University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

Publications from USDA-ARS / UNL Faculty

U.S. Department of Agriculture: Agricultural
Research Service, Lincoln, Nebraska

1999

Accomplishments and Impact from Breeding for Increased Forage Nutritional Value

M. D. Casler

University of Wisconsin-Madison, michael.casler@ars.usda.gov

Kenneth P. Vogel

University of Nebraska-Lincoln, kvogel1@unl.edu

Follow this and additional works at: <https://digitalcommons.unl.edu/usdaarsfacpub>

Casler, M. D. and Vogel, Kenneth P., "Accomplishments and Impact from Breeding for Increased Forage Nutritional Value" (1999). *Publications from USDA-ARS / UNL Faculty*. 1919.
<https://digitalcommons.unl.edu/usdaarsfacpub/1919>

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Agricultural Research Service, Lincoln, Nebraska at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in Publications from USDA-ARS / UNL Faculty by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.

Accomplishments and Impact from Breeding for Increased Forage Nutritional Value

M. D. Casler* and K. P. Vogel

ABSTRACT

Despite considerable rhetoric, there were no serious efforts to improve genetically the nutritional value of forage crops until the 1960s when advances in analytical chemistry and rumen fermentation technology allowed breeders to adapt meaningful laboratory techniques for repeatedly screening thousands of samples in a short time period. Genetic increases in some measure of digestibility, typically in vitro dry matter digestibility (IVDMD), have been documented in new cultivars of at least seven forage crops, including legumes, cool-season grasses, warm-season grasses, annuals, and perennials. The rate of gain for IVDMD ranges from 8 to 45 g kg⁻¹ cycle⁻¹, which, on a percentage basis (0.7–2.5% yr⁻¹), is similar to long-term gains for grain yield of many cereal crops. In asexually propagated species, in which all genetic variance can be utilized in a single cycle of selection, gains as high as 11.8% cycle⁻¹ have been reported. Generally, gains in IVDMD are repeatable across a wide range of environments and management systems, including on-farm tests. Averaged across species, a 1% increase in IVDMD generally leads to a 3.2% increase in average daily gains of beef cattle (*Bos taurus*). Because increased IVDMD generally does not decrease forage yield per se, and sometimes occurs with increased forage yield, these gains also translate to improved beef production per hectare. The ability to document increased animal performance associated with breeding for increased forage nutritional value can greatly enhance the value of a new cultivar to forage producers, which can lead to rapid adoption of new cultivars.

FORMAL FORAGE feeding began in the late 1880s. Records dating back at least 200 yr prior to that describe the concept of phenotypic differences among strains of a single forage species (Casler et al., 1996). Contemporary literature includes references to selection of strains or genotypes for superior “quality” of forage and the concept of superior strain selection dating back at least 300

yr. While these early selectionists did not use laboratory techniques and animal evaluations as we do today, there is some evidence that they were on the same track as we. Their selection criteria consisted of improved plant vigor, reduced disease symptoms, reduced senescence, and perhaps palatability or acceptability to livestock. Generally these plant traits are either positively correlated with laboratory measures of forage quality or they act to protect forage quality (Casler et al., 1996; Edwards et al., 1981; Lenssen et al., 1991). Thus, some of the initial conscious selection practiced on forage crops may have enhanced forage quality per se or protected it from degradation by pathogens.

The Forage Quality Revolution

The most important single event in the history of forage grass breeding was the publication of the in vitro dry matter digestibility analysis of Tilley and Terry (1963). Conversely, the Tilley and Terry technique has not revolutionized legume breeding because many legumes have persistence problems that are far more limiting to animal production than any lack of forage quality. Without persistence, the level of quality the legume possesses does not matter. Furthermore, most legumes are higher for most measures of forage quality than most grasses, although there are some exceptions to this generalization. Thus, the vast majority of the literature related to breeding for increased forage quality derives from grasses. Nevertheless, some important gains have been made and principles elucidated from research on forage legumes. These will be discussed herein. While the Kjeldahl test for N concentration and the relatively recent advancements in sequential fiber analysis are

M.D. Casler, Dep. of Agronomy, Univ. of Wisconsin-Madison, Madison, WI 53706-1597; K.P. Vogel, USDA-ARS, Dep. of Agronomy, Univ. of Nebraska, Lincoln, NE 68583. Received 31 March 1998.
*Corresponding author (mdcasler@facstaff.wisc.edu).

Published in Crop Sci. 39:12–20 (1999).

Abbreviations: ADF, acid detergent fiber; ADL, acid detergent lignin; CP, crude protein; IVDMD, in vitro dry matter digestibility; IVNDFD, in vitro neutral detergent fiber digestibility; NDF, neutral detergent fiber.

important for commercial forage analysis (Undersander et al., 1993), they have had relatively little impact on forage breeding programs. As described later, these techniques present some interesting challenges and potentials to forage breeders and will likely see greater attention in the future.

