY}/ly + \sigma^2_{FR/L}/rl + \sigma^2_e/rly)$$

where $\sigma^2_F$ = HSF variance, $\sigma^2_{FL}$ = HSF × location variance, $\sigma^2_{FY}$ = HSF × year variance, $\sigma^2_{FLY}$ = HSF × location × year variance, $\sigma^2_{FR/L}$ = HSF × replication within location variance, $\sigma^2_e$ = residual variance, and r, l, y equal the number of replicates, locations, and years, respectively (Nguyen and Sleper, 1983).

Genetic correlations were estimated as

$$r_{G(xy)} = \sigma_{G(xy)}/[\sigma_{G(x)} \times \sigma_{G(y)}]$$

where $\sigma_{G(xy)}$ is the genetic covariance among clonal lines for trait x and y, and $\sigma_{G(x)}$ and $\sigma_{G(y)}$ are the genetic standard deviations for traits x and y, respectively. Genetic covariance was calculated using the manova statement of SAS Institute (1999) to obtain the cross products between traits. The genetic component of the cross products were partitioned using the appropriate linear combination of mean cross products. Prior to computation of genetic correlations, data were standardized by substracting the mean and dividing by the standard deviation to nullify effects due to large differences in magnitude and scaling among the individual traits.

## RESULTS AND DISCUSSION

### Main Effects and Interactions

The variation among clonal lines was significant ($P < 0.05$) for the four mineral elements evaluated, KRAT, CP, NDF, and IVDMD at Logan and Swift Current (Table 1), and in the analyses of data combined across

**Table 1. Variance components from ANOVA of mineral concentrations and forage quality parameters for 21 Russian wildrye clonal lines and their polycross progenies, combined across 2 yr and four replications; all effects are random.**

| | Logan | | | Swift Current | | | Mandan | | |
|---|---|---|---|---|---|---|---|---|---|
| | E† | Y‡ | E × Y | E | Y | E × Y | E | Y | E × Y |
| | g $ka^{-1}$ | | | | | | | | |
| | Parents | | | | | | | | |
| K | 1.0411* | 0.1179 | 0.5606** | 1.1905** | 18.0062** | 0.6997** | 0.6218 | 0.1465 | 0.4054 |
| Ca | 0.0649** | 0.0321* | 0.0164** | 0.0363** | 0.1076** | 0.0071* | 0.0078 | 0.0198 | 0.0030 |
| Mg | 0.0549** | 0.0459** | 0.0132** | 0.0321** | 0.0899** | 0.0014 | 0.0023 | 0.0116* | 0.0045 |
| KRAT§ | 0.0675** | 0.0627** | 0.0188** | 0.0419** | 0.5596** | 0.0220** | 0.0000 | 0.0000 | 0.0096 |
| P | 0.0184** | 0.0019 | 0.0045** | 0.0183** | 0.1114** | 0.0024 | 0.0037 | 0.0302** | 0.0038 |
| CP¶ | 106.8700** | 0.0000 | 16.8830* | 50.2787* | 170.4100** | 37.6529** | 39.7012 | 316.8900** | 8.2390 |
| NDF# | 219.7000** | 862.9700** | 35.9109** | 112.6700** | 204.4500** | 58.9231** | 23.8553 | 18.4210 | 13.1981 |
| IVDMD†† | 193.4500** | 681.1000** | 29.7221* | 52.7872* | 49.0279** | 48.0976** | 26.4767 | 0.0000 | 0.0000 |
| | Progenies | | | | | | | | |
| K | 0.03894 | 0.0000 | 0.2875* | 0.3593 | 2.8660* | 0.0000 | 0.0000 | 5.2384** | 0.3042 |
| Ca | 0.03069** | 0.1419** | 0.0000 | 0.0249** | 0.2447** | 0.0000 | 0.0068 | 0.0000 | 0.0074 |
| Mg | 0.02162** | 0.0759** | 0.0022 | 0.0033 | 0.0951** | 0.0005 | 0.0000 | 0.0000 | 0.0026* |
| KRAT | 0.0201* | 0.0856** | 0.0000 | 0.0209* | 0.4258 | 0.0000 | 0.0048 | 0.0539 | 0.0000 |
| P | 0.0057* | 0.0000 | 0.0011 | 0.0000 | 0.1014** | 0.0008 | 0.0000 | 0.0483** | 0.0005 |
| CP | 21.4225* | 5.2745 | 10.6319 | 36.1555 | 256.4900 | 0.0000 | 0.0000 | 0.0000 | 12.7401 |
| NDF | 2.3714 | 469.6400** | 63.2627** | 0.0000 | 75.1737 | 53.3409 | 0.0753 | 682.2900** | 0.0000 |
| IVDMD | 0.0000 | 296.3200* | 71.7024** | 0.0000 | 90.4612 | 27.4075 | 9.7219 | 74.0732 | 4.5377 |

