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1993

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Hopkins, Andrew A.; Vogel, Kenneth P.; and Moore, Kenneth J., "Predicted and Realized Gains from Selection for In Vitro Dry Matter Digestibility and Forage Yield in Switchgrass" (1993). *Publications from USDA-ARS / UNL Faculty*. 1902.
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Predicted and Realized Gains from Selection for In Vitro Dry Matter Digestibility and Forage Yield in Switchgrass

Andrew A. Hopkins, Kenneth P. Vogel,* and Kenneth J. Moore

ABSTRACT

Improved forage yield and quality, which can lead to more efficient livestock production, are important goals in switchgrass (*Panicum virgatum* L.) breeding. Objectives of this study were to determine the effectiveness of multiple cycles of recurrent restricted phenotypic selection (RRPS) in improving forage yield in switchgrass and in improving in vitro dry matter digestibility (IVDMD), and to compare predicted and realized gains from selection. Six switchgrass populations were developed by selecting a base population for one cycle of low and three cycles of high IVDMD and two cycles for high yield. Half-sib progenies of parents selected from the base population for high and low IVDMD were used to estimate heritability for IVDMD by parent-progeny regression. Realized gains from selection were determined in a seeded sward trial that included the base and six selected populations. Estimated and realized heritabilities for IVDMD were 0.40 and 0.31, respectively. Predicted gains and (in parenthesis) realized gains from selection for IVDMD in grams per kilogram per cycle were -21 (-15) for the Low IVDMD Cycle 1, 16 (15) for the High IVDMD Cycle 1 ('Trailblazer'), 14 (4) for the High IVDMD Cycle 2, and 19 (18) for the High IVDMD Cycle 3 populations. There was a low but positive genetic correlation between forage yield and IVDMD of 0.10. Forage yield was not improved by RRPS, probably because of lack of genetic variability for forage yield in the base population. It is concluded that RRPS is effective for improving IVDMD in switchgrass, but was not effective in improving forage yield in the populations evaluated, and that predicted gains exceeded realized gains from selection for IVDMD due to limited selection for traits other than IVDMD.

IMPROVING forage yield and quality are important objectives in breeding switchgrass. Gain from selection in a breeding program for a cross-pollinated species such as switchgrass depends on genetic variation within a population for a given trait, heritability of that trait, and selection intensity (Falconer, 1981).

Previous research indicates that substantial genetic variation for IVDMD exists in switchgrass. Both Talbert et al. (1983) and Godshalk et al. (1986) reported moderately high heritabilities, calculated on an among and within half-sib family basis, for IVDMD in lowland switchgrass types originating from floodplains. Vogel et al. (1981) observed realized heritabilities of 0.59 for high IVDMD and 0.55 for low IVDMD in upland switchgrass types, which are shorter and finer stemmed than lowland types.

Heritabilities for forage yield in switchgrass are very low to moderately low. Using parent-progeny regression, Newell and Eberhart (1961) obtained a heritability estimate of 0.05 for forage yield from a set of late-maturing tall green upland accessions. Other heritabilities

for forage yield have ranged from 0.20 (Godshalk et al., 1986) to 0.59 (Talbert et al., 1983).

Utilizing a base population similar in origin and maturity to the tall green population described by Eberhart and Newell (1959), Vogel et al. (1981) achieved significant shifts in switchgrass IVDMD in a single cycle of divergent RRPS, which is a form of stratified mass selection. In a replicated grazing trial, Anderson et al. (1988) reported that the two-percentage-unit increase in IVDMD for the High IVDMD Cycle 1 population, later released as the cultivar Trailblazer (Vogel et al., 1991), led to a >20% increase in steer (*Bos taurus*) gains per hectare compared with 'Pathfinder', a switchgrass cultivar similar in origin to the base population. Forage yield was not changed by divergent selection for IVDMD.

The effectiveness of RRPS (Burton, 1974) in improving forage yield in switchgrass has not been tested, nor has its effectiveness in improving IVDMD in multiple cycles of selection. Information is also lacking on direct comparisons between predicted and realized gains from selection in switchgrass, after either single or multiple cycles of selection. Our objectives were to determine the effectiveness of multiple cycles of RRPS in improving forage yield, and alternatively IVDMD, in an upland switchgrass population, and to determine predicted and realized gains from selection in this same population.

