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Selection strategies for developing smooth bromegrass cell wall ideotypes

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Summary. A random sample of 80 families of the B8HD smooth bromegrass (*Bromus inermis* Leyss.) population were tested in three environments for forage yield and cell wall constituents. Expected progress from one cycle of family selection was computed for single-trait selection and multiple-trait restricted selection. Expected gains were compared to desired goals and actual results from one cycle of phenotypic selection. Desired goals were: Model I = reduced lignin and cellulose, with increased hemicellulose, resulting in no change in cell wall content; Model II = reduced lignin and cellulose with no change in hemicellulose; or Model III = reduced lignin, cellulose, and hemicellulose. Single-trait selection for high hemicellulose in first harvest or low cellulose in second harvest had the best expected responses, of any single trait, for Model I. Possible undesirable effects of selection for low cellulose would be a reduction in forage yield potential. Multiple-trait restricted selection was judged to be more effective, with responses all in the desired direction, by specifying increased hemicellulose in index development. Selection in second harvest was expected to have similar responses as first harvest, except for a greater increase in forage yield. Development of Models II or III is expected to be difficult due to a negative correlation estimate between first and second harvest cell wall concentration.

Key words: Cell wall – Ideotype breeding – Selection – Smooth bromegrass

Introduction

The ability of plant breeders to improve nutritive value of forage species has been demonstrated in several species (e.g., Burton et al. 1967; Coors et al. 1986; Ehlke et al. 1986). Improvements in laboratory measures of forage nutritive value have led to improved animal performance (e.g., Anderson et al. 1988; Burton et al. 1967; Eichhorn et al. 1986). Improvements in animal performance, through the use of new cultivars, is passed as pure profit to producers of animal products, provided the cultivar does not possess some trait that reduces its forage yield and persistence or substantially increases seed prices.

Research on the quantitative genetics of traits related to forage nutritive value has provided information on the role of plant cell wall constituents in limiting digestion of forage tissue by rumen microorganisms. Using in vitro dry matter digestibility (IVDMD) as a laboratory index of forage nutritive value, reductions in the concentrations of lignin and cellulose and an increase in hemicellulose concentration are expected to have the greatest beneficial effect toward increasing forage nutritive value (Casler 1986). This model (Model I), for changing cell wall composition, was proposed as an ideotype goal in breeding smooth bromegrass, *Bromus inermis* Leyss. (Casler 1986). A second model (II) was also proposed, in which lignin and cellulose would be reduced, but without the concurrent increase in hemicellulose concentration, thereby decreasing total cell wall concentration (Casler 1986). A third potentially desirable model (III) would be reduced lignin, cellulose, and hemicellulose.

The objective of this study was to investigate various strategies for selecting genotypes with the goal of developing populations characteristic of these three ideotype models. Selection strategies included single-trait selection for several criteria at two harvest dates, and multiple-trait restricted selection with several restriction patterns (based on the specification of desired gains) at two harvest dates. Development of populations characteristic of these models would allow three questions to be

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answered: (1) are genetic changes toward these ideotype goals attainable, (2) if so, will they lead to improved animal performance without increasing producer input costs, and (3) are these genetic gains achieved at more or less cost than selecting for improved IVDMD? These populations will also be useful in determining why genetic variation exists in forage species for digestibility of dry matter or cell walls and how cell wall constituents interact to limit digestion by rumen microorganisms. Testing hypotheses related to these questions will require careful and controlled manipulation of cell wall constituents.

Single-trait selection criteria were investigated because selection is simple and assays can be done rapidly. Multiple-trait selection indices were investigated because it is desirable to change the level of several traits, and unfavorable genetic correlations may prevent or hinder desirable correlated responses when using single-trait selection. One cycle of single-trait phenotypic selection on spaced plants, in the same population as used in this study, led to the desired changes for Model III, but not for Model I (Carpenter 1988). Among the significant selection responses, selection for low lignin decreased all cell wall constituents (Model III); selection for low cell wall concentration decreased cellulose; selection for low cellulose was unsuccessful; and selection for high hemicellulose decreased only lignin concentration (Carpenter 1988).

Restricted selection indices were the only type investigated because the relative changes for each trait in the index could be specifically stated prior to application of the index (Baker 1986; Harville 1975; Tai 1977). Baker (1986) stated that restricted indices should be considered when specific changes are required in primary traits or when certain primary traits must be maintained at fixed levels. Forage yield is a trait that probably must be maintained at least at its original level during selection for improved nutritive value.