The mid-20th century brought about some radical changes to the concept of breeding for increased quality of forage, notably the introduction of laboratory analyses for crude fiber and protein concentration. While numerous studies addressed the question of genetic variation, there are no reports of actual selection and breeding for improved quality until J.M.A. Tilley and R.A. Terry collaborated with J.P. Cooper of the Welsh Plant Breeding Station (Cooper et al., 1962). Their procedure represented the laboratory breakthrough that catalyzed "the forage quality revolution" that is the subject of this paper. It met nearly all characteristics that plant breeders needed in a selection criterion: rapid, repeatable, amenable to small sample size, heritable, and directly correlated with animal performance. The dominance of the Tilley and Terry procedure and its many modifications can be seen in any literature review of the topic, "breeding for increased forage quality" (Burton, 1989; Buxton and Casler, 1993; Clark and Wilson, 1993; Hacker, 1982; Hanna, 1993; Marten, 1989; Vogel and Sleper, 1994).

New Cultivars or Germplasm with Increased Animal Performance

Measures of Digestibility

Most efforts to improve forage quality by breeding have been based on some modification of the Tilley and Terry procedure. Genetic variation has been documented in at least 17 species (Buxton and Casler, 1993) and several more that are described in more recent publications. Most populations that have been investigated show considerable genetic variation for IVDMD. It is typical to observe a range of variation of 100 g kg⁻¹ between the lowest- and highest-ranked individuals, although ranges of up to 377 g kg⁻¹ have been observed within populations (Buxton and Casler, 1993). This wealth of genotypic variation and its ubiquitous nature suggests that forage quality traits have played little role in the evolution and domestication of forage crops. Little selection pressure has been applied to IVDMD and related traits until the advent of the forage quality revolution, effectively preserving this genotypic variation for our use in developing new and unique cultivars and germplasm.

Two methods have been principally used to increase IVDMD: phenotypic recurrent selection in sexually propagated species and hybridization followed by selection of individual clones or hybrids in asexually propagated species. Genetic progress has been documented in seven sexually propagated species: smooth brome grass, *Bromus inermis* Leyss.; orchardgrass, *Dactylis glomerata* L.; perennial ryegrass, *Lolium perenne* L.; switchgrass, *Panicum virgatum* L.; alfalfa, *Medicago sativa* L. (Buxton and Casler, 1993); timothy, *Phleum pratense* L. (Sur-

prenant et al., 1990); and maize, *Zea mays* L. (Barrière et al., 1995). The rate of genetic progress in these species has ranged from 8 to 45 g kg⁻¹ cycle⁻¹ (1.3 to 12.1% cycle⁻¹ or 0.7 to 2.5% yr⁻¹). In the perennials, selection is typically conducted on a single-plant basis and usually has realized heritability of about 0.2 to 0.3. Genetic progress has been documented in two asexually propagated species: bermudagrass, *Cynodon dactylon* (L.) Pers. (Buxton and Casler, 1993; Vogel and Sleper, 1994) and *Digitaria milaniana* (Hacker, 1986). Genetic gains up to 11.8 % per cycle of crossing and evaluation have been reported in bermudagrass (Fig. 1).

Generally, selection for increased IVDMD has not led to correlated responses for forage yield (Buxton and Casler, 1993; Casler et al., 1996; Casler, 1998). The third cycle of selection for high IVDMD in 'Pathfinder' switchgrass is a notable exception, but its yield loss appeared to be due to a sudden loss of cold tolerance in Cycle 3 rather than a yield reduction per se (Buxton et al., 1995; Hopkins et al., 1993). Other notable exceptions are forage quality mutants such as brown-midrib and

Fig. 1. Genetic differences in average daily gain (ADG), forage availability, and animal production per hectare for 10 cultivars that represent increased in vitro dry matter digestibility (IVDMD) compared with the population from which they were selected or to a standard cultivar which they were intended to replace. Each variable is plotted against the observed genetic change in IVDMD. Literature citations can be found as follows: 'Coastcross-1,' 'Tifton 78,' 'Tifton 84,' 'Trailblazer,' 'Manska,' and 'Badger' (Vogel and Sleper, 1994); 'Alpha' (Casler and Drolsom, 1995); 'Mascot,' 'Siriol,' and 'Cambria' (Munro and Walters, 1986).

dwarf genes which provide large and rapid increases in whole-plant IVDMD, but with large reductions in forage yield (Casler, 1998).