MATERIALS AND METHODS

Population Development

Population development, as summarized in Table 1 and Fig. 1, took place at the Nebraska Agricultural Experiment Station near Mead, 55 km northeast of Lincoln in southeast Nebraska on a Sharpsburg silt loam (fine, montmorillonitic, mesic Typic Argiudoll). All strains were developed from the ey and ff upland type populations described by Newell and Moline (1978), which together constitute the base population. Separate space-planted nurseries were used to select for IVDMD and forage yield. All space-planted selection nurseries were sampled or harvested the first or second year following establishment and fertilized annually with NH_4NO_3 at rates of 90 to 112 kg N ha^{-1} . The method of Moore et al. (1991) for describing morphological development stage of perennial grasses will be used in this report.

A description of the nursery and the methods used to initiate RRPS for IVDMD is given by Vogel et al. (1981). The restrictions imposed were as follows. In all cycles of selection for IVDMD, the nursery was stratified into rows, and the most leafy, vigorous plants in a row ($\approx 20\%$) were sampled at panicle emergence (R1 stage). For each row, the sampled plants with the highest IVDMD were selected. Of these, only disease-free plants with adequate spring vigor were placed in a replicated polycross isolation (two replications). An equal amount of seed was then bulked from each genotype in the polycross isolation to start the next cycle of selection.

Selection for forage yield differed slightly from selection for IVDMD. In the High Yield Cycle 1 selection nursery, the restrictions included harvesting every plant for forage yield, stratifying the nursery into rectangular 32-, 20-, or 25-plant

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Table 1. Number of plants, means, standard deviations, and selection intensities for four cycles of selection for in vitro dry matter digestibility (IVDMD) and two cycles of selection for forage yield in switchgrass.

Population	Selection nursery† <i>n</i>	Sampled plants‡			Selected plants			<i>i</i> §
		<i>n</i>	$\bar{x}$	<i>s</i>	<i>n</i>	$\bar{x}$	<i>s</i>	
IVDMD, g kg ⁻¹								
Low IVDMD Cycle 1	2240	220	511	45	25	458	15	1.68
High IVDMD Cycle 1 (Trailblazer)	2240	220	511	45	25	551	35	1.68
High IVDMD Cycle 2	1056	283	484	34	88	518	23	1.13
High IVDMD Cycle 3	900	195	527	46	48	574	24	1.27
Forage yield, g plant ⁻¹								
High yield Cycle 1	690	682	680	193	64	937	122	1.79
High yield Cycle 2	740	157	1115	252	49	1300	228	1.13

† *n* = number of plants.

‡ $\bar{x}$ = mean; *s* = phenotypic standard deviation.

§ *i* = standardized selection differential.

selection blocks (differences due to an uneven number of rows), and basing selections on 2-yr means. Plants were harvested with a flail-type plot harvester at anthesis (R4) in 1976 and at the R1 stage in 1977. The phenotypic correlation between forage yields for 1976 and 1977 was $r = 0.65$ ($P < 0.01$). The repeatability estimate, calculated using years as replications (Falconer, 1981, p. 126–127), was 0.98 for forage yield. In the High Yield C2 selection nursery, the top 25% of plants were visually chosen based on vigor for harvesting and, due to the high correlation and repeatability estimates calculated for Cycle 1, final selections were made on the basis of a single year's forage yield. Plants were harvested at the R4 stage in 1981 in the High Yield C2 selection nursery. In both selection cycles, dry matter percentages were determined on a portion of the plants harvested and used to adjust forage yields to a dry-weight basis. Polycrossing restrictions were the same as those used in selecting for IVDMD.

Progeny Trials for Heritability Estimates

A replicated progeny trial was conducted to obtain heritability estimates, to predict gain from selection for IVDMD, and to determine genetic correlations between forage yield and