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† E = entry.
‡ Y = year.
§ KRAT = K/(Ca + Mg) ratio, expressed as moles of charge.
¶ CP = crude protein.
\# NDF = neutral detergent fiber.
†† IVDMD = in vitro dry matter digestibility.

**Table 2. Variance components from ANOVA of mineral concentrations and forage quality parameters for 21 Russian wildrye clonal lines and their polycross progenies combined across three locations, two years, and four replications. Locations were treated as a fixed effect, and entries, years, and replications as random in the analyses.**

| | L† | E‡ | Y§ | E × L | E × Y | Y × L | E × Y × L |
|---|---|---|---|---|---|---|---|
| | g kg$^{-1}$ | | | | | | |
| | | | | Parents | | | |
| K | ns¶ | 0.9555** | 0.0000 | 0.0000 | 0.1206 | 6.3790** | 0.4972* |
| Ca | ns | 0.0188** | 0.0001 | 0.0170** | 0.0050* | 0.0694** | 0.0039 |
| Mg | ns | 0.0169** | 0.0002 | 0.0127** | 0.0016 | 0.0770** | 0.0048** |
| KRAT# | ns | 0.0178* | 0.0004 | 0.0166** | 0.0053 | 0.2849** | 0.0118** |
| P | ns | 0.0078** | 0.0003 | 0.0057** | 0.0000 | 0.0706** | 0.0044** |
| CP†† | ns | 33.125* | 44.225 | 31.385** | 6.0061 | 116.55** | 15.763* |
| NDF‡‡ | ns | 89.945** | 218.71 | 26.531 | 0.0000 | 141.81** | 44.035** |
| IVDMD§§ | ns | 57.365** | 56.921 | 30.655** | 0.0000 | 185.15** | 24.600** |
| | | | | Progenies | | | |
| K | ns | 0.0000 | 0.0000 | 0.1003 | 0.0299 | 4.0759** | 0.1232 |
| Ca | ns | 0.0149** | 0.0001 | 0.0059 | 0.0002 | 0.1899** | 0.0014 |
| Mg | ns | 0.0035 | 0.0002 | 0.0048* | 0.0008 | 0.0854** | 0.0009 |
| KRAT | ns | 0.0108** | 0.0004 | 0.0044 | 0.0004 | 0.2852** | 0.0000 |
| P | ns | 0.0030** | 0.0003 | 0.0000 | 0.0000 | 0.0734** | 0.0017* |
| CP | * | 0.7670 | 0.0005 | 18.118 | 0.0000 | 88.966* | 0.3950 |
| NDF | ns | 2.9221 | 359.34* | 0.0000 | 13.177 | 49.695 | 25.296* |
| IVDMD | ns | 9.2477 | 159.61* | 0.0000 | 0.0024 | 0.0000 | 34.547** |

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† L = location.
‡ E = entry.
§ Y = year.
¶ ns = not significant.
# KRAT = K/(Ca + Mg) ratio, expressed as moles of charge.
†† CP = crude protein.
‡‡ NDF = neutral detergent fiber.
§§ IVDMD = in vitro dry matter digestibility.

the three locations (Table 2). However, the variance components were much smaller and differences among mean squares from which the variances were computed were nonsignificant at the Mandan location (Table 1). As would be expected, the variance components associated with differences among the progenies were considerably smaller than those for the parental clones. At Logan, differences among progeny lines were significant for all traits evaluated except K, NDF, and IVDMD. At Swift Current, differences among progeny lines were significant only for Ca and KRAT. No significant differences were detected among the progeny lines at Mandan.

