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Performance of Meadow Fescue Accessions under Management-Intensive Grazing

Michael D. Casler* and Edzard van Santen

ABSTRACT

Meadow fescue (*Festuca pratensis* Huds.) is a pasture grass that has been little used in North America since the introduction of its higher yielding relative, tall fescue (*F. arundinacea* Schreb.). The objectives of this study were to quantify genotypic variation for traits related to performance under management-intensive grazing (MIG) within the USDA-NPGS collection of meadow fescue accessions, to relate that variation to the geographic sources, and to compare these meadow fescue accessions to a range of tall fescue cultivars. One hundred-sixty meadow fescue accessions and 10 tall fescue cultivars were grazed for 2 yr under a free-choice MIG system. Meadow fescue accessions were an average of 3.0% lower in net herbage accumulation (NHA; 8.33 vs. 8.60 Mg ha^{-1}), but 14.7% higher in apparent intake (3.13 vs. 3.58 Mg ha^{-1}) and 15.1% higher in apparent preference (31.7 vs. 36.4%) compared with tall fescue cultivars. Naturalized meadow fescue accessions had greater apparent intake and preference and were lower in crown rust resistance than cultivated meadow fescue accessions. Cultivated meadow fescue accessions were less variable for all traits than naturalized accessions, reflecting nearly a century of breeding activity in Europe. Most of the variability among accessions was accounted for by geographic sources. Naturalized accessions from the Russian Black Sea region generally ranked most favorably for all traits.

Meadow fescue may be more useful than tall fescue in northern North American MIG systems which are typically based on forage mixtures in which relatively unpalatable species are chronically refused. Meadow fescue is a diploid ($2n = 2x = 14$) forage grass widely adapted to lowlands of central and northern Europe. It is used primarily for grazing or in a frequent-cutting hay management system. Cytogenetic studies suggest that it is the source of the P genome of tall fescue (Sleper and West, 1996). It is partially sympatric with tall fescue in the southern portion of its distribution. Molecular marker analysis suggests that it is also closely related to perennial ryegrass, *Lolium perenne* L. (Xu and Sleper, 1994). It hybridizes readily with both perennial and Italian ryegrass, *L. multiflorum* Lam. (Thomas and Humphreys, 1991).

Meadow fescue was first introduced into North America prior to 1800 (Kennedy, 1900) and spread throughout the USA during the 19th century (Buckner et al., 1979). Continued introduction of new species and accessions, followed by extensive forage yield testing in the late 19th and early 20th centuries led to the conclusion that tall fescue had vigor and resistance to crown rust (caused by *Puccinia coronata* Corda) superior to that of meadow fescue (Buckner et al., 1979). As a result, cultivation of meadow fescue in the USA began a steady decline at the beginning of the 20th century. By the early 1940s, only 560 000 kg yr^{-1} of meadow fescue seed was produced in the USA (Hoover et al., 1948). By 1954, meadow fescue was no longer listed in the USDA Statistical Reporting Service's list of seed crops and tall fescue had reached a total seed production of 44 000 ha and 11 million kg yr^{-1} in the USA, more than any other perennial grass (USDA, 1954).

Numerous cultivars of meadow fescue have been developed by European breeding programs where meadow fescue is highly adapted and widely utilized. Of 233 *F. pratensis* accessions listed by the Germplasm Resources Information Network (GRIN; internet address: http://www.ars-grin.gov/npgs/; June 12, 2001), 79 either have a cultivar name or otherwise appear to be derived from breeding programs. Meadow fescue germplasm has also been used extensively in the improvement of *Lolium* × *Festuca* hybrids (Thomas and Humphreys, 1991). Thus, it is highly likely that considerable progress has been made in breeding meadow fescue for crown rust resistance and other important agronomic traits. The presence of large amounts of additive genetic variation for crown rust resistance in closely related species (Mansat and Betin, 1979; Wilkins, 1978; Wofford and

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Abbreviations: GRIN, Germplasm Resources Information Network; NHA, net herbage accumulation; NPGS, USDA National Plant Germplasm System; MIG, management-intensive grazing.

Watson, 1982) implies that crown rust resistance also exists within meadow fescue. A considerable amount of variation for morphological and agronomic traits exists within the USDA National Plant Germplasm System (NPGS) collection of meadow fescue accessions (Casler and van Santen, 2000). Variation in crown rust reaction within the collection had been demonstrated in two studies (Braverman, 1977; Casler and van Santen, 2000).