IVDMD. In this study, the populations designated Low IVDMD C1 and High IVDMD C1 are the same as those designated Low IVDMD PC and High IVDMD PC, respectively, by Vogel et al. (1981). The Low IVDMD PC and High IVDMD PC populations were derived by placing parental clones in polycross isolation. Open-pollinated seed was also harvested from the parental clones in the original selection nursery. These populations are identified as Low IVDMD OP and High IVDMD OP by Vogel et al. (1981). Seed from individual clones was used to plant progeny rows of the four populations (Fig. 1) near Mead, NE, in the spring of 1978 as a randomized complete block experiment with two replications. Plots consisted of seeded rows 0.76 m apart and 4.5 m long. Atrazine [6-chloro-*N*-ethyl-*N'*-(1-methylethyl)-1,3,5-triazine-2,4-diamine] was applied at a rate of 2.2 kg a.i. ha⁻¹ shortly after planting. The experiment was burned in early spring of 1979 and 1980 to remove residue; plots were fertilized with 112 and 128 kg N ha⁻¹ as NH₄NO₃ on 14 May 1979 and 28 Apr. 1980, respectively, as well as with 26 kg P ha⁻¹ on 5 May 1980. Dacthal [dimethyl tetrachloroterephthalate] was applied for weed control at the rate of 13 kg a.i. ha⁻¹ in May 1979. Plots were sampled on 25 July 1979 and on 5 Aug. 1980 at the R1 stage by cutting tillers at ≈10 cm height at random locations within a plot. Plots were harvested with a flail-type harvester on the

Fig. 1. Development of switchgrass populations used in determining predicted and realized gains from selection.

respective sampling dates; yield was adjusted for dry matter and plot length.

Estimating Gain from Selection

Realized gain from selection was determined using a replicated sward trial planted near Mead. The yield test included the base population, the four populations selected for IVDMD, and the two populations selected for high forage yield. Sward plots 4.6 m long by 1.2 m wide were planted on 30 May 1986. A plot drill was used for seeding at a rate of 430 PLS m⁻². The experiment was planted as a randomized complete-block design using six replications. Atrazine was applied on 30 May 1986 at a rate of 2.2 kg a.i. ha⁻¹ for weed control. Plant residue from the first year of growth was burned in early spring of 1987. A mixture of 2.2 kg a.i. ha⁻¹ alachlor [2-chloro-*N*-(2,6-diethylphenyl)-*N*-(methoxymethyl) acetamide], and 1.1 kg a.i. ha⁻¹ atrazine was applied on 8 May 1987. In 1988, plant residue was mowed 7 April; a mixture of 1.1 kg a.i. ha⁻¹ atrazine and 2.2 kg a.i. ha⁻¹ metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)acetamide] was applied in early spring. On 21 June 1988, 2,4-D amine [(2,4-dichlorophenoxy) acetic acid] was applied at 0.45 kg a.i. ha⁻¹ for weed control. Plant residue was burned in early spring 1989. Metolachlor and atrazine (2.2 kg a.i. ha⁻¹) and 2,4-D amine (0.45 kg a.i. ha⁻¹) were applied on 3 May 1989. Each spring plots were fertilized with 112 kg N ha⁻¹ applied as NH₄NO₃.

Forage was sampled three times during both 1987 and 1988 and once in 1989. All samples were taken by cutting tillers with hand sickles at ≈10 cm height at random locations within a plot. Sample 1 was taken at early stem elongation (E0 to E2) on 15 June 1987 and 14 June 1988, Sample 2 was taken at the boot stage (R0) on 30 June 1987 and 12 July 1988, and Sample 3 was at heading (R3; when 50% of the panicles in a plot had emerged) on 11 Aug. 1987 and 1988. Care was taken not to sample regrowth. In 1989, a single sample was taken at R3 on 27 July 1989 for dry matter determination only. Forage was harvested using a plot flail harvester within 1 or 2 d after the final forage sample was collected. The harvester cut a swath 0.9 m wide, the length of the plots. Cutting height was 10 cm. Forage yield was adjusted to a dry-matter basis, using the dry matter percentage from the previously collected forage sample. Dry weight of the samples taken during the season was added to the dry weight of harvested plot yield to give a total dry weight yield.

Plot stands were estimated after unharvested borders of plots were removed. A 1-m² grid, divided into 25 equally sized subsquares, was placed randomly within a plot and the number of squares not containing a live switchgrass plant were counted. The procedure was repeated in a different area of the same plot. The total number of squares not containing a plant was multiplied by 2, and the resulting number was subtracted from 100 to give percent stand.

Forage Quality Analyses

All forage samples from selection nurseries, progeny test, and the sward yield trial were dried in a forced-air oven at ≈65 °C, and ground in a Wiley¹ mill to pass through a 1-mm screen. To determine IVDMD, the Tilley and Terry (1963) procedure was modified by adding 6 g of urea to every 3.5 L of rumen fluid and deleting HgCl₂ and Na₂CO₃ after the first stage. Samples from the sward trial were reground to uniformity using a UDY cyclone mill.