Materials and methods

Open-pollinated family seed of 500 random genotypes from the B8HD smooth bromegrass population was produced at Arlington, Wisconsin, USA in July 1982. The B8HD population is a nine-clone synthetic previously selected for high IVDMD, resistance to seedling damping off (caused by *Pythium* spp.) and brown leafspot [caused by *Pyrenophora bromi* (Died.) Drechsl.], and persistence in mixture with alfalfa, *Medicago sativa* L. (Ehlke et al. 1986). Genotypes in the isolated crossing block were 1 year old, spaced on 1-m centers, and unreplicated. Seed from the plants comprising the perimeter row were discarded, leaving 352 families for testing. Plots of each family were seeded at Arlington [Plano silt loam (fine-silty, mixed, mesic Typic Argiudoll)] and Marshfield, Wisconsin [Withee silt loam (fine-loamy, mixed, frigid Aeric Glossoboralf)] in April 1983. The seeding rate was 20 kg ha^{-1}. The experimental design was two randomized complete blocks with a restriction on randomization: the 352 families were randomly divided into 22 sets of 16 families, and each set was planted as a 16-plot incomplete block within each complete replicate. Each plot was 0.9 × 1.35 m and composed of five seeded rows, which were indistinguishable by September 1983 due to tillering.

Plots at both locations were clipped twice to control annual weeds in the seeding year and fertilized with 56 kg N ha^{-1} after each clipping. In the fall of 1983 and 1984, P and K were applied at rates recommended by soil test results. In 1984 and 1985, plots were clipped for yield determination twice, in early June and early September. Nitrogen fertilizer was applied at 112 kg N ha^{-1} in April and after the first cutting in 1984 and 1985. Forage yield of each plot was determined on a dry matter basis, using approximately a 0.5 kg fresh forage sample from each plot for determination of dry matter concentration.

Due to an infestation of quackgrass [*Elytrigia repens* (L) Nevski] at Marshfield, only five sets of families were completely uncontaminated in both replicates. Therefore, all genetic parameter estimates were based on the 80 families in these five sets; data collected from all other families were not used in the analyses. Due to the increased severity of the quackgrass infestation, no data were collected from Marshfield in 1985.

From the 960 forage samples collected on families in the five sets to be analyzed, 90 were drawn as a stratified random sample; 7 or 8 samples were randomly drawn from within each of the 12 location-year-replicate-harvest combinations. These 90 samples were assayed for neutral and acid detergent fiber (NDF and ADF) and acid detergent lignin (Robertson and Van Soest 1981), using 0.5 g forage samples. Based on wet-laboratory data on the sample of 90 forage samples, a near-infrared reflectance spectrometer was calibrated and used to predict NDF, ADF, and lignin contents of all 960 forage samples (Norris 1985). Hemicellulose concentration was computed as NDF-ADF and cellulose concentration was computed as ADF-lignin (Goering and Van Soest 1970). These values of cellulose and hemicellulose were slightly biased from what would be obtained from more sophisticated analytical procedures (Morrison 1980). However, the Robertson and Van Soest (1981) procedure is judged adequate for breeding and genetic studies because (1) its rapidity and ease-of-application make it ideal for screening large numbers of genotypes or families, (2) cell wall constituents measured in this fashion are readily amenable to genetic manipulation (Carpenter 1988; Coors et al. 1986) and are useful for studying ruminal degradation of forage tissue (Casler 1987; Ehlke et al. 1986), and (3) the bias is probably relatively constant within species and within stages of maturity, so that genotype rankings and variances would differ little from use of other techniques.

Data were analyzed using a random effects model. The linear model for analysis of variance was

$$Y_{ijkl} = \mu + \lambda_i + (\varrho/\lambda)_{ij} + \beta_k + (\lambda\,\beta)_{ik} + (\beta\,\varrho/\lambda)_{ijk} + (\alpha/\beta)_{kl} + (\lambda\,\alpha/\beta)_{ikl} + \varepsilon_{ijkl}$$

where

Y_{ijkl} = the $i\,j\,k\,l^{\text{th}}$ observation,

μ = the overall mean,

λ_i = the effect of the i^{th} environment (locations and years together),

$(\varrho/\lambda)_{ij}$ = the effects of the j^{th} replicate in the i^{th} environment,

β_k = the effect of the k^{th} set,

$(\lambda\,\beta)_{ik}$ = $i\,k^{\text{th}}$ set × environment interaction effect,

$(\beta\,\varrho/\lambda)_{ijk}$ = the $i\,j\,k^{\text{th}}$ set × replicate/environment interaction effect,

$(\alpha/\beta)_{kl}$ = the effect of the l^{th} family in the k^{th} set,

$(\lambda\,\alpha/\beta)_{ikl}$ = the $i\,l^{\text{th}}$ family × environment interaction effect in the k^{th} set,

and ε_{ijkl} = $j\,l^{\text{th}}$ error effect within the k^{th} set and the i^{th} environment.