A sufficient number of grazing experiments comparing high-IVDMD cultivars with check or standard cultivars have been conducted to allow some cautious generalizations about the effects of breeding for increased IVDMD (Fig. 1). Some caution is warranted because inconclusive grazing experiments and/or those that do not show the expected improvement in animal gain associated with IVDMD may not have been published. Genetic improvement in IVDMD generally results in improved animal daily gains and the relationship is broadly positive, with a 3.2% increase in daily gains for each 1% increase in IVDMD (Fig. 1A). Genetic changes in IVDMD appear to be negatively correlated with changes in forage availability (on this broad scale), but forage availability increased in nine of 10 cultivars, compared with their checks (Fig. 1B). Finally, the combination of increased animal daily gains and forage availability always led to increased animal production per hectare (Fig. 1C). Again, with the caution that there may be less positive unpublished results, selection for increased IVDMD appears to be an almost foolproof means of improving animal performance on forage crops. A study on crested wheatgrass (*Agropyron* spp.) has shown that cultivar differences in IVDMD do not always lead to expected differences in animal performance (Vogel et al., 1993). Because there are numerous genetic traits that differ between cultivars that have no shared pedigree, such as these two crested wheatgrass cultivars, there are likely many factors other than IVDMD contributing to animal performance differences. The best way to document improved animal performance due to plant breeding is to conduct a direct comparison of a new cultivar or population, bred for improved forage nutritional value, with the population from which it was developed, or secondarily, with a standard cultivar of similar phenotype, origin, and use.

The ultimate test of a new cultivar with a genetic improvement in IVDMD is an on-farm test of its feeding value compared with a standard, lower quality cultivar. Unfortunately, only one cultivar, Augusta perennial ryegrass, has been tested in such a manner (Table 1). Previous research has established a 3% advantage in *in vitro* organic matter digestibility and a 27% advantage

in organic matter intake of Augusta over "RvP" (Munro and Walters, 1986). In a six-farm test, the advantage of Augusta over RvP ranged from 0.02 to 0.26 kg animal⁻¹ d⁻¹ (3.2–31.0%) for mean daily gains of beef cattle and from 0.11 to 1.47 kg ha⁻¹ d⁻¹ for mean live-weight production (Table 1). While these results indicate that the expression of improved digestibility can be variable, the mean benefits were large enough to give a positive response on all farms, with some being very substantial.

Breeding for increased IVDMD can lead to rapid financial benefits to the agricultural community and society (Table 2). "Trailblazer" switchgrass (released in 1984) and "Manska" intermediate wheatgrass, *Thinopyrum intermedium* (Host) Barkw. & D.R. Dewey, (released in 1992) were both documented to have increased IVDMD, available forage, average daily gains, and animal production per hectare in grazing evaluations (Vogel and Sleper, 1994). Since 1985, there have been a minimum of 63 096 ha seeded to Trailblazer and 7088 ha seeded to Manska forage production (K.P. Vogel, 1997, unpublished data based on certified seed production). Combining these data and assuming the value of pasture-finished beef to be \$0.88 kg⁻¹, 1 yr of production on all Trailblazer and Manska pasture would net \$3.22 and \$0.25 million, respectively. For Trailblazer this far surpasses the entire cost of the breeding program, while for Manska, it would require approximately 2 yr of production for the net increase in profits to exceed the cost of developing the cultivar. Because both cultivars are perennial and typically used as such, these benefits to society represent only the "tip of the iceberg." Furthermore, these figures do not include non-certified production, which may be significant. Use of Trailblazer seed exceeds the total of the next three most popular switchgrass cultivars for the Great Plains, while use of Manska seed exceeds that of "Reliant" by five times (K.P. Vogel, 1997, unpublished data). The popularity of these cultivars is directly related to their superior animal performance.

While these values provide an extremely positive outlook for the potential benefits of forage breeding, they oversimplify a complex system. Economic benefits to increased forage nutritional value are extremely difficult to quantify because of numerous assumptions, differential responses for widely differing animal systems, and the need to evaluate their impact on whole-farm systems

Table 1. Mean liveweight gain and production of two perennial ryegrass cultivars with contrasting *in vitro* organic matter digestibility and intake, evaluated by beef cattle on six farms (data adapted from Walters, 1984).

Farm	Mean liveweight gain			Mean liveweight production		
	RvP	Augusta	Increase	RvP	Augusta	Increase
	kg animal ⁻¹ day ⁻¹		%	kg ha ⁻¹ d ⁻¹		%
1	0.87	1.01	16.1	4.94	5.73	16.0
2	0.99	1.25	26.3	5.70	7.17	25.8
3	0.88	0.96	9.1	4.80	5.23	9.0
4	0.70	0.76	8.6	3.28	3.58	9.1
5	0.62	0.64	3.2	2.53	2.64	4.3
6	0.42	0.55	31.0	4.52	5.92	31.0
Mean	0.75	0.86	15.4	4.30	5.05	17.5

(Ford, 1999). In reality, genetic increases in forage nutritional value may not accrue from increased meat or milk production per se, but rather from reductions in required protein or energy supplementation, decreases in acreage of alternative crops, or simply increased flexibility in whole-farm enterprise management and organization (Ford, 1999).

The ability to transform plants by inserting cloned genes from other organisms has allowed the development of many new ideas for improving digestibility of forage crops. Most current efforts are focused on down-regulation of enzymes in the lignin biosynthesis pathway by cloned antisense genes for these enzymes. Transformed alfalfa or stylo (*Stylosanthes* spp.) plants have been shown to have reduced lignin concentration and/or increased IVDMD compared with control plants (Ni et al., 1993; Rae et al., 1996). Although these plants have yet to be incorporated into breeding programs, they may prove to be useful sources of improved forage quality in the future.