The greatest potential utility for meadow fescue in North America appears to be for MIG systems. A limited evaluation of seven meadow fescue and 15 tall fescue cultivars under free-choice MIG showed meadow fescue cultivars to have a range of apparent dry matter intake similar to that of the tall fescue cultivars, despite an average 11% lower forage availability (Casler et al., 1998). The objectives of this study were to quantify genotypic variation for traits related to performance under MIG within the USDA-NPGS collection of meadow fescue accessions, to relate that variation to the geographic source of the accessions, and to compare these meadow fescue accessions with a range of tall fescue cultivars.

MATERIALS AND METHODS

Seed Increase

This study was initiated with 213 meadow fescue accessions from the USDA-NPGS collection stored at Pullman, WA. Seed originating from the collection site or the original donation was used whenever possible (75 accessions). Accessions were otherwise represented by a first- or second-generation seed increase, which was conducted at Pullman, WA, mostly in 1986. Accessions were classified according to country of origin, on the basis of information obtained from GRIN, and cultivated status (cultivar or breeding material vs. wild or naturalized collection; on the basis of published accounts of collecting expeditions: USDA, 1969a,b, 1970, 1982, 1986, 1991).

Seeds were germinated in a greenhouse in January 1991 and raised as individual seedlings. Seedlings were transplanted to isolated crossing blocks at Arlington, WI, in April 1991. Each crossing block consisted of 100 plants spaced on 0.9-m centers in a 10 by 10 grid. Adjacent crossing blocks were a minimum of 10 m apart. Weeds were controlled in the crossing blocks by hand weeding. The land between all crossing blocks was planted to winter rye (*Secale cereale* L.) in September 1991 to form a pollen barrier in spring 1992.

Crossing blocks were fertilized with 60 kg N ha^{-1} in early spring 1992. Preemergence herbicide was applied for weed control prior to the initiation of spring growth as described by Falkner and Casler (1998). Prior to anthesis of meadow fescue, the winter rye pollen barrier was uniformly 30 to 40 cm higher than most meadow fescue plants. Seed was harvested on all meadow fescue plants. Seed of each plant was threshed, cleaned and weighed. Individual-accession seed increases were created by bulking equal amounts of seed of each plant from an individual crossing block.

Grazing Trial

Of the 213 seed increases, only 150 produced sufficient seed to establish replicated plots for grazing. The remaining 63 accessions were excluded from the grazing trial because of poor seed production, an insufficient number of plants in the crossing block, winter injury, or poor seed quality (fungal infections or poor germination per se). An additional 10 European meadow fescue cultivars were included in the trial and they were similarly classified according to country of origin. These cultivars were treated identically to all accessions classified as cultivated germplasm. Ten tall fescue seed lots, representing eight cultivars, were also included in the grazing trial [Advance, Barcel, Dovey, Elfina, GA5(E+), GA5(E−), Johnstone, KY31(E+), KY31(E−), and Malik].

A total of 170 populations were planted in drilled plots in April 1996 at Arlington, WI. Seeding rate was 500 pure live seeds m^{-2}, which was approximately equal to 11 kg ha^{-1} for meadow fescue and 14 kg ha^{-1} for tall fescue. The experimental design was a randomized complete block with four blocks. Plots were 0.9 by 1.3 m. A border row of meadow fescue was planted around the entire perimeter of the experiment. Alleys between rows of plots were seeded to a blend of Kentucky bluegrass (*Poa pratensis* L.), perennial ryegrass (*Lolium perenne* L.), and red fescue (*Festuca rubra* L.) to allow rapid visual identification of plots. The experiment was clipped three times for weed control, and fertilized twice with 40 kg N ha^{-1} during the seeding year.

The experiment was fertilized in early spring 1997 with 40 kg N ha^{-1}. Bulk density of herbage in each plot was measured with a pasture plate meter before and after each of 10 grazing events. The plate meter was built from aluminum with a mass of 1.25 kg and a circular plate area of 0.2 m^2. Plate height was measured approximately 3 s after allowing the plate to rest on the plot canopy, in three different places within each plot. Plate height was also measured at ten places on border plots. Following each border measurement, the 0.2-m^2 measured area was clipped at a 2-cm height. These samples were dried at 60°C and weighed. Because border plots were seeded with remnant seed from the accessions in the test and all accessions were of similar growth habit and morphology, border plots were highly representative of the test plots.