All estimates of family and family × environment variances were estimated within sets and then pooled over sets. Error effects in analyses of variance were tested for normality and randomness; no evidence of non-normality or non-randomness was found. Family and family × environment variance components were used to compute expected progress from one cycle of selection on a family mean basis, where means were based on two replicates in each of three environments. Expected selection progress was computed based on single-trait selection for each of nine selection criteria (season total forage yield, and NDF, lignin, cellulose, and hemicellulose determined on both first and second harvests). All computations were done in matrix formulation as follows:

$$\boldsymbol{R} = 1.659\, \boldsymbol{h}\, \boldsymbol{r_g}\, \boldsymbol{g_d}$$

where

- $\boldsymbol{R}$ = the matrix of expected direct and correlated selection responses (diagonal elements are direct selection responses and off-diagonal elements are correlated selection responses, rows are selection criteria, and columns are response criteria),
- 1.659 = the standardized selection differential for a 12.2% selection intensity [this was the selection intensity used by Carpenter (1988) for phenotypic selection in this population],
- $\boldsymbol{h}$ = a matrix in which the diagonal elements are the square root of heritability estimates and the off-diagonal elements are zeros,
- $\boldsymbol{r_g}$ = the genetic correlation matrix, which was formulated as $\boldsymbol{g_i}\, \boldsymbol{G}\, \boldsymbol{g_i}$ (Searle 1982), where $\boldsymbol{G}$ = the genetic variance/covariance matrix and $\boldsymbol{g_i}$ = a matrix in which the diagonal elements are the inverses of the genetic standard deviations and the off-diagonal elements are zeros, and
- $\boldsymbol{g_d}$ = a matrix in which the diagonal elements are the genetic standard deviations and the off-diagonal elements are zeros.

Knowles (1969, 1980) has reported non-random cross-pollination and limited pollen travel in smooth bromegrass crossing blocks. Based on these studies, it is expected that the genetic variation among families includes a paternal effect, deriving from variable paternal contributions to each maternal source. Thus, families would be intermediate between half-sib and full-sib families for genetic variance expectations. Assuming normal and disomic inheritance, with no epistasis, the expected genetic variance among families (σ_F^2) would be: $(1/4)\,\sigma_A^2 \leq \sigma_F^2 \leq (1/2)\,\sigma_A^2 + (1/2)\,\sigma_D^2$ (Hallauer and Miranda 1981).

Therefore, expected genetic gains may be biased upwards, to the extent that family structures approach a full-sib mating design, and this bias would be greatest for traits affected by dominance. Previous research has suggested that forage nutritive value in smooth bromegrass is controlled mainly by additive genetic variation (Ross et al. 1970; Sleper et al. 1973). Because no complete incompatability was observed (Knowles 1980) and at least 6% cross-pollination between genotypes can occur at a distance of 8 m within a crossing block (Knowles 1969), family structure and subsequent estimates of genetic variances for the B8HD families probably approximated a half-sib family mating design more closely than the full-sib design.

The nine selection criteria were also formulated into 12 restricted selection indices. The 12 different indices were the result of a $3 \times 2 \times 2$ factorial combination of factors (Table 1). Indices 1–6 restricted forage yield to an increase of 1 Mg ha^{-1}; indices 7–12 restricted forage yield to no change. Indices 1, 2, 7, and 8 restricted NDF to no change but specified decreases in lignin and cellulose and a compensatory increase in hemicellulose (Model I); indices 3, 4, 9, and 10 restricted hemicellulose concentration to no change and specified decreases in lignin and cellulose, thereby decreasing NDF (Model II); indices 5, 6, 11, and 12 specified decreases in lignin, cellulose, and hemicellulose (Model III). Odd-numbered indices specified changes in lignin and cellulose approximately in proportion to their population means in this study (last line in Table 2); even-numbered indices specified equal changes in lignin and cellulose. The absolute value of the coefficients specifies the genetic covariance to be imposed between the restricted trait and the index (Baker 1986). Changes in the overall scale of Table 1 coefficients would not affect expected selection responses. The set of 12 indices was applied in three manners: (1) restrictions on seasonal total forage yield and first harvest cell wall constituents with no restrictions on second harvest cell wall constituents (first five columns of Table 1), (2) restrictions on seasonal total forage yield and second harvest cell wall constituents with no restrictions on first harvest cell wall constituents (last five columns of Table 1), and (3) specified restrictions on all nine traits (all columns of Table 1).