Relative differences among the clonal lines were not consistent across locations as indicated by the significant ($P < 0.01$) entry × location interactions for all but one of the mineral elements (K) and for two of the three forage quality attributes (CP and IVDMD) (Table 2). The entry × location mean squares were generally nonsignificant in the progenies. Pearson correlation coefficients ($r$) among entry means between locations provides some insight on this interaction in the clonal lines (Table 3). Correlations between Swift Current and Logan clonal means were all significant ($P < 0.05$), ranging from $r = 0.53$ to 0.72. Correlations between Mandan and Swift Current and Mandan and Logan were generally low and nonsignificant. Even in those instances where the $r$ values were significant (Swift Current vs Logan), the coefficient of determination ($r^2$) indicated that <50% of the variation among clonal lines at Swift Current was associated with that at Logan. The $r$ values among progeny lines between locations were mostly nonsignificant, and in some cases negative.

**Table 3. Correlation coefficients among three locations for mineral concentrations and attributes associated with forage quality in 21 Russian wildrye clonal lines, based on entry × location means ($n = 21$).**

| | $r$ | | |
|---|---|---|---|
| | ND† vs. SC‡ | ND vs. UT§ | SC vs. UT |
| K | 0.41 | 0.49* | 0.65** |
| Ca | 0.25 | 0.56** | 0.53** |
| Mg | 0.31 | 0.34 | 0.68** |
| KRAT¶ | 0.15 | 0.31 | 0.60** |
| P | 0.34 | −0.06 | 0.69** |
| CP# | 0.26 | 0.22 | 0.60** |
| NDF†† | 0.51* | 0.42 | 0.72** |
| IVDMD‡‡ | 0.47* | 0.41 | 0.71** |

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† ND = Mandan, North Dakota.
‡ SC = Swift Current, Saskatchewan, Canada.
§ UT = Logan, Utah.
¶ KRAT = K/(Ca + Mg) ratio, expressed as moles of charge.
# CP = crude protein.
†† NDF = neutral detergent fiber.
‡‡ IVDMD = in vitro dry matter digestibility.

The presence of entry × year interactions at Logan and Swift Current provides additional evidence of the inconsistent performance of the clonal lines across environments. These interactions were generally nonsignificant however, among the clonal lines at Mandan, the progeny lines at each of the three locations, and among both parent and progeny lines in the analyses of data combined across locations (Table 1, 2).

## Genetic Parameters

### Mineral Elements

The potential to genetically decrease incidence of grass tetany through breeding, determined on the basis of the magnitude of the broad- and narrow-sense heritability values, parent-progeny correlations ($r$), and range

**Table 4. Means, ranges, broad- ($H$) and narrow-sense ($h^2$) heritability values, and phenotypic parent-progeny correlations for mineral concentrations and attributes associated with forage quality in 21 Russian wildrye clonal lines and their polycross progenies, combined across 2 yr.**