Heritability Estimates and Statistical Analysis

Parent–progeny regression was used to determine two separate heritability estimates for IVDMD, one based on poly-

crossed progeny and the other based on open-pollinated progeny. Two-year means from the open-pollinated progeny rows were regressed on the 3-yr parental means from the Cycle 1 selection nursery. This same procedure was used with the Low IVDMD PC and High IVDMD PC populations as well. Heritability was then calculated as twice the regression coefficient; the standard error for heritability was calculated as twice the standard error of the regression coefficient.

Variance component analysis was also used to determine heritabilities on a half-sib family mean basis as described by Nguyen and Sleper (1983):

$$h^2 = \frac{\sigma_F^2}{[\sigma_F^2 + \sigma_{FY}^2/y + \sigma_{FR}^2/r + \sigma_e^2/ry]} \quad [1]$$

where σ_F^2 is the variance among half-sib families, σ_{FY}^2 and σ_{FR}^2 are the variances for the family × year and family × replication interactions, σ_e^2 is the error variance, and r and y represent the number of replications and years, respectively. The experimental design was a split plot in time, with all effects being random. Standard errors for heritability estimates obtained using variance component analysis were calculated using the method outlined by Nyquist (1991).

Predicted gain from selection was calculated according to Falconer (1981) as:

$$Gs_1 = h^2S \quad [2]$$

where S is the selection differential, or as:

$$Gs_2 = ih^2\sigma_p \quad [3]$$

where i is the standardized selection differential from Becker (1975) and σ_p is the phenotypic standard deviation from the respective selection nursery. Parent–progeny regression heritability estimates were used in predicting gain from selection.

Genetic correlations between forage yield and IVDMD were calculated according to Falconer (1981), using progeny row data and the formula:

$$r_{gyd} = \frac{\sigma_{gyd}}{\sqrt{(\sigma_{yy}^2 \sigma_{dd}^2)}} \quad [4]$$

where r_{gyd} is the genetic correlation between forage yield and IVDMD, σ_{gyd} is the genetic covariance between forage yield and IVDMD, σ_{yy}^2 is the genetic variance of forage yield, and σ_{dd}^2 is the genetic variance of IVDMD. Realized heritabilities for IVDMD and forage yield were calculated according to Falconer (1981).

Analyses of variance procedures were used to analyze the results of the sward trial. Individual year data for forage yield, heading date, and stand percentages were analyzed using a mixed model, with populations as fixed effects and replicates as random effects. Combined years data (1987–1989) for these variables were analyzed as a split plot in time with population as the whole plot and years as the split plot. A mixed model was used, with populations as fixed effects, and replications and years as random effects. Individual year data for IVDMD were analyzed as a split plot in time with population as the whole plot and sampling stage as the split plot to test for entry × sampling stage interactions within a year. A mixed model was used, with populations and sampling stage as fixed effects and replications random. Combined years data (1987 and 1988) for IVDMD, using means across sampling stages, were analyzed as a split plot in time, with population as the whole plot and year as the split plot. Populations were fixed effects, and replications and years were random. For the combined years analyses, an error term was synthesized and approximate F -tests were used to test hypotheses regarding population effects

¹ Names of products are included for the benefit of the reader and do not imply endorsement by the USDA or the University of Nebraska.

Table 2. Estimates of heritability (h^2) ($\pm$ SE) for in vitro dry matter digestibility (IVDMD) and forage yield in the base population of switchgrass.

	h^2	
	OP progeny†	PC progeny
IVDMD		
Parent-progeny regression	0.40 $\pm$ 0.48	0.68 $\pm$ 0.28
Variance component analysis	0.04 $\pm$ 0.10	0.47 $\pm$ 0.07
Forage yield		
Variance component analysis	0.00‡	0.22 $\pm$ 0.001

† OP progeny are progeny of open-pollinated parents; PC progeny are progeny of closed-pollinated or polycross (PC) parents.

‡ Variance component for progenies from analysis of variance was negative.

according to Neter et al. (1985); approximate degrees of freedom were calculated according to Satterthwaite (1946). The SAS statistical analysis package (SAS Institute, 1985) was used for all data analyses.

RESULTS AND DISCUSSION

Selection Procedures

Phenotypic variation existed in all selection nurseries for either IVDMD or forage yield, as indicated by the phenotypic standard deviations for the plants sampled for quality or harvested for forage yield (Table 1).