Matrix computations for index formulation were as presented on p. 117 of Baker (1986). Expected selection responses from

Table 1. Restrictions on desired selection responses placed on individual traits included in first or second harvest selection indices

Selection index	First harvest restrictions					Second harvest restrictions				
	Yield	NDF[a]	Lig.	Cel.	Hem.	Yield	NDF[a]	Lig.	Cel.	Hem.
1	1	0	−1	−11	12	1	0	−1	−10	11
2	1	0	−1	− 1	2	1	0	−1	− 1	2
3	1	−12	−1	−11	0	1	−11	−1	−10	0
4	1	− 2	−1	− 1	0	1	− 2	−1	− 1	0
5	1	−22	−1	−11	−10	1	−20	−1	−10	−9
6	1	− 3	−1	− 1	− 1	1	− 3	−1	− 1	−1
7	0	0	−1	−11	12	0	0	−1	−10	11
8	0	0	−1	− 1	2	0	0	−1	− 1	2
9	0	−12	−1	−11	0	0	−11	−1	−10	0
10	0	− 2	−1	− 1	0	0	− 2	−1	− 1	0
11	0	−22	−1	−11	−10	0	−20	−1	−10	−9
12	0	− 3	−1	− 1	− 1	0	− 3	−1	− 1	−1

[a] NDF is neutral detergent fiber

Table 2. Expected selection responses for single-trait selection on a half-sib family mean basis with a selection intensity of 12.2%

Selection criterion	Direction of selection	Selection response criterion								
		Total forage yield	Harvest 1				Harvest 2			
			NDF[a]	Lig.	Cel.	Hem.	NDF[a]	Lig.	Cel.	Hem.
		Mg ha^{-1}	g kg^{-1}							
Forage yield	+	2.42[b]	3.6	0.7	3.9	4.0	3.8	1.1	2.2	3.5
Harvest 1										
NDF	−	−2.82	−2.4	−0.2	−1.4	−0.8	0.8	0.0	0.2	0.6
Lignin	−	−5.71	−1.3	−0.4	−1.0	0.1	0.2	−0.5	0.1	0.6
Cellulose	−	−4.44	−2.1	−0.2	−2.4	0.5	1.3	−0.1	−0.4	1.9
Hemicell.	+	3.77	0.9	0.0	−0.4	1.3	0.2	−0.2	−0.6	1.0
Harvest 2										
NDF	−	−4.77	1.3	0.0	1.4	−0.2	−1.9	−0.3	−0.2	−1.5
Lignin	−	−5.47	0.2	−0.4	−0.4	1.0	−0.9	−0.7	−0.2	0.0
Cellulose	−	−3.12	0.3	0.0	−0.5	0.8	−0.2	−0.1	−0.6	0.5
Hemicell.	+	3.72	−0.8	−0.1	−1.8	1.1	1.3	0.0	−0.4	1.7
Pop. mean		11.43	605	26	299	280	592	31	295	266

[a] NDF is neutral detergent fiber
[b] Direct selection responses are underlined

index selection were computed, for each index, as follows:

$$RI = 1.659\ Cov_{iI}(V_I)^{-1/2}$$

where

RI = the vector of expected responses for the nine traits based on one cycle of family selection for the index,
1.659 = the standardized selection differential,
Cov_{iI} = the vector of genetic covariances between individual traits in the index and the index, which was computed as $b'G$ (Baker 1986) (b = the 9 × 1 vector of index coefficients and b' was its transpose), and
V_I = the phenotypic variance of the index.

Results and discussion

There was no genetic variation for maturity in this population, either in the progeny test or in the original parental crossing block. Family variation was significant for all traits except hemicellulose at the second harvest. Family × environment interaction was not significant for any trait, despite 150 degrees of freedom for this mean square. This result supports other results that indicate the general lack of genotype × location and genotype × year interactions for traits related to forage nutritive value (e.g., Christie 1977; Ehlke et al. 1986; Reich and Casler 1985; Ross et al. 1970; Sleper et al. 1973). Heritability, on a family mean basis, was 0.71 for forage yield, 0.18–0.40 for first harvest cell wall constituents, and 0.13–0.36 for second harvest cell wall constituents. Heritability estimates for cell wall constituents were similar to realized heritability for IVDMD of unreplicated spaced plants (0.30; Casler and Carpenter 1989).

Single-trait selection

Expected direct selection responses were low for cell wall constituents; only two values exceeded 1% of the mean value, first and second harvest lignin (1.5% and 2.3% of the mean, respectively) (Table 2). Expected direct selection response for forage yield was high (21% of the mean). These expectations contrast with experimental results from one cycle of phenotypic selection based on unreplicated spaced plants in B8HD (Carpener 1988). Realized gains for higher forage yield and higher or lower hemicellulose were zero (Carpenter 1988). Conversely, significant realized gains for lower NDF, lignin, or cellulose were 1.6 to 4.2 times larger than expectations based on the progeny test. Apparently more genetic variation exists for some traits of smooth bromegrass than can be estimated using standard quantitative genetic models based on disomic inheritance, and/or spaced plants are a more effective screening tool for these traits than solid-seeded plots.