Within 18 h of the pregraze plate-meter measurements, the entire experiment was stocked with 70 to 90 dry Holstein cows and heifers (*Bos taurus*) for 4 to 6 h, depending on net herbage accumulation and the animals' appetites (mean stocking density of 345–445 animal units ha^{-1}). Postgraze pasture plate height measurements were made approximately 24 h after grazing. The experiment was grazed in mid-May, mid-June, early July, early August, and early September 1997 and mid-May, late May, late June, early August, and early September 1998. Each grazing event occurred when the average canopy height across all plots was approximately 30 cm. Data and sample collection were similar for all 10 grazing events. The entire experiment was mowed to 5 cm following each postgrazing measurement to equalize the residue of each accession prior to each regrowth cycle. All plots remained in a vegetative growth stage throughout the duration of the experiment.

Crown rust reaction was rated on each plot prior to the third and fourth grazing events of each year. Ratings were made on a scale of 0 to 10, where each value was a decile of pustule coverage on leaf blades of the visible canopy (i.e., 0 = none, 1 = 1–10% coverage, 2 = 11–20% coverage,..., 10 = 100% of visible leaves completely covered with pustules).

Statistical Analysis

Pre- and postgrazing plate height measurements were converted into estimates of available herbage by means of the calibration developed from border plots. Net herbage accumulation (NHA) was defined as the sum of available herbage (pregraze measurements) over five grazing events during the growing season. Apparent dry matter intake was defined as the difference between pre- and postgrazing available herbage, summed over five grazing events. Apparent preference was defined as apparent intake expressed as a percentage of NHA and averaged over five grazing events.

Each variable was analyzed by analysis of variance using the split-plot-in-time-and-space model (Steel et al., 1996). All effects were assumed to be random. Contrasts were used to test differences between the means of naturalized meadow fescue accessions, cultivated meadow fescue accessions, and tall fescue cultivars. Contrasts were also used to test differences between endophyte-infected and endophyte-free meadow fescue accessions, and were based on infection data of Holder et al. (1994). Accession or cultivar variance components for the three groups were estimated by equating mean squares to their expectations (Gaylor et al., 1970). Confidence intervals for variance component estimates were computed according to Milliken and Johnson (1984). Separate from the contrast analysis, the sum of squares for meadow fescue accessions was partitioned into among- and within-country sources of variation. Variance components and confidence intervals for among- and within-country sources were estimated as described above. Because of the large number of accessions from Russia and its large geographic size, accessions from this country were split into four convenient groups for the country-germplasm-source analysis: 19 cultivated accessions, 12 naturalized accessions from the Altai Mountains, 18 naturalized accessions from the Black Sea region, and four naturalized accessions from northwestern Russia.

Genotypic correlation coefficients between variables were computed separately for meadow fescue accessions and tall fescue cultivars, by the procedures of Mode and Robinson (1959). Principal components analysis was conducted on the 4 by 160 matrix of accession means for four variables measured on meadow fescue accessions.

RESULTS AND DISCUSSION

Calibrations of pasture plate meter height to estimates of available herbage were similar for pre- and postgrazing measurements. Regression equations were $Y = 0.042 + 0.103x$, $r^2 = 0.74$, $P < 0.01$ for pregrazing and $Y = 0.053 + 0.098x$, $r^2 = 0.70$, $P < 0.01$ for postgrazing. The slopes of these two regressions were homogeneous by *t*-test ($P = 0.58$), so pre- and postgrazing samples were pooled to form a single regression calibration equation, $Y = 0.003 + 0.104x$, $r^2 = 0.85$, $P < 0.01$. Homogeneity of pre- and postgrazing calibration equations has been reported previously for grazing experiments conducted with similar grazing pressure and herbage utilization rates (Casler et al., 1998). However, as grazing pressure and/or herbage utilization rates increase, pre- and postgrazing calibrations are less likely to be homogeneous. This was observed by Murphy et al. (1995) for pastures that received significantly heavier grazing pressure than applied in this study.

Mean squares for meadow fescue accessions were significant ($P < 0.01$) for all variables. The accession × year interaction was significant only for net herbage accumulation (NHA), but accounted for only 7.5% of the phenotypic variance among accession means for NHA. Mean squares for accessions within both naturalized and cultivated meadow fescue groups were significant ($P < 0.01$), but accession × year interactions within both groups were significant only for NHA at $P < 0.05$. Mean squares for tall fescue cultivars were all nonsignificant ($P = 0.09$–0.27), perhaps reflecting the low number

Table 1. Means over 2 yr and four replicates and *P*-values for contrasts among naturalized and cultivated meadow fescue accessions and tall fescue cultivars.