Measures of Intake

There has been relatively little effort focused on improving intake per se. The relative inattention to improving intake is an important oversight given its greater importance to animal performance compared with digestibility (Fahey and Hussein, 1999). There are two main reasons for this: (i) the natural communication and knowledge gap that still exists between many animal nutritionists and plant breeders, and (ii) confusion among plant breeders over methods to predict efficiently intake on thousands of laboratory samples. Neutral detergent fiber (NDF) concentration is generally considered to be the single laboratory measure most closely correlated with voluntary intake (Van Soest, 1994). Selection experiments for IVDMD generally show little or no genetic correlated response for NDF, indicating that genetic correlations between these two traits are typically low or zero (Buxton and Casler, 1993; Gabrielson et al., 1990). This is advantageous because it suggests that both intake and digestibility of forages can be increased through breeding. However, it can also be a disadvantage because it may require considerably more effort to improve both intake and digestibility than either trait alone.

The concentration of NDF in forage crops appears to be under genetic control in a manner similar to that

of IVDMD. Ranges of variation within populations, realized heritability, and genetic gains, although reported for fewer species, are similar to those for IVDMD. Genetic progress toward reduced NDF concentration has been reported for smooth brome grass (Casler, 1995), reed canarygrass, *Phalaris arundinacea* L. (Surprenant et al., 1988), and maize (Wolf et al., 1993). Genetic progress has ranged from 9 to 26 g kg⁻¹ cycle⁻¹ (1.6–4.0 % cycle⁻¹).

Unlike results from IVDMD selection, there have been two distinct and potentially serious correlated responses related to reduced NDF concentration. In smooth brome grass and reed canarygrass, a reduction in NDF concentration was associated with a reduction in forage yield. Three cycles of selection for low NDF concentration in smooth brome grass reduced forage yield by an average of 0.41 Mg ha⁻¹ (4.7%), while one cycle of selection in reed canarygrass reduced forage yield by 0.06 to 0.31 Mg ha⁻¹ (2.7–6.1%), despite simultaneous selection for high forage yield in the latter study. Casler (1998) argued that this may be a physiologically necessary correlation, given that fiber is such an important and abundant component of forage crop dry matter. Nevertheless, this is an area for some potentially important future research: to determine whether this association can be broken by selection. Because recurrent selection for any forage quality trait will involve some inbreeding as a natural consequence of intercrossing a limited number of related individuals, the losses in forage yield may be partly due to inbreeding depression. Separation of the effects of inbreeding and selection can be accomplished with complex mating designs that traditionally have not been applied to forage crop breeding.

In maize, selection for resistance to European corn borer (*Ostrinia nubilalis* Hübner) led to dramatic increases in NDF concentration (Buendgeon et al., 1990). Although the reciprocal correlated response must be more fully tested, this suggests that corn borer resistance may decline with selection for reduced NDF concentration in maize. Initial results show an increase in first-generation, but no change in second-generation corn borer damage associated with selection for low fiber (Buendgeon et al., 1990). Although none of the low-NDF materials have entered feeding or grazing experiments, they show potential promise for delivering improved feeding value to the grower. Future efforts must

Table 2. Increase in in vitro dry matter digestibility (IVDMD), animal performance, and profit from 1 year of beef production for Trailblazer switchgrass and Manska intermediate wheatgrass compared to control cultivars (data adapted from Vogel and Slepser, 1994, and from K.P. Vogel, 1997, unpublished data).

Measurement†	Cultivar‡	
	Trailblazer	Manska
Genetic increase in IVDMD (g kg ⁻¹)	40	16
Genetic increase in daily liveweight gains (kg)	0.15	0.17
Genetic increase in animal production (kg ha ⁻¹)	67	40
Genetic increase in profit (\$ ha ⁻¹)§	59	35
Area seeded between 1986 and 1997 (ha)	63 096	7 088
Added profit from 1 year of beef production on all seeded ha (\$)	3 720 000	250 000

† Trailblazer released in 1984, Manska released in 1992.

‡ All except seeded area are measured as the difference between Trailblazer or Manska and their control cultivar.

§ Based on a price of pasture-finished beef of \$0.88 kg⁻¹.

include economic analyses to determine if the apparent genetic correlations between NDF and yield and between NDF and insect resistance represent economic liabilities.

Divergent selection for leaf shear strength in perennial ryegrass shows potential for improving intake or ruminants. High and low shear-strength populations that differed by 32% showed a negative association with intake by sheep (*Ovis aries*) in two studies, although the effect on intake was not significant in the more recent study (Inoue et al., 1993; MacKinnon et al., 1988). Inoue et al. (1993) suggested that correlated responses toward longer leaves per unit dry weight for the low shear-strength population may have indirectly increased masticatory load, offsetting much of the benefit of low shear-strength leaves.