Selection for increased forage yield was expected to give the greatest responses for all cell wall constituents (Table 2). Similarly, selection for any cell wall constituent was expected to give a greater absolute magnitude change in forage yield than selection for forage yield; lignin, which was present in the lowest concentration, had the largest of these expected responses. The large magnitude of these responses involving forage yield was due to

the fact that genetic correlation estimates between forage yield and all cell wall constituents were all > 1.0, and forage yield heritability was approximately 2 to 5 times larger than for cell wall constituents. Due to the unrealistically large genetic correlation coefficients, the sum of lignin + cellulose + hemicellulose responses did not equal the NDF response for yield selection. These results suggested that the magnitude of expected correlated responses involving forage yield were probably not realistic. While estimates of their absolute magnitude may not be reliable, they were all positive, a result that was probably realistic. Without placing restrictions on any other trait, family selection for increased forage yield would have the favorable effect of increasing hemicellulose concentration, but the unfavorable effect of also increasing NDF, lignin, and cellulose concentrations. These expectations are quite contrary to previous results from two cycles of phenotypic selection on spaced plants of B8HD and its parent population (Carpenter 1988; Casler and Ehlke 1986; Ehlke et al. 1986).

Spaced-plant forage yield is generally considered to be an unreliable predictor of yield in solid-seeded plots (e.g., Casler and Hovin 1985; Petersen 1976; Rotili et al. 1976). Furthermore, plant spacing and the degree of intergenotypic competition can influence the genetic relationships among traits which are affected by competition (Casler and Hovin 1985; Rogers and Lazenby 1966). For cell wall constituents and other forage quality traits, spaced plant evaluations of smooth bromegrass provide excellent predictive capabilities of performance in solid plots (Carpenter 1988; Ehlke et al. 1986). Spaced-plant evaluations of forage nutritive value traits provide an adequate selection environment (adequate genetic variance and heritability and a high genetic correlation with solid-seeded plots), without allowing manifestation of usable genetic variance for forage yield. Low genetic correlations between forage yield and nutritive value of spaced plants (Casler 1986) indicate that any forage yield changes associated with selection for forage nutritive value of spaced plants would be due to drift. Since effective population sizes in the Carpenter (1988) study were 75, drift was not likely a factor. It could also be hypothesized that small plot size and large error variances in the Carpenter (1988) study prevented a reliable assessment of variation among entries for forage yield. This is probably not the case since forage yield was highly heritable in the current study, it was conducted in a manner similar to that of Carpenter (1988), had similar error variances for forage yield, and shared two of Carpenter's three locations.

Development of populations in the direction of cell wall ideotype Model I would be extremely difficult and time-consuming using single-trait selection (Table 2). All cell wall selection criteria, except hemicellulose, led to decreased NDF in the harvest upon which selection was based and little change or an opposite change in the other harvest. Selection for low NDF reduced all components in the selection harvest, but gave variable results in the other harvest. For development of Model III, NDF would be the best expected single-trait selection criterion. Selection for high hemicellulose or low cellulose would be expected to have similar and favorable results toward Model I development for all harvests, with the exception that lower cellulose would lead to reduced forage yield. Based on either criterion, hemicellulose always increased, cellulose always decreased, and lignin either decreased or showed no change. Selection for hemicellulose of first harvest or cellulose of second harvest gave the smallest expected responses for NDF. The dissimilarity of responses between the two harvests, which was not observed by Ehlke et al. (1986), may pose a potential problem for development of populations with consistent differences when using only single-trait selection.

Multiple-trait selection

When restrictions were placed on both first and second harvests in the same selection indices, expected selection gains were all < 0.06 Mg ha^{-1} for forage yield and < 0.3 g kg^{-1} for cell wall constituents (data not shown). These low responses were apparently due to the extreme severity of restrictions when those restrictions were placed on both harvests simultaneously, and to the negative genetic correlation between first and second harvest for NDF ($r_g = -0.46$). Other cell wall constituents were positively correlated between harvests ($r_g = 0.81$ for lignin, 0.40 for cellulose, and 0.70 for hemicellulose). Expected responses for first or second harvest restrictions, each placing no restrictions on the other harvest, are presented in Tables 3 and 4.