Source and species	*n*	Net herbage accumulation	Apparent intake	Apparent preference	Crown rust rating†
		Mg ha^{-1}		%	
Naturalized meadow fescue	78	8.34	3.65	37.0	5.1
Cultivated meadow fescue	82	8.33	3.52	36.0	4.7
Cultivated tall fescue	10	8.60	3.13	31.7	3.1
Meadow fescue vs. tall fescue		<0.0001	<0.0001	<0.0001	<0.0001
Naturalized vs. cultivated meadow fescue		0.5915	<0.0001	<0.0001	<0.0001

† 0 = none, 1 = 1–10%,..., 10 = 90–100% of leaf canopy covered with pustules.

of cultivars and/or low degrees of freedom. Cultivar × year interactions for tall fescue cultivars were also nonsignificant. Means over years were used in all subsequent analyses.

Meadow Fescue and Tall Fescue

Tall fescue cultivars had 3.1% higher average NHA than meadow fescue accessions (Table 1). This was approximately one quarter of the mean difference observed between 15 tall fescue cultivars and seven meadow fescue cultivars in a previous grazing study (Casler et al., 1998). The smaller difference in the current experiment likely reflects the vastly greater assemblage of meadow fescue germplasm, increasing the frequency of highly vigorous and adapted germplasm with NHA similar to or exceeding that of tall fescue. Indeed, 14 meadow fescue accessions (two cultivated and 12 naturalized) ranked higher than the highest-ranking tall fescue cultivar (Johnstone) for NHA (Fig. 1).

Naturalized and cultivated meadow fescue accessions did not differ in mean NHA (Table 1). However, natu-

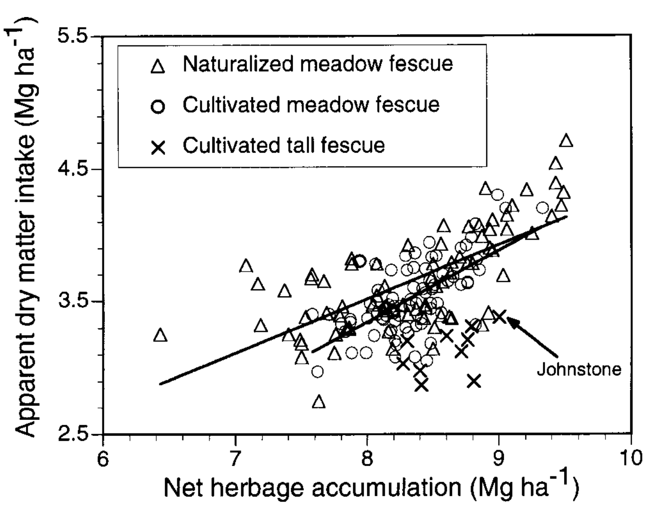

Fig. 1. Scatterplot of apparent dry matter intake vs. net herbage accumulation for 78 naturalized meadow fescue accessions (regression: $Y = 0.262 + 0.407X$, $r^2 = 0.48$, $P < 0.01$), 82 cultivated meadow fescue accessions (regression: $Y = -0.069 + 0.538X$, $r^2 = 0.41$, $P < 0.01$), and 10 tall fescue cultivars (regression: $P > 0.05$). Each data point represents a mean over 2 yr and four replicates.

Table 2. Accession or cultivar variance components and 95% confidence intervals for naturalized and cultivated meadow fescue accessions and tall fescue cultivars.

Variable and group	Variance component	Lower 95% limit	Upper 95% limit
Net herbage accumulation (Mg ha^{-1})			
Naturalized meadow fescue	0.360	0.219	0.583
Cultivated meadow fescue	0.040	−0.006	0.102
Cultivated tall fescue	0.027	0.007	0.053
Apparent dry matter intake (Mg ha^{-1})			
Naturalized meadow fescue	0.093	0.037	0.174
Cultivated meadow fescue	0.018	−0.017	0.064
Cultivated tall fescue	0.008	−0.003	0.020
Apparent preference (%)			
Naturalized meadow fescue	3.432	1.194	6.677
Cultivated meadow fescue	1.584	−0.085	3.880
Cultivated tall fescue	0.920	0.348	1.643
Crown rust rating			
Naturalized meadow fescue	1.764	1.221	2.669
Cultivated meadow fescue	0.870	0.582	1.342
Cultivated tall fescue	0.069	0.022	0.127

ralized meadow fescue accessions were nine times more variable for NHA than cultivated meadow fescue accessions, a statistically significant difference, as indicated by confidence intervals of variance component estimates (Table 2). It appears that meadow fescue breeding programs have significantly narrowed the genetic base without altering mean NHA of cultivated meadow fescue germplasm, relative to that available from naturalized sources.