Protein Concentration and Composition

Crude protein (CP) concentration has received relatively little attention, likely because inexpensive nitrogen fertilizer for grasses is very effective at increasing CP concentration of forage. Furthermore, fertilization with nitrogen fertilizer can negate the progress achieved through breeding for increased CP concentration in grasses, which is most obvious at relatively low nitrogen fertilizer levels (Arcioni et al., 1983). In addition, some of the early selection experiments showed that genetic increases in CP concentration were achieved at the expense of forage yield (Arcioni et al., 1983; Clements, 1969), although a timothy population was an exception to this (Surprenant et al., 1990). Selection for increased CP concentration can also lead to increased IVDMD (Clements, 1969; Surprenant et al., 1990).

A long-term selection program for increased CP concentration, combined with reduced acid detergent fiber (ADF) concentration, has been undertaken in alfalfa at Cornell University in New York. Two cycles of selection have increased CP concentration by an average of 14 g kg⁻¹ (6.9%) and decreased ADF concentration by an average of 15 g kg⁻¹ (4.4%) (Vaughn et al., 1990). Combined, these genetic changes increased digestibility by 16 g kg⁻¹ (2.1%). However, despite selection of the most vigorous plants during the selection phase, forage yield decreased by an average of 0.67 Mg ha⁻¹ (4.8%), which is similar to the decrease observed in the low-NDF smooth brome grass selection. Again, part of this decrease in yield may be caused by inbreeding depression, but the consistency and large magnitude of these yield reductions following selection for increased CP and/or reduced fiber concentration suggest a true genetic correlation. Genetic correlations may be due to linkage of genes controlling different traits, which can be broken or reduced by selection and recombination, or pleiotropy, which is caused by one gene having a direct effect on more than one trait. The preponderance of negative correlated responses for reduced forage yield points to pleiotropy, but continued selection and detailed mating designs designed to detect these genetic phenomena will be required to determine if these effects can be ameliorated.

Most current efforts to modify genetically forage-crop protein are focusing on increasing protein quality and/or the quantity of rumen-non-degradable protein. Protein ingested by ruminants is often used inefficiently. Most soluble protein is degraded to ammonia in the rumen, much of which is absorbed into the bloodstream and eventually excreted as urea. Non-degradable protein passes through the rumen where it is more efficiently utilized in the lower digestive tract. Because native proteins differ dramatically in their rumen degradability, plant transformation may be an effective mechanism for inserting genes coding for non-degradable proteins into forage crops (McNabb et al., 1993). This method has been demonstrated, in principle, as a means of increasing the concentration of sulfur-rich proteins in subterranean clover, *Trifolium subterraneum* L. (Khan et al., 1996). Genetic variation for ruminal protein degradation parameters is present within alfalfa (Broderick and Buxton, 1991), suggesting the possibility that traditional breeding methods may also be useful for improving protein quality.

Alkaloid Concentration and Type

One of the more remarkable stories in breeding cool-season forage grasses has been the development of improved cultivars in reed canarygrass (Marten et al., 1976) and phalaris, *Phalaris tuberosa* L. (Oram et al., 1985). In reed canarygrass, the presence of tryptamine or β -carboline alkaloids was associated with a 13-fold increase in the incidence of diarrhea of sheep. While variation in gramine concentration did not cause differential animal health, a 68% reduction in gramine concentration was associated with an average of 185% greater lamb gains and 136% greater steer gains. Recent cultivars of reed canarygrass all have reduced gramine concentration, combined with no tryptamine/ β -carboline alkaloids. These cultivars have excluded all others from the reed canarygrass pasture seed market.

Mineral Element Concentration and Balance

Hypomagnesaemia is likely the most serious ruminant disease caused by mineral imbalance of forage crops. It is caused by a deficiency of Mg and/or an excess of K in the forage tissue. Two breeding programs have attacked this problem by selecting for increased Mg uptake. In Italian ryegrass (*L. multiflorum* Lam.), a 56% increase in Mg concentration of the forage led to a 13% increase in blood serum Mg and a 12% increase in dry matter intake of grazing ewes (Mosely and Baker, 1991). Ewe and lamb live-weight gains increased by 10%, while the proportion of clinical cases of hypomagnesaemia was reduced by 88% with no fatalities among 120 ewes grazing the high-Mg population. In tall fescue (*Festuca arundinacea* Schreb.), selection for increased Mg and a reduction in the mineral ratio K/(Ca+Mg) led to a reduction in the mineral ratio of 18% (Mayland and Sleper, 1993). This resulted in a 12% increase in blood serum Mg levels of grazing cattle and an 8% reduction in the blood serum mineral ratio K/(Ca+Mg) (Sleper et al., 1997, personal communication).

An Improved Understanding of Forage Quality Traits

Much of the literature establishing the validity of laboratory techniques for predicting forage quality was based on non-genetic relationships. Forages with a wide range in laboratory predictors of forage quality and animal performance were generated by sampling at a number of maturity stages and/or using a number of different species. While considerable progress was made, allowing the foundation of numerous breeding programs to be developed, many details of interrelationships among traits and the nature of variation for forage quality traits was not applicable to breeding programs. Many of the selection studies cited above have allowed some of these genetic relationships to be refined and quantified, separate from the effects of environmental factors.