| | K | Ca | Mg | KRAT† | P | CP‡ | NDF§ | IVDMD¶ |
|---|---|---|---|---|---|---|---|---|
| | g kg$^{-1}$ | | | | | | | |
| **Logan** | | | | | | | | |
| Parents: | | | | | | | | |
| Mean | 28.0 | 2.46 | 2.18 | 2.46 | 2.60 | 248 | 508 | 825 |
| Range min. | 24.8 | 1.86 | 1.56 | 1.87 | 2.35 | 226 | 478 | 798 |
| Range max. | 30.8 | 2.91 | 2.69 | 3.27 | 2.90 | 267 | 539 | 858 |
| $H$# | 0.53 | 0.81 | 0.66 | 0.69 | 0.76 | 0.82 | 0.85 | 0.83 |
| Progenies: | | | | | | | | |
| Mean | 28.1 | 2.55 | 2.21 | 2.39 | 2.61 | 252 | 502 | 830 |
| Range min. | 26.3 | 2.01 | 1.85 | 2.09 | 2.46 | 241 | 483 | 817 |
| Range max. | 29.8 | 2.95 | 2.66 | 2.89 | 2.88 | 264 | 515 | 849 |
| $h^2$†† | 0.04 | 0.62 | 0.55 | 0.47 | 0.53 | 0.46 | 0.03 | 0.00 |
| $r$‡‡ | 0.43* | 0.72** | 0.50* | 0.62** | 0.83** | 0.71** | 0.63** | 0.69** |
| **Swift Current** | | | | | | | | |
| Parents | | | | | | | | |
| Mean | 31.04 | 2.44 | 2.10 | 2.79 | 2.27 | 237 | 490 | 850 |
| Range min. | 28.0 | 2.02 | 1.75 | 2.32 | 1.94 | 221 | 467 | 831 |
| Range max. | 33.4 | 2.81 | 2.51 | 3.18 | 2.54 | 255 | 512 | 867 |
| $H$# | 0.67 | 0.76 | 0.93 | 0.73 | 0.82 | 0.59 | 0.73 | 0.62 |
| Progenies: | | | | | | | | |
| Mean | 31.6 | 2.65 | 1.94 | 2.86 | 2.21 | 212 | 503 | 834 |
| Range min. | 30.2 | 2.31 | 1.81 | 2.43 | 2.12 | 190 | 491 | 820 |
| Range max. | 33.6 | 3.13 | 2.12 | 3.14 | 2.32 | 231 | 516 | 843 |
| $h^2$ | 0.39 | 0.60 | 0.43 | 0.60 | 0.00 | 0.33 | 0.00 | 0.00 |
| $r$ | 0.01 | 0.56* | 0.28 | 0.41 | 0.76** | 0.01 | 0.45* | 0.47* |
| **Mandan** | | | | | | | | |
| Parents: | | | | | | | | |
| Mean | 29.2 | 2.69 | 2.03 | 2.54 | 2.21 | 250 | 523 | 836 |
| Range min. | 26.0 | 2.48 | 1.81 | 2.30 | 2.01 | 234 | 505 | 819 |
| Range max. | 31.2 | 3.05 | 2.28 | 2.76 | 2.39 | 269 | 534 | 848 |
| $H$ | 0.29 | 0.36 | 0.22 | 0.00 | 0.31 | 0.46 | 0.31 | 0.52 |
| Progenies: | | | | | | | | |
| Mean | 34.6 | 2.56 | 2.04 | 3.04 | 2.56 | 283 | 501 | 856 |
| Range min. | 33.1 | 2.19 | 1.86 | 2.83 | 2.43 | 271 | 491 | 843 |
| Range max. | 36.5 | 2.81 | 2.16 | 3.31 | 2.68 | 293 | 518 | 867 |
| $h^2$ | 0.00 | 0.20 | 0.00 | 0.20 | 0.00 | 0.00 | 0.00 | 0.23 |
| $r$ | 0.23 | 0.31 | 0.57** | 0.19 | 0.23 | 0.48* | 0.33 | 0.23 |
| **Combined across locations** | | | | | | | | |
| Parents: | | | | | | | | |
| Mean | 29.4 | 2.53 | 2.10 | 2.60 | 2.36 | 245 | 507 | 837 |
| Range min. | 26.9 | 2.24 | 1.78 | 2.23 | 2.16 | 227 | 488 | 821 |
| Range max. | 31.7 | 2.88 | 2.45 | 3.01 | 2.56 | 260 | 528 | 852 |
| $H$ | 0.72 | 0.61 | 0.65 | 0.55 | 0.68 | 0.58 | 0.81 | 0.74 |
| Progenies: | | | | | | | | |
| Mean | 31.4 | 2.59 | 2.06 | 2.76 | 2.46 | 249 | 502 | 840 |
| Range min. | 30.6 | 2.24 | 1.91 | 2.56 | 2.38 | 240 | 494 | 831 |
| Range max. | 32.1 | 2.82 | 2.26 | 3.06 | 2.60 | 257 | 515 | 847 |
| $h^2$ | 0.00 | 0.65 | 0.41 | 0.60 | 0.83 | 0.04 | 0.12 | 0.43 |
| $r$ | 0.23 | 0.71** | 0.52* | 0.59** | 0.83** | 0.52* | 0.71** | 0.69** |

* Significant at the 0.05 probability level.
** Significant at the 0.01 probability level.
† KRAT = K/(Ca + Mg) ratio, expressed as moles of charge.
‡ CP = crude protein.
§ NDF = neutral detergent fiber.
¶ IVDMD = in vitro dry matter digestibility.
# $H$ = Broad-sense heritabilities derived from variance components among clonal lines.
†† $h^2$ = Narrow-sense heritabilities computed from variance components among polycross progenies (half sib families).
‡‡ $r$ = Pearson correlation coefficients between progeny and parental means.