Despite their inferior mean NHA, meadow fescue accessions had 14.7% higher apparent dry matter intake and 15.1% higher apparent preference than tall fescue cultivars (Table 1). Naturalized meadow fescue accessions averaged 4.0 and 2.8% higher in apparent intake and preference, respectively, than cultivated meadow fescue accessions. Johnstone was the highest-ranked tall fescue cultivar for apparent intake, but ranked only 114th among all meadow and tall fescue entries (Fig. 1). Tall fescue cultivars formed a tight grouping within the bivariate distribution of NHA and apparent intake, showing relatively little overlap with the distribution of meadow fescue accessions. For apparent preference, 'Grasslands Advance' was the highest-ranked tall fescue cultivar, ranking 143rd among all entries (Fig. 2). Naturalized meadow fescue accessions were more variable for both apparent intake and preference than cultivated meadow fescue and tall fescue germplasm (Table 2). Thus, breeding programs have also significantly reduced genotypic variability for apparent intake and preference. Part of this response may have been an indirect consequence of reduced genotypic variability for NHA.

Tall fescue cultivars had a 37% lower mean crown rust rating than meadow fescue accessions, while cultivated meadow fescue accessions had 8% lower mean crown rust rating than naturalized meadow fescue accessions (Table 1). Again, naturalized meadow fescue accessions were the most variable group, followed by cultivated meadow fescue accessions and tall fescue cultivars (Table 2). The small variability for crown rust rating among tall fescue cultivars led to a tight clustering within the overall distribution of mean crown rust ratings (ranks 5 through 50, Fig. 3).

The superior mean crown rust ratings and reduced genotypic variability of the two cultivated groups appear to be the result of selection for crown rust resistance in both species, particularly tall fescue. Meadow and tall fescue researchers have placed considerable emphasis on inheritance and genetic improvement of crown rust resistance. Crown rust resistance is moderately to highly heritable in both species and phenotypic selection for resistance is generally highly effective (Cagas, 1989; Enquist and Jönsson, 2001; Wofford and Watson, 1982). Both meadow and tall fescue have served as successful donors of crown rust resistance in interspecific hybrids with Italian ryegrass (Oertl and Matzk, 1999). Excessive susceptibility to crown rust was one factor leading to the nearly complete elimination of meadow fescue from commercial markets in the USA (Buckner et al., 1979). Crown rust decreases forage yield, water-soluble carbohydrate concentration, and in vitro dry matter digestibility in meadow fescue and tall fescue (Berry and Gudauskas, 1972; Cagas, 1979; Simons, 1970).

Sources of Variation among Meadow Fescue Accessions

For a subset of 67 meadow fescue accessions, mean crown rust reaction in this study was highly correlated

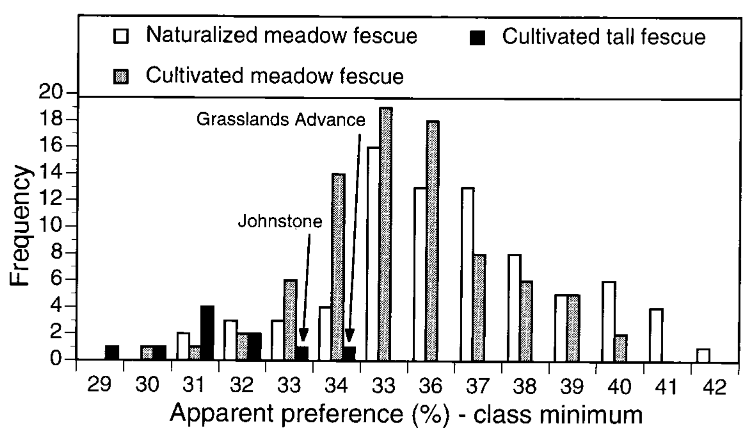

Fig. 2. Distribution of mean apparent preference (over 2 yr and four replicates) for 78 naturalized meadow fescue accessions, 82 cultivated meadow fescue accessions, and 10 tall fescue cultivars.

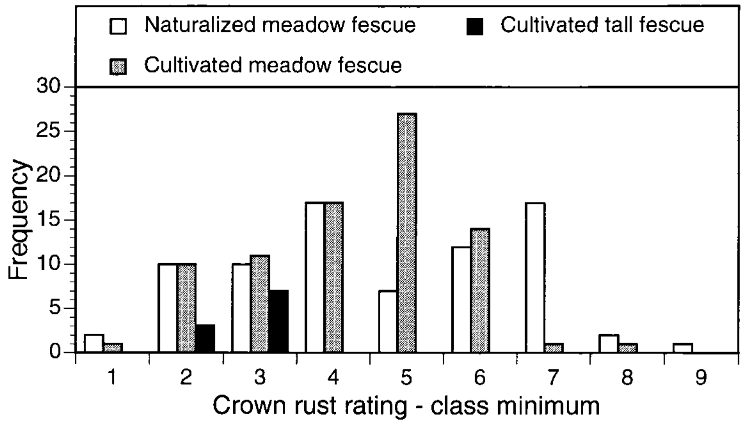

Fig. 3. Distribution of mean crown rust rating (over 2 yr and four replicates) for 78 naturalized meadow fescue accessions, 82 cultivated meadow fescue accessions, and 10 tall fescue cultivars.