Maturity

Maturity is the most notable of these factors. Numerous changes occur as forage plants mature, most notably that all positive measures of forage quality decline (IVDMD, protein), while negative measures of forage quality increase (NDF, lignin, silica). Some of the initial selection experiments further confused the issue of maturity, when it was observed that genetic changes in IVDMD were due to genetic changes in maturity (Buxton and Casler, 1993). Selection for increased IVDMD based on sampling plants on a given day, ignoring maturity stage, may lead to a later heading date. Conversely, selection for increased IVDMD based on sampling plants at a given maturity stage, ignoring calendar date, may lead to an earlier heading date.

Van Wijk et al. (1993) erroneously concluded that "The progress we have witnessed in breeding for improved nutritive value largely consists of chance findings as well as of early-maturing selections from within a population." and that "Once the gross variation due to maturity classes has been taken care of by maturity-grouping there is little net variation left to be measured accurately within these maturity groups." Their conclusions were apparently based on a large number of published animal feeding trials in which genetic differences among cultivars for IVDMD were shown to be positively associated with increased animal performance, measured either by daily meat or milk production (Munro and Davies, 1989; Munro and Walters, 1986; Munro et al., 1992). These cultivars were not developed specifically by selection for increased IVDMD, but rather, their increased IVDMD was serendipitous and unexpected. Many of these cultivars expressed a wide range in relative maturity, but direct relationships between maturity and IVDMD or animal performance were not consistent or not evident. The studies summarized by Munro and colleagues further support the existence of genetic variation for IVDMD that is independent of the timing of reproductive maturity. Furthermore, many of these cultivars have shown increased popularity among growers and increased use in further breeding efforts, solely due to the a posteriori discovery

of their improved IVDMD or animal performance. The improved IVDMD of Manska intermediate wheatgrass was discovered a posteriori in small-plot trials, after which it was included in a grazing trial to evaluate its feeding value (Vogel and Sleper, 1994). It was not released until after its improved feeding value had been documented.

Experience has shown that recurrent selection for increased IVDMD rarely results in correlated responses for timing of reproductive maturity (Buxton and Casler, 1993; Casler, 1998; Vogel and Sleper, 1994). In populations that are highly variable for maturity, potential correlations with maturity can be ameliorated by selecting only within maturity classes or by adjusting forage quality data to a constant maturity stage. Forage quality increases can be achieved by genetic changes in maturity, but there is considerable genetic variation for forage quality traits, in many species, that is independent or only weakly dependent on maturity.

Disease Resistance

Relatively little attention has been given to potential relationships between IVDMD and disease resistance. However, because lignin concentration and/or composition may play an important role in both of these types of traits, plant breeders need to be cognizant of these potential relationships. Most results to date (summarized by Buxton and Casler, 1993 and Casler, 1998) suggest that small increases in IVDMD do not result in losses of fungal disease resistance. However, preliminary results suggest a potential loss of resistance to some fungal pathogens associated with reduced lignin concentration (Casler et al., 1997, unpublished data). Such relationships may complicate forage breeding programs by forcing additional breeding efforts toward increasing or maintaining disease resistance while selecting for increased forage quality. For example, an initial correlation between high water-soluble carbohydrate concentration and crown rust (*Puccinia coronata* Corda.) susceptibility in perennial ryegrass was broken by recombination and selection for desirable levels of both traits (Humphreys, 1997, personal communication).

The Genetic Nature of Digestibility

Digestibility is not a plant trait per se. It can only be defined in terms of a plant-microbe interaction, i.e., the gravimetric determination of disappearance during fermentation with rumen microorganisms or fungal cellulase. As such, any genetic control of digestibility (whether it be dry matter, organic matter, or fiber) must be determined by plant traits that affect the efficiency and rate of tissue degradation by rumen microorganisms or fungal cellulases. While maturity is certainly one of these plant traits, there are numerous others that have been shown to be the apparent cause of genetic variation for IVDMD and related traits.

Variation in chemical composition is most frequently identified as influencing the IVDMD of forage crops. A series of experiments on smooth brome grass showed a strong and consistent relationship between IVDMD

Fig. 2. Relationship between neutral detergent fiber (NDF) digestibility (IVNDFD) and lignin concentration or esterified ferulic acid concentration for nine high-IVDMD and nine low-IVDMD smooth brome grass clones (data adapted from Jung and Casler, 1990).