in entry means, varied among locations (Table 4). For example, at Logan, broad-sense heritabilities ($H$) computed from variance components among the clonal lines ranged from 0.53 to 0.81 for the mineral elements, and was 0.69 for KRAT. Narrow-sense heritabilities derived from variance components among the polycross progenies (half-sib families) at Logan were more variable, ranging from 0.04 for K to 0.55 for Mg, 0.62 for Ca, and 0.47 for KRAT. Parent-progeny correlations from the Logan trials were significant for all mineral elements and KRAT ($r$ = 0.43 to 0.72). The KRAT values ranged from 1.87 to 3.27 for the clonal lines, and from 2.09 to 2.89 in the progenies at Logan. These data suggest that in an environment similar to the Logan site, Russian wildrye cultivars with KRAT values below the threshold value of 2.2 could be obtained through intense selection in this breeding population.

Heritability values and parent-progeny relationships for parameters associated with grass tetany from the Swift Current trials also suggested that selection for

reduced grass tetany potential would be effective (Table 4). Broad-sense heritability values ranged from 0.67 for K, to 0.93 for Mg, and was 0.73 for the KRAT ratio. Narrow-sense heritability values for the mineral elements ranged from 0.39 for K, to 0.60 for Ca, and was 0.60 for KRAT. Parent-progeny correlations were all positive, but significant only for Ca ($r = 0.56$). The $r$ value for the KRAT (0.41) approached significance ($P = 0.06$). The range in means among the parental clones and progenies for the KRAT ratio were much less encouraging at Swift Current. These values ranged from 2.32 to 3.18 in the parental clones, and from 2.43 to 3.14 in the progenies, well above the 2.2 threshold level.

Genetic variation for parameters relating to grass tetany was less definitive at the Mandan site, possibly because poorer stands were obtained at that location. Broad- and narrow-sense heritabilities were more variable and substantially smaller than at the other two locations. The parent-progeny correlation was significant only for Mg ($r = 0.57$, $P < 0.01$). The range in KRAT values (2.30 to 2.76 for the clones, and 2.83 to 3.31 for the progenies) provided additional evidence that selection in this breeding population for KRAT values below the established danger level would not be a feasible objective in the northern Great Plains.

In the analyses of data combined across locations (Table 4), the presence of genotype × location interactions would be expected to mask the genetic variation among the clonal and progeny lines. Although this did occur to some degree, heritability values were relatively high for traits related to grass tetany. Broad-sense heritabilities ranged from 0.61 to 0.72 for the three minerals, and was 0.55 for the KRAT; $h^2$ values ranged from 0 to 0.65 for the minerals, and was 0.60 for KRAT. Parent-progeny correlations were significant ($P < 0.05$ or $< 0.01$) in all but one instance, and was 0.59 for KRAT ($P < 0.01$). This confirms earlier conclusions (Asay and Mayland, 1990), that although parameters associated with grass tetany potential can apparently be effectively altered in this Russian wildrye breeding population through recurrent selection, KRAT at or below the 2.2 target level would likely be achieved only through infusion of a broader germplasm base.

The significant correlation ($r = 0.83$, $P < 0.01$) between parents and progenies along with an $H$ value of 0.68 suggests that breeding for increased concentrations of P would also be a realistic breeding approach in this Russian wildrye population (Table 4). Ranges in P, 2.16 to 2.56 in the parents, and 2.38 to 2.60 in the progenies (Table 4), are similar to those found in other forage grasses and tend to be on the low end of concentrations needed for livestock production. Nevertheless, P deficiencies or Ca:P imbalance are not likely in livestock grazing this species (Mayland and Cheeke, 1995).

### Forage Quality Determinations

As in the mineral analyses, conclusions from the forage quality parameters (CP, NDF, and IVDMD) also are complicated by some inconsistencies across the three environments, and should be interpreted with caution. At Logan, the magnitude of the $H$ and $r$ values suggested that some genetic progress could be made through selection (Table 4). The $H$ values indicated that the genetic variance constituted from 82 to 85% of the phenotypic variance among clonal lines for CP, NDF, and IVDMD. The parent-progeny $r$ values (0.71 for CP, 0.63 for NDF, and 0.69 for IVDMD) were significant ($P < 0.01$). The $h^2$ values were much less, 0.46 for CP, but essentially 0 for NDF and IVDMD. Opportunities for selection based on ranges in mean values also were greater for CP than NDF and IVDMD. The range in clonal means was 17% of the overall mean for CP, compared with 12% for NDF and 7% for IVDMD. Corresponding ranges for the progenies were 9% for CP, 6% for NDF, and only 4% for IVDMD.