($r = 0.71$, $P < 0.01$) with mean crown rust reaction from natural field inoculations at Geneva, NY (Braverman, 1977). However, neither the mean Braverman rating nor the mean rating described in this paper was correlated ($r = 0.03$, $n = 87$; $r = 0.06$, $n = 135$, respectively) with mean crown rust reaction from two northern Wisconsin locations (Casler and van Santen, 2000). *Puccinia coronata* is capable of considerable host specialization, both within and between host species (Simons, 1970). Strains of *P. coronata* originating on tall or meadow fescue had differential pathogenicity on a range of tall and meadow fescue cultivars (Cagas, 1984; Nakada et al., 1976; Schmidt, 1980). Furthermore, mean infection levels were markedly lower in the northern Wisconsin study (3.0 vs. 5.0 for the current study and 5.3 for Braverman). Thus, the strain of crown rust that infects meadow fescue in northern Wisconsin may be less virulent or have different host specialization than either the southern Wisconsin strain or the strain prevalent near Geneva, NY, in 1975 and 1976.

Crown rust rating had a high negative genotypic correlation coefficient with NHA ($r_g = -0.705 \pm 0.049$). A similar relationship was observed between forage yield and crown rust reaction in a collection of perennial ryegrass accessions (Casler, 1995). Because meadow fescue accessions expressed differential crown rust infection, it cannot be concluded unequivocally that NHA and crown rust reaction truly share a high negative genotypic correlation. Accessions with high crown rust reaction may have been incapable of expressing their potential for higher NHA simply becaue of the debilitating effects of infection. Indeed, the *reduction* in forage yield between fungicide-protected and rust-infected plants was correlated positively with crown rust reaction in meadow fescue (Cagas, 1979), suggesting that at least some observed variation in forage yield may be created by the rust infection. Thus, rust infection may potentially inflate estimates of genetic variation for NHA, apparent intake, and apparent preference. Because crown rust was abundant in mid- to late summer and absent during the remainder of the growing season, and because these variables were expressed as totals or means over five grazing events within the season, this potential bias is probably small in this study.

Apparent intake and NHA shared a moderately high genotypic correlation coefficient for meadow fescue accessions ($r_g = 0.631 \pm 0.082$). This result was similar to that from a grazing evaluation of seven meadow fescue cultivars, and suggests that a significant part of the variation for apparent intake was due to variation in available herbage (Casler et al., 1998). This correlation is very much a function of herbage utilization rate (mean apparent preference): as herbage utilization rate approaches 100%, apparent intake and NHA approach each other; as herbage utilization rate approaches 0%, genetic variation for apparent intake approaches zero. The existence of this correlation suggests that antiquality factors, such as toxins produced by endophytic fungi, had little influence on apparent intake of meadow fescue accessions in this study. Indeed, the relationship between apparent intake and NHA of meadow fescue accessions was largely linear, except for a small group of accessions that had higher-than-expected mean apparent intake for their relatively low mean NHA (Fig. 1). Holder et al. (1994) found that 23 of 150 meadow fescue accessions were infected with the endophyte *Neotyphodium uncinatum* (W. Gams, Petrini & D. Schmidt) Glenn, C.W. Bacon & Hanlin. In our evaluation, these 23 accessions averaged slightly higher in intake and crown rust reaction than the other 127 accessions (Table 3). Although

Table 3. Variance components, 95% confidence intervals, and sum of squares percentages for the partition of meadow fescue accession sums of squares among and within countries.

Variable and source of variation†	Variance component	Lower 95% limit	Upper 95% limit	Sum of squares (%)
Net herbage accumulation				
Among countries	0.344	0.159	0.780	59
Within countries	0.059	0.018	0.112	
Apparent dry matter intake				
Among countries	0.106	0.039	0.259	47
Within countries	0.017	−0.009	0.049	
Apparent preference				
Among countries	5.195	2.071	12.348	50
Within countries	0.627	−0.440	1.961	
Crown rust rating				
Among countries	1.995	0.966	4.451	63
Within countries	0.534	0.382	0.754	

† Among countries (26 df), within countries (133 df).

we did not conduct an endophyte evaluation in this experiment, these results suggest that there was little or no causal relationship between endophyte infection and apparent intake or preference of meadow fescue accessions. This was expected, because *N. uncinatum* does not produce ergot alkaloids which are toxic and unpalatable to livestock (Daccord et al., 1995).