Harvest 1. Expected responses for all restricted traits were proportional to the restrictions placed upon them and were zero when the restriction was zero (Table 3). There was some variation among expected selection responses due to the different methods of setting restrictions, but all methods gave some expectation of progress. The magnitude of expected responses was also similar to those observed with single-trait selection.

Specifying an increase in hemicellulose appeared the best approach to Model I development, particularly since results were rather consistent for both harvests. Specifying no change or a decrease in hemicellulose (Models II and III) appeared to be effective, except for some inconsistency between harvests. Differences in hemicellulose restrictions had only slight effects on forage yield responses, but all gave some positive average response.

Specification of restrictions proportional to lignin and cellulose concentrations gave the best expectations for Model II development, but not for Models I or III

Table 3. Expected selection responses for restricted selection indices based on selection for total forage yield and first harvest traits

Selection index	Selection response criterion							
	Total forage yield	Harvest 1				Harvest 2		
		NDF[a]	Lig.	Cel.	Hem.	NDF[a]	Lig.	Cel.	Hem.
	Mg ha^{-1}	g kg^{-1}							
1	0.14	0.0	−0.1	−1.5	1.6	0.7	−0.3	−0.7	1.6
2	0.44	0.0	−0.4	−0.4	0.9	−0.6	−0.8	0.0	0.2
3	0.23	−2.8	−0.2	−2.5	0.0	1.8	0.1	−0.1	1.8
4	0.41	−0.8	−0.4	−0.4	0.0	−0.4	−0.6	0.3	−0.1
5	0.11	−2.4	−0.1	−1.2	−1.1	1.2	0.2	0.4	0.5
6	0.36	−1.1	−0.4	−0.4	−0.4	−0.2	−0.4	0.4	−0.2
Hem. restrict									
Increase (1, 2, 7, 8)	0.14	0.0	−0.3	−1.0	1.3	0.0	−0.5	−0.4	0.9
No change (3, 4, 9, 10)	0.16	−1.8	−0.3	−1.5	0.0	0.7	−0.2	0.1	0.9
Decrease (5, 6, 11, 12)	0.12	−1.8	−0.2	−0.8	−0.7	0.5	−0.1	0.4	0.1
Lignin and Cel.									
Prop. (odd nos.)	0.08	−1.7	−0.2	−1.8	0.2	1.2	0.0	−0.1	1.3
Equal (even nos.)	0.20	−0.6	−0.4	−0.4	0.2	−0.4	−0.6	0.2	0.0
Forage yield									
No change (7–12)	0.00	−1.2	−0.3	−1.1	0.2	0.4	−0.3	0.1	0.6
Increase (1–6)	0.28	−1.2	−0.3	−1.1	0.2	0.4	−0.3	0.1	0.6

[a] NDF is neutral detergent fiber

Table 4. Expected selection responses for restricted selection indices based on selection for total forage yield and second harvest traits

Selection index	Selection response criterion							
	Total forage yield	Harvest 1				Harvest 2		
		NDF[a]	Lig.	Cel.	Hem.	NDF[a]	Lig.	Cel.	Hem.
	Mg ha^{-1}	g kg^{-1}							
1	0.08	0.3	0.0	−0.8	1.1	0.0	−0.1	−0.8	0.9
2	0.64	−0.3	−0.3	−1.4	1.5	0.0	−0.6	−0.6	1.3
3	0.07	1.2	0.1	0.2	0.8	−0.8	−0.1	−0.7	0.0
4	0.62	1.1	−0.2	0.1	1.2	−1.2	−0.6	−0.6	0.0
5	0.06	1.6	0.2	0.9	0.5	−1.2	−0.1	−0.6	−0.6
6	0.55	1.6	−0.1	0.7	1.0	−1.6	−0.5	−0.5	−0.5
Hem. restrict									
Increase (1, 2, 7, 8)	0.18	0.0	−0.1	−1.1	1.3	0.0	−0.4	−0.7	1.1
No change (3, 4, 9, 10)	0.17	1.2	−0.0	0.2	1.0	−1.0	−0.3	−0.7	0.0
Decrease (5, 6, 11, 12)	0.15	1.6	0.1	0.8	0.8	−1.4	−0.3	−0.6	−0.6
Lignin and Cel.									
Prop. (odd nos.)	0.04	1.0	0.1	0.1	0.8	−0.7	−0.1	−0.7	0.1
Equal (even nos.)	0.30	0.8	−0.2	−0.2	1.2	−1.0	−0.6	−0.6	0.0
Forage yield									
No change (7–12)	0.00	0.9	0.0	−0.1	1.0	−0.8	−0.3	−0.7	0.2
Increase (1–6)	0.34	0.9	0.0	−0.1	1.0	−0.8	−0.3	−0.7	0.2

[a] NDF is neutral detergent fiber

(Table 3), on the average. The effect of proportional versus equal restrictions was not consistent for the two harvests. Proportionality put a greater constraint on concurrent improvements in forage yield than did equality. Specification of changes in forage yield did not affect selection responses for cell wall constituents of any index (i.e., responses for cell wall constituents for indices 1–6 were identical to the corresponding indices 7–12). The mean difference in expected forage yield improvement with a specified increase in forage yield was 2.4% of the population mean.