and acid detergent lignin (ADL) concentration, in which each 10 g kg^{-1} increase in IVDMD was apparently caused by a 1.3 g kg^{-1} decrease in ADL concentration (Casler, 1998). This relationship typically accounted for over 80% of the variation in IVDMD. As selection has proceeded, a degree of non-linearity in the relationship has appeared (Fig. 2). Digestibility of NDF was closely associated with lignin concentration following selection for high IVDMD, but only moderately associated with lignin following selection for low IVDMD. In the low IVDMD direction, the concentration of ferulic acid accounts for as much variation in NDF digestibility as does the concentration of lignin per se. In switchgrass, the ratio of ferulic acid to *p*-coumaric acid was closely associated with genetic progress for IVDMD, while lignin concentration was not related to IVDMD (Gabrielson et al., 1990). Although there have been no genetic studies to date, cell wall structure, including lignin-polysaccharide and lignin-phenolic covalent bonds are important determinants of forage availability to rumen microorganisms (Hatfield et al., 1999). A greater understanding of the molecular structure of the cell wall and its genetic control will be extremely useful to forage breeding programs that focus on improving forage nutritional value.

In some crops, such as alfalfa, for which leaves have considerably higher IVDMD than stems, selection for increased whole-plant forage quality results primarily from changes in leaf/stem ratio. Selection for low lignin

Table 3. Effects of selection (means of selected populations minus standards) measured on three variables (ADF = acid detergent fiber, IVTD = in vitro true digestibility, and CP = crude protein concentration) of alfalfa at two locations under three management systems (Vaughn et al., 1990).

Variable	Location/Management†					
	McGowan			Helfer		
	A	B	C	A	B	C
ADF	-17**	-17**	-14**	-13**	-18**	-10**
IVTD	18**	17**	17**	16**	20**	8*
CP	14**	15**	15**	12**	17**	10**

*, ** Selection effect different from zero at $P < 0.05$ or 0.01 , respectively.

† A = three harvests at 6-wk intervals, B = three harvests with a 5-wk first interval and a 6-wk second interval, and C = three harvests with a 10-d delay in first harvest and two 6-wk intervals.

concentration in alfalfa led to increased IVDMD, but because of an 18 to 53% increase in leaf/stem ratio and an associated 11 to 22% reduction in forage yield (Kephart et al., 1989). Conversely, in grasses, for which leaves and stems are similar in IVDMD, selection has little effect on leaf/stem ratio. In smooth brome grass, divergent-IVDMD plants differed little morphologically but showed some differences in anatomy, including the number of vascular bundles per leaf blade and the proportion of rapidly vs. slowly digestible cell types (Casler and Carpenter, 1989; Ehlerke and Casler, 1985).

Genotype × Environment Interactions

Genetic progress from breeding for increased forage quality is reasonably consistent across environments and harvest managements. Numerous studies have evaluated populations selected for increased forage quality in a range of environments, including multiple sites, years, and harvests. In general, their findings have consistently indicated that genotype × environment interaction is relatively unimportant in determining the progress from breeding for increased forage quality. Several examples are cited by Casler (1998). Forage quality selections in alfalfa have also shown similar responses under differential harvest management systems (Table 3).

Nearly all of the successful selection experiments reported by Buxton and Casler (1993) were based on a single sample of a plant at a single point in time. When evaluating the progress from selection for improved forage nutritional value, the plant breeder cannot repeat the environment in which the original superior plants were identified, simply due to year-to-year variation in weather patterns. Therefore, any measure of progress must be made in new environments, a harsh restriction if the genetic progress is sensitive to genotype × environment interactions. Thus, a simple documentation of genetic progress for increased forage nutritional value, in itself, partially attests to the relative unimportance of genotype × environment interaction in determining forage quality. This may be a remarkable statement to some researchers, given the large potential environmental effects on forage quality traits. However, it reinforces the point that environmental effects per se and genotype

× environment interaction effects are statistically independent of each other in most experiments. In documenting the value of plant breeding programs, environmental effects are far less important than genotype × environment interaction. While it might be a desirable goal to minimize environmental effects on forage nutritional value per se, creating a cultivar with greater environmental stability of feeding value, this is unlikely to be achieved by plant breeding.

Thus, an improved cultivar will usually have increased forage quality, compared with its predecessor, under most environmental or management conditions to which it is subjected. This makes the processes of breeding for increased forage quality and modification of management to increase forage quality act in an additive manner. Furthermore, a perennial crop cultivar with increased forage quality often represents a permanent one-time increase in forage quality, whereas a management scheme to increase forage quality must continually be re-applied each year or growing season.

Summary and Conclusions

There is a wealth of heritable variation for many plant traits affecting forage nutritional value, most likely in all species potentially useful as forage crops. Measurable and meaningful progress can be achieved in short periods of time, resulting in observable improvements in animal gains on pasture. On average, a 1% genetic increase in IVDMD has led to a 3.2% increase in average daily live-weight gains. Such progress is typically achieved without loss in agricultural fitness or undesirable shifts in plant maturity. Genetic gains in forage nutritional value, if documented by increased animal performance, can improve overall profit margins associated with a new cultivar, compared with older cultivars, by literally millions of dollars. Breeding for increased nutritional value has resulted in great benefits to the livestock community and rural society. There is no sign that the genetic progress achieved during the past 40 yr of plant breeding will not continue for at least the next 40 yr.