At Swift Current, the $H$ values indicated that a relatively large proportion of the phenotypic variance for forage quality traits among the clonal lines was due to genetic effects, ranging from 0.59 for CP to 0.73 for NDF (Table 4). The parent-progeny $r$ values were significant ($P < 0.05$) for NDF ($r = 0.45$) and IVDMD ($r = 0.47$), but was near 0 for CP. As was the case at Logan, $h^2$ was 0 for NDF and IVDMD, and somewhat higher (0.33) for CP. The range in clonal and progeny means at Swift Current also reflected those from the Logan location, indicating that more genetic variability was available for selection for CP than NDF and IVDMD. The ranges in CP among the clonal and progeny means were 14% and 19% of their respective general means; whereas the corresponding ranges for NDF and IVDMD were all less than 10%.

The ratio of the genetic variance to the phenotypic variance among the clonal lines for forage quality determinations at Mandan ranged from 0.31 for NDF to 0.52 for IVDMD. Parent-progeny $r$ values were significant ($P < 0.05$) only for CP, $r = 0.48$, and the $h^2$ values were 0 for CP and NDF, and 0.23 for IVDMD. The range among clonal and progeny means at Mandan followed a trend similar to that observed at the other two locations, with substantially greater ranges for CP than for NDF and IVDMD.

Results from the analyses of the forage quality data combined across environments (Table 4) suggested that selection in this breeding population of Russian wildrye on the basis of evaluations averaged across these three locations would be a worthy objective. In the combined analyses, broad-sense heritabilities among the clonal lines were relatively high, ranging from 0.58 for CP, to 0.81 for NDF, and 0.74 for IVDMD. Parent-progeny correlations computed from means across locations ($r = 0.52$ for CP, 0.71 for NDF, and 0.69 for IVDMD) were all significant ($P < 0.05$ or $<0.01$). As was the case in the individual analyses, $h^2$ values computed from variance components among the progeny lines were variable, ranging from 0.04 for CP to 0.43 for IVDMD. On the basis of ranges in mean values at the individual locations, opportunities for selection would be relatively good for CP, and somewhat limited for the other two quality parameters, particularly IVDMD.

### Intercharacter Relationships

Genetic correlation coefficients computed from the clonal data combined across locations (Table 5) sug-

**Table 5. Genetic correlation coefficients among parameters associated with grass tetany and forage quality in 21 Russian wildrye clonal lines, based on data combined across three locations and two years.**

| | Ca | Mg | KRAT† | P | CP‡ | NDF§ | IVDMD¶ |
|---|---|---|---|---|---|---|---|
| K | 0.71 | 0.25 | 0.02 | −0.11 | 0.50 | −0.51 | 0.89 |
| Ca | | 0.75 | −0.57 | 0.58 | 0.82 | −0.19 | 0.47 |
| Mg | | | −0.91 | 0.33 | 0.64 | −0.38 | 0.44 |
| KRAT | | | | −0.58 | −0.56 | 0.05 | 0.01 |
| P | | | | | 0.22 | 0.29 | 0.05 |
| CP | | | | | | −0.53 | 0.87 |
| NDF | | | | | | | −0.72 |

† KRAT = K/(Ca + Mg) ratio, expressed as moles of charge.
‡ CP = crude protein.
§ NDF = neutral detergent fiber.
¶ IVDMD = in vitro dry matter digestibility.

gested that KRAT could be reduced most effectively by selection for higher levels of Mg and Ca. Correlation values also indicated that selection for reduced KRAT per se would not significantly alter the two estimates of forage quality, NDF and IVDMD; however, a weak negative relationship was found between KRAT and CP. Crude protein also was positively associated with Ca and Mg, and to lesser degree with K. Genetic correlation values strongly indicate that selection for higher levels of CP would be accompanied by increased IVDMD. Crude protein and IVDMD were both negatively correlated with NDF.

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