Mean squares for countries, as a source of meadow fescue germplasm, were significant ($P < 0.01$) for all four variables. Variance components for among countries were 3.7 to 8.3 times larger than variance components for accessions within countries and the confidence intervals for pairs of variance components showed little or no overlap (Table 3). Country sources of germplasm explained 47 to 63% of the sums of squares for accessions, far more than the 16% of accession degrees of freedom among countries. These results strongly suggest regional geographic differentiation of phenotype for meadow fescue accessions. An evaluation of morphological and agronomic traits of these accessions under hay management led to similar conclusions, although the geographic differentiation was less striking in that study (Casler and van Santen, 2000).

Country means ranged from 7.45 to 9.10 Mg ha^{-1} for NHA, 3.24 to 4.20 Mg ha^{-1} for apparent intake, 31.7 to 40.4% for apparent preference, and 2.8 to 8.0 for crown rust rating. Despite this range and overwhelming statistical significance of country means, conclusions about the value of germplasm from most countries cannot be drawn becaue of the limited number of accessions. Fifteen of the 27 country sources had fewer than five accessions.

Table 4. Eigenvectors of the first two principal components for four variables measured on 160 meadow fescue accessions over four replicates and 2 yr.

Variable	First principal component	Second principal component
Net herbage accumulation	0.58	−0.36
Apparent dry matter intake	0.65	0.29
Apparent preference	0.34	0.66
Crown rust rating	−0.35	0.59
Variance explained (%)	49	41

Principal components analysis resulted in two components that accounted for 90% of the variability among accessions (Table 4). The first component (PRIN1) was associated with high NHA, high apparent intake, high apparent preference, and low crown rust rating. The second component (PRIN2) was associated with low NHA, high apparent intake, high apparent preference, and high crown rust rating. The association of high NHA with low crown rust rating in both components reflects the strong negative correlation between these two variables within these accessions. High values of PRIN1 are clearly desirable, while low values of PRIN2 are probably most desirable, although they would reflect relatively low mean intake and preference.

The scatterplot of PRIN1 vs. PRIN2 clearly demonstrates the considerable amount of geographic differentiation within this group of accessions (Fig. 4). As a group, the Russian Black Sea accessions ranked highest for PRIN1, while eight of the nine individual accessions with the highest values of PRIN1 were from this region. All 16 of the Russian Black Sea accessions had positive