Heritability Estimates

Four different heritability estimates were obtained for IVDMD (Table 2). The heritability estimates obtained by parent-progeny regression are suitable for predicting gain from selection for a mass-selection breeding scheme such as RRPS. Heritability estimates obtained on a half-sib family-mean basis are suitable for selection of parents based on a half-sib family progeny test or on the family portion of a between- and within-family breeding scheme (Empig et al., 1972; Nguyen and Sleper, 1983). Heritability estimates obtained using either method were lower using the OP row data than those obtained using the PC row data (Table 2). The single generation of selection and intermating separated means of the high and low populations sufficiently to increase heritability estimates determined by parent-progeny regression and by variance component analyses. Polycrossing-selected high and low IVDMD clones in separate isolations produced progenies that more closely resembled the phenotype of the parents than did the OP progeny, resulting in an increase in the parent-progeny regression coefficient. The heritability estimate (h^2) used to predict gain from selection was obtained by regressing performance of OP progeny on performance of parents. This estimate was used because it was not biased by environmental covariances (Vogel et al., 1980; Casler, 1982) or possibly inflated by separate mating of high and low parents.

The heritability estimate for IVDMD obtained using variance component analyses of open-pollinated half-sib progenies was only 0.04. This indicates that gains in

selecting for IVDMD in this switchgrass population could not be made without pollination control.

Heritability estimates for forage yield determined by parent-progeny regression were not determined from the set of progenies used in this study, because forage yield data were not collected from parental clones. A heritability estimate of 0.05 as estimated by Newell and Eberhart (1961) using parent-progeny regression in the parental germplasm of the base population was used to predict gain from selection for forage yield.

Parents whose progeny were evaluated in the progeny test were not selected for forage yield and thus could be considered random plants from the population in regard to this trait, assuming no genetic linkages exist between IVDMD and forage yield in the base population. At least half of the parents, the males, of both the High and Low IVDMD OP populations were random, due to unregulated pollination. However, the variance component estimate for families was negative for the OP progenies, while a heritability estimate of 0.22 $\pm$ 0.001 for forage yield was obtained for the PC progenies. This heritability estimate is consistent with the findings of Talbert et al. (1983), who reported a lower heritability estimate, on a family basis, for forage yield compared with IVDMD in switchgrass. Genetic correlations between IVDMD and forage yield were 0.10 for the PC progenies and 0.0 for the OP progenies. These low values provide evidence that few genes influencing forage yield in switchgrass are linked to genes affecting IVDMD.

Gain from Selection

Gain from selection was determined using a replicated sward trial in which forage samples were collected at three stages of plant development. Significant differences ($P < 0.05$) existed among the populations for IVDMD at every sampling for both 1987 and 1988 (Table 3). No significant entry $\times$ sampling stage interactions for IVDMD were present in either 1987 or 1988 (data not shown), indicating that relative genetic differences among the populations for IVDMD remained constant during different growth stages and climatic periods. This consistency in relative forage quality is important to note, from both a breeding and a management standpoint, because switchgrass forage can decrease in IVDMD by >200 g kg⁻¹ as it matures during the growing season (Gabielsen et al., 1990).

Table 3. In vitro dry matter digestibility (IVDMD) for seven switchgrass populations sampled at three growth stages in 1987 and 1988.

Population	IVDMD					
	1987 sample			1988 sample		
	1	2	3	1	2	3
	IVDMD, g kg ⁻¹					
Low IVDMD Cycle 1	595	529	351	553	406	355
Base population	611	535	367	577	426	369
High IVDMD Cycle 1 (Trailblazer)	627	558	373	579	441	398
High IVDMD Cycle 2	629	569	382	594	446	385
High IVDMD Cycle 3	661	582	403	605	468	397
High yield Cycle 1	609	517	355	541	412	375
High yield Cycle 2	611	537	359	568	418	359
LSD ($\alpha = 0.05$)	18	35	32	21	21	14

Table 4. Forage yield, in vitro dry matter digestibility (IVDMD) averaged across years† and sampling stages, and predicted and realized gains from selection (G_{s1} and G_{s2})‡, for seven switchgrass populations.