For Model I development, selection index number 1 would pobably be the most useful; it had the highest and most consistent responses across harvests and some expected increase in forage yield. Model II and III development would be more difficult than Model I due to the negative genetic correlations beween cellulose and hemicellulose and between first and second harvest NDF. Selection indices 4 and 6 were most consistent between harvests, but gave low responses for NDF. Selection indices 3 and 5 gave good first harvest responses, but were poor for second harvest and lower in forage yield response.

Harvest 2. When restrictions were placed on second harvest traits and not on first harvest traits, response patterns were similar to selection with restrictions on first harvest traits (Table 4). The main difference observed for second harvest restriction versus first harvest restriction was a smaller effect of lignin and cellulose proportionality versus equality, particularly in second harvest. The negative genetic correlation between first and second harvest NDF again posed the problem of inconsistency between harvests. Only selection with NDF restricted to zero change (Model I) was immune to this effect. Model I development, based on second harvest restrictions, would be best when based on selection index number 2. This index gave similar cell wall constituent responses as index number 1, but an eight-fold greater forage yield response.

Conclusions

Due to the presence of significant genetic variability and limited family × environment interaction, selection for forage yield or cell wall constituents, on a family mean basis, should be successful in the B8HD population. However, selection on the basis of solid-seeded family plots should not be conducted for forage yield alone, due to the presence of seriously unfavorable genetic correlations with forage nutritive value traits. Due to low expected gains and large input costs, progeny test selection, for forage yield and nutritive value together, is expected to be considerably less cost-effective and efficient than phenotypic selection for forage nutritive value of spaced plants. However, selection for forage yield should not be based on spaced plants, because of low selection progress (Carpenter 1988) and low correlations with solid-stand performance (Casler and Hovin 1985; Petersen 1976; Rotili et al. 1976).

The success of phenotypic selection for forage nutritive value traits, on a spaced-plant basis (Carpenter 1988; Ehlke et al. 1986), suggests that a combined form of phenotypic-genotypic selection would be most effective in efficiently improving both forage yield and nutritive value. Samples for laboratory analysis can be clipped from each plant in the parental crossing block at heading, several weeks before progeny families are produced. Selection would be based on parental (spaced-plant) nutritive value and progeny (solid-stand) forage yield, minimizing the risks associated with either selection method when used alone. This would require less time than a normal progeny test, because laboratory analyses of parents would be completed long before all yield determinations were made on the progeny, rather than after the last cutting was taken. Finally, the efficiency of this phenotypic-genotypic selection system may be improved further by the use of multistage selection indices (Godshalk et al. 1988). Selection among parents for forage nutritive value would reduce the number of families to be yield tested, allowing for greater replilcation of families and higher heritability of progeny forage yield.

Both single and multiple-trait selection schemes can be expected to give selection responses toward development of Model I or Model III ideotypes, with Model I the most likely candidate for rapid success due to considerably greater consistency between harvests. Model I development could be based on single-trait selection (high hemicellulose of first harvest or low cellulose of second harvest), but with potential loss of forage yield due to correlated changes with the low cellulose criterion. Model II appears to be an unrealistic goal, based on single-trait selection. Based on multiple-trait selection approaches, selection index number 1 (for first harvest restrictions) or 2 (for second harvest restrictions) would give the most favorable changes for all traits investigated in this study. Restrictions need not and should not be placed on both harvests simultaneously. The decision to base selection restrictions on first or second harvest traits probably depends on the breeder's objectives and resources. For example, we have a greater work force for first harvest, but it is also our busiest time of the year. Since second harvest restrictions had the greatest forage yield responses and similar cell wall constituent responses to first harvest restrictions, this might be enough information to warrant choosing second harvest as the restriction environment.