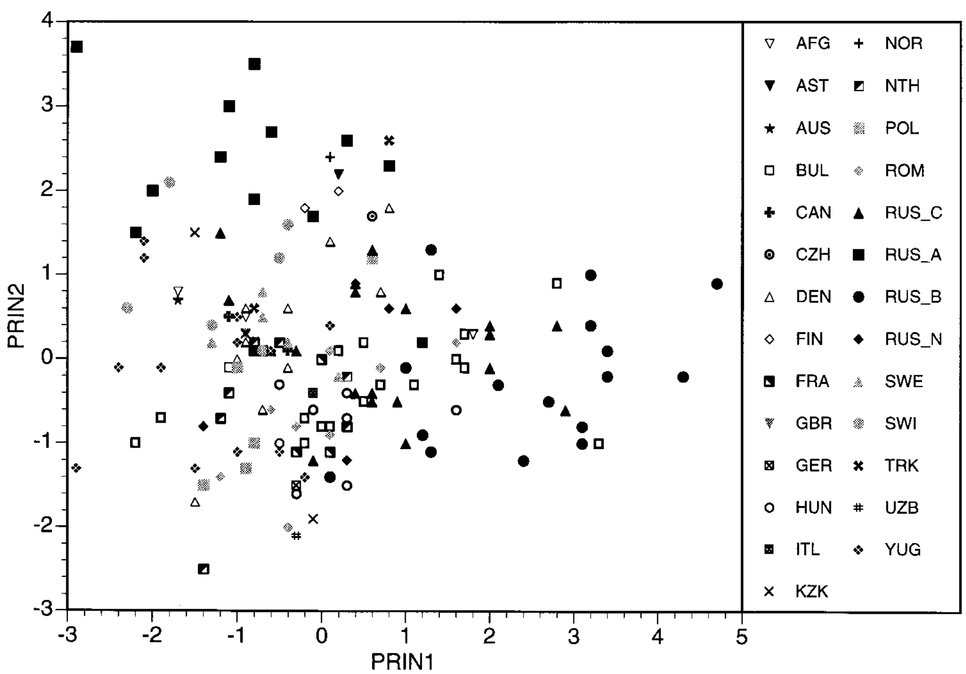

Fig. 4. Scatterplot of the first two principal components (PRIN1 and PRIN2) describing 90% of the phenotypic variability for four variables measured on 160 meadow fescue accessions. Country abbreviations are: AFG = Afghanistan, AST = Australia, AUS = Austria, BUL = Bulgaria, CAN = Canada, CZH = Czech Republic, DEN = Denmark, FIN = Finland, FRA = France, GBR = Great Britain, GER = Germany, HUN = Hungary, ITL = Italy, KZK = Kazahkstan, NOR = Norway, NTH = Netherlands, POL = Poland, ROM = Romania, RUS−C = Russia (cultivated), RUS−A = Russia (Altai Mtns.), RUS−B = Russia (Black Sea region), RUS−N = Russia (northwest), SWE = Sweden, SWI = Switzerland, TRK = Turkey, UZB = Uzbekistan, and YUG = the former Yugoslavia.

values of PRIN1. Six of the eight highest ranked Russian Black Sea accessions for PRIN1 and 13 of the 16 accessions from this region were generated from original seed, indicating that the apparent adaptive advantage of accessions from this region was not due to genetic shifts during seed multiplication. Of the 20 accessions ranked highest for PRIN1, 11 were from the Russian Black Sea region, five were Russian cultivars, three were from Bulgaria (one cultivated), and one was from Afghanistan (Fig. 4). Russian Black Sea accessions, Russian cultivars, and Bulgarian accessions were similarly diverse for both PRIN1 and PRIN2 with each group expressing approximately two-thirds of the range of PRIN1 and half the range of PRIN2. Yugoslavian accessions were uniformly low for PRIN1.

The 10 accessions with the lowest values of PRIN2 originated from nine countries, representing highly diverse geographic regions from Scandinavia to Southern Asia (Fig. 4). Seven of these accessions were represented by cultivated germplasm. Dutch and Hungarian accessions clustered together with relatively low values of PRIN2. Russian Altai accessions were tightly clustered at the high end of the PRIN2 scale, while Swiss accessions clustered just below Altai accessions, and Swedish accessions clustered just above the mean of PRIN2. Danish, Kazakh, Polish, and Yugoslavian accessions were highly variable for PRIN2.

The group of Russian cultivars formed a cluster that was intermediate between Russian Black Sea and Altai groups, acting as a phenotypic transition between these extreme groups, for the traits measured in this study. Many of these Russian cultivars may have germplasm from both Russian regions in their pedigrees. Alternatively, these cultivars may represent selections from within each region toward some common intermediate phenotypic goal. While the Black Sea accessions appeared the most useful for rotational grazing in Wisconsin-type environments, some of the Russian cultivars appeared to be nearly as advantageous.

The Russian Black Sea accessions derive from at least five collecting expeditions: Q. Jones and W. Keller in 1965, W.H. Skrdla in 1967, D.R. Dewey and A.P. Plummer in 1977, M.D. Rumbaugh in 1982, and one or more expeditions by Russian personnel of the Vavilov Institute of St. Petersburg (USDA, 1969a,b, 1970, 1982, 1986, 1991). Most of these accessions appear to have been collected in a relatively small region bounded loosely by the triangle of Rostov, Krasnodar, and Stavropol between the Black and Caspian Seas. Given the relatively small geographic area (less than 1000 km^2) and the tendency of germplasm explorers to collect near major roads to maximize their efficiency, it is possible that some of the accessions are duplicates or repeated samples from individual or neighboring meadows or pastures. At best, the narrow geographic range suggests relatively narrow genetic diversity within this group.

Because of the dominance of Black Sea accessions in this study, it will be difficult to maintain a high level of geographic diversity within a meadow fescue breeding program focused on rotational grazing for the northern USA. The geographic clustering in Fig. 4 suggests that geographic diversity largely equates to phenotypic diversity, which ultimately is related to genetic diversity. Thus, dominance of a gene pool by Black Sea accessions will likely lead to severe restrictions in genetic diversity and a possible genetic bottleneck. The germplasm from the Black Sea region may be suitable for short-term development of a new cultivar for use in MIG systems in temperate regions of North America. However, to ensure a high probability of long-term genetic gains, germplasm pools for recurrent selection should include accessions from additional geographic regions. Additional accessions to be added to the gene pool for long-term selection should focus primarily on NHA, intake, and preference, because crown rust resistance can be improved rapidly by relatively rapid and inexpensive phenotypic selection methods.

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