Selection criterion	Population	Forage yield kg ha ⁻¹	IVDMD g kg ⁻¹	Predicted gain		Realized gain
				G_{s1}	G_{s2}	
				IVDMD, g kg ⁻¹		
IVDMD	Low IVDMD Cycle 1	9632	466	-21	-30	-15
IVDMD	Cycle 0 (base population)	8422	481			
IVDMD	High IVDMD Cycle 1 (Trailblazer)	9923	496	16	30	15
IVDMD	High IVDMD Cycle 2	9901	501	14	15	4
IVDMD	High IVDMD Cycle 3	7885	519	19	24	18
				Forage yield, % of mean		
Yield	High yield Cycle 1	9181	468	2.0	2.5	9.0
Yield	High yield Cycle 2	8938	476	1.0	1.2	-2.6
	LSD ($\alpha = 0.05$)	1427	13			

† Average across 3 and 2 yr, respectively, for forage yield and IVDMD.

‡ Predicted gain from selection $G_{s1} = h^2 S$ and $G_{s2} = i h^2 \sigma_p$, where h^2 is the heritability estimates, S is the selection differential, i is the standardized selection differential, and σ_p is the phenotypic standard deviation from the respective selection nursery.

Digestibility responded favorably to selection, as evidenced by significant differences ($P < 0.05$) for IVDMD among the populations, and the consistency of rankings with cycle of selection (Table 4). The High IVDMD C3 population was 37 g kg⁻¹ greater in IVDMD than the base population. Thus, RRPS as practiced in this study was an effective breeding procedure for improving forage quality in switchgrass. Increased digestibility was not accompanied by changes in maturity, as evidenced by nonsignificant differences for heading date among the populations (data not shown).

Realized gains for IVDMD were similar, or slightly lower than, predicted gains for all cycles of selection (Table 4). We used two methods to predict gains from selection, to see which method was most similar to realized gains from selection. Predicted gains from selection using the equation $G_{s1} = h^2 S$ were smaller and closer in value to realized gains from selection than gains predicted using the equation $G_{s2} = i h^2 \sigma_p$, possibly because S was determined using measured values and i is based on theoretical expectations. Averaged across cycles, a realized heritability estimate of 0.31 for high IVDMD was obtained, which is less than the 0.59 value reported by Vogel et al. (1981) for a single cycle of selection. Realized gains may have been less than predicted gains because some plants were not selected for sampling or for polycrossing because of undesirable agronomic traits such as presence of leaf diseases, or poor spring vigor following the sampling year. However, substantial increases in digestibility were possible even with limited selection pressure for traits other than IVDMD.

Significant differences ($P < 0.05$) were found among the populations for forage yield (Table 4). Differences in establishment ability or persistence probably did not influence forage yield, as percent stand was not significantly different among the populations (data not shown). The High IVDMD C3 population was not significantly lower yielding than the base population, indicating that digestibility was increased without sacrificing forage yield.

No significant differences for forage yield were found between the base population and the populations selected for yield. The reason for the failure of RRPS to increase forage yield was probably due to little genetic variability for forage yield. The negative variance component estimate for families, determined from open-pollinated progeny, provides evidence for this situation. Breeding

for improved forage yield in switchgrass will require the development of populations with more genetic variability for forage yield than exists in this population. Between- and within-family selection has increased forage yield in lowland switchgrass types (Godshalk et al., 1988) and may be needed to improve forage yield of upland switchgrass types.

CONCLUSIONS

Predicted gain exceeded realized gains from selection for IVDMD, possibly because RRPS, as practiced in this study, was not strictly for IVDMD; however, RRPS effectively improved IVDMD on a sustained basis during three cycles of positive selection. Increased IVDMD was achieved without significantly decreased forage yield. Improvements in IVDMD were consistent for three stages of maturity. This study clearly shows that a single sample collected in a single year can be used to identify genetically superior high IVDMD switchgrass plants in a recurrent selection breeding program. Trailblazer switchgrass (High IVDMD C1) increased animal gains and beef production by 17% in comparison with the Low IVDMD C1 population in a replicated grazing trial (Anderson et al., 1988). The improved IVDMD of the High IVDMD Cycle 3 should result in additional gains in animal performance and beef production per hectare. Breeding for both improved yield and IVDMD in switchgrass may require between- and within-family selection, and use of a selection index as indicated by Godshalk et al. (1988). This study demonstrates that the efficacy of a breeding procedure such as RRPS is limited by the available genetic variability in a population.

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