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References

Anderson B, Ward JK, Vogel KP, Gorz HJ, Haskins FA (1988) Forage quality and performance of yearlings grazing switchgrass strains selected for differing digestibility. J Anim Sci 66:2239–2244

Baker RJ (1986) Selection indices in plant breeding. CRC Press, Boca Raton

Burton GW, Hart RH, Lowrey RS (1967) Improving forage quality in bermudagrass by breeding. Crop Sci 7:329–332

Carpenter JA (1988) Divergent phenotypic selection for forage yield and nutritive value traits in smooth bromegrass. PhD thesis, University of Wisconsin-Madison (Diss Abstr ADG88-09020)

Casler MD (1986) Causal effects among forage yield and quality measures of smooth bromegrass. Can J Plant Sci 66:591–600

Casler MD (1987) In vitro digestibility of dry matter and cell wall constituents of smooth bromegrass forage. Crop Sci 27:931–934

Casler MD, Carpenter JA (1989) Morphological and chemical responses to selection for in vitro digestibility in smooth bromegrass. Crop Sci 29:924–928

Casler MD, Ehlke NJ (1986) Forage yield and yield component changes with divergent selection for in vitro dry matter digestibility of smooth bromegrass. Crop Sci 26:478–481

Casler MD, Hovin AW (1985) Predicting forage yield from morphological traits in reed canarygrass. Crop Sci 25:783–787

Christie BR (1977) Effectiveness of one cycle of phenotypic selection on in vitro digestibility in bromegrass and orchardgrass. Can J Plant Sci 57:57–60

Coors JG, Lowe CC, Murphy RP (1986) Selection for improved nutritional quality of alfalfa forage. Crop Sci 26:843–848

Ehlke NJ, Casler MD, Drolsom PN, Shenk JS (1986) Divergent selection for in vitro dry matter digestibility in smooth bromegrass. Crop Sci 26:1123–1126

Eichhorn MM Jr, Oliver WM, Hallmark WB, Young WA, Davis AV, Nelson BC (1986) Registration of 'Grazer' bermudagrass. Crop Sci 26:835

Godshalk EB, Timothy DH, Burns JC (1988) Application of multistage selection indices to crop improvement. Crop Sci 28:23–26

Goering HK, Van Soest PJ (1970) Forage fiber analysis (apparatus, reagents, procedures, and some applications). USDA-ARS Agric Handb 379, US Govt Print Off, Washington, DC

Hallauer AR, Miranda Fo, JB (1981) Quantitative genetics in maize breeding. Iowa State University Press, Ames

Harville DA (1975) Index selection with proportionality constants. Biometrics 31:223–225

Knowles RP (1969) Nonrandom pollination in polycrosses of smooth bromegrass, *Bromus inermis* Leyss. Crop Sci 9:58–61

Knowles RP (1980) Seedling pubescence as a genetic marker in smooth bromegrass (*Bromus inermis* Leyss.). Can J Plant Sci 60:1173–1180

Morrison IM (1980) Hemicellulosic contamination of acid detergent residues and their replacement by cellulose residues in cell wall analysis. J Sci Food Agric 31:639–645

Norris KH (1985) Definition of NIRS analysis. In: Marten GC, Shenk JS, Barton FE II (eds) Near infrared reflectance spectroscopy (NIRS): analysis of forage quality. USDA-ARS Agric Handb 643, US Govt Print Off, Washington/DC, p 6

Petersen HL (1976) Competition in *Lolium perenne* L. as measured by yield and persistency. In: Dennis B (ed) Breeding methods and variety testing in forage plants. Proc EUCARPIA Fodder Crops Sec, 7–9 September. Royal Veterinary and Agricultural University Højbakkegård, pp 129–140

Reich JM, Casler MD (1985) Effect of maturity and alfalfa competition on expected selection response for smooth bromegrass forage quality traits. Crop Sci 25:635–640

Robertson JB, Van Soest PJ (1981) The detergent system of analysis and its application to human foods. In: James WPT, Theander O (eds) The analysis of dietary fiber in food. Marcel Dekker, New York, pp 123–158

Rogers HH, Lazenby A (1966) Selection criteria in the breeding of grasses. In: Hill AGG (ed) Proc 10th Intl Grassl Congr, 7–16 July, Helsinki. Finnish Grassland Assn, Salomonkatu, pp 630–633

Ross JG, Bullis SS, Lin KC (1970) Inheritance of in viro digestibility in smooth bromegrass. Crop Sci 10:710–712

Rotili P, Zannone L, Gnocchi G (1976) Effects of association and density in clones of tall fescue (*Festuca arundinacea* L.). In: Dennis B (ed) Breeding methods and variety testing in forage plants. Proc EUCARPIA Fodder Crops Sec, 7–9 September. Royal Veterinary and Agricultural University, Højbakkegård, pp 141–151

Searle SR (1982) Matrix algebra useful for statistics. Wiley, New York

Sleper DA, Drolsom PN, Jorgensen NA (1973) Breeding for improved dry matter digestibility in smooth bromegrass (*Bromus inermis* Leyss.). Crop Sci 13:556–559

Tai GC (1977) Index selection with desired gains. Crop Sci 17:182–183