REFERENCES

- Arcioni, S., F. Veronesi, D. Mariotti, and M. Falcinelli. 1983. Evaluation of the possibility of improving protein yield in *Lolium perenne* L. Z. Pflanzenzüchtg. 91:203-210.
- Barrière, Y., J.-C. Émile, R. Traineau, and Y. Hébert. 1995. Genetic variation in the feeding efficiency of maize genotypes evaluated from experiments with dairy cows. Plant Breeding 114:144-148.
- Broderick, G.A., and D.R. Buxton. 1991. Genetic variation in alfalfa for ruminal protein degradability. Can. J. Plant Sci. 71:755-760.
- Buendgen, M.R., J.G. Coors, A.W. Grombacher, and W.A. Russell. 1990. European corn borer resistance and cell wall composition of three maize populations. Crop Sci. 30:505-510.
- Burton, G.W. 1989. Progress and benefits to humanity from breeding warm-season forage grasses. p. 21-29. In D.A. Sleper et al. (ed) Contributions from breeding forage and turf grasses. CSSA Spec. Publ. 15. CSSA, Madison, WI.
- Buxton, D.R. and M.D. Casler. 1993. Environmental and genetic effects on cell wall composition and digestibility. p. 685-714. In H.G. Jung et al. (ed) Forage cell wall structure and digestibility. ASA., Madison, WI.
- Buxton, D.R., K.P. Vogel, M.D. Casler, and K.J. Moore. 1995. Field survival of perennial forages divergently selected for digestibility. p. 163. In Agronomy abstracts. ASA, Madison, WI.
- Casler, M.D. 1995. Selection for low fiber concentration in smooth brome grass. p. 161. In Agronomy abstracts. ASA, Madison, WI.
- Casler, M.D. 1998. Breeding for improved forage quality: potentials and problems. In Proc. XVIII Intl. Grassl. Congr. 8-19 June 1997. Winnipeg, Manitoba and Saskatoon, Saskatchewan. (in press).
- Casler, M.D., and J.A. Carpenter. 1989. Morphological and chemical responses to selection for in vitro dry digestibility in smooth brome grass. Crop Sci. 29:924-928.
- Casler, M.D., and P.N. Drolsom. 1995. Registration of 'Alpha' smooth brome grass. Crop Sci. 35:1508.
- Casler, M.D., J.F. Pedersen, G.C. Eizenga, and S.D. Stratton. 1996. Germplasm and cultivar development. p. 413-469. In L.E. Moser et al. (ed) Cool-season forage grasses. ASA, Madison, WI.
- Clark, D.A. and J.R. Wilson. 1993. Implications of improvements in nutritive value on plant performance and grassland management. p. 165-171. In M.J. Baker (ed) Grasslands for our world. SIR Publ., Wellington, NZ.
- Clements, R.J. 1969. Selection for crude protein content in *Phalaris tuberosa* L. I. Response to selection and preliminary studies on correlated response. Aust. J. Agric. Res. 20:643-652.
- Cooper, J.P., J.M.A. Tilley, W.F. Raymond, and R.A. Terry. 1962. Selection for digestibility in herbage grasses. Nature 195:1276-1277.
- Edwards, M.T., D.A. Sleper, and W.Q. Loegering. 1981. Histology of healthy and diseased orchardgrass leaves subjected to digestion in rumen fluid. Crop Sci. 21:341-343.
- Ehlke, N.J. and M.D. Casler. 1985. Anatomical characters of smooth brome grass clones selected for in vitro dry matter digestibility. Crop Sci. 25:513-517.
- Fahey, G.C., Jr., and H.S. Hussein. 1999. Forty years of forage quality research: accomplishments and impact from an animal nutrition perspective. Crop Sci. 39:4-12 (this issue).
- Ford, S.A. 1998. Economic evaluation of forage quality gains: Past and future. Crop Sci. 39:21-27 (this issue).
- Gabrielson, B.C., K.P. Vogel, B.E. Anderson, and J.K. Ward. 1990. Alkali-labile cell-wall phenolics and forage quality in switchgrass selected for differing digestibility. Crop Sci. 30:1313-1320.
- Hacker, J.B. 1982. Selecting and breeding better quality grasses. p. 305-326. In J.B. Hacker (ed) Nutritional limits to animal production from pastures. St. Lucia, Australia. 24-28 Aug. 1981. Commonwealth Agric. Bureaux, Farnham House, Farnham Royal, Slough, England.
- Hacker, J.B. 1986. Selection for nutritive value in *Digitaria milanjiana*. 1. Breeding of contrasting full-sib clones differing in leaf digestibility. Aust. J. Exp. Agric. 26:543-549.
- Hanna, W.W. 1993. Improving forage quality by breeding. p. 671-675. In D.R. Buxton et al. (ed) International crop science I. CSSA, Madison, WI.
- Hatfield, R.D., J. Ralph, and J.H. Grabber. 1998. Cell wall structural foundations: molecular basis for improving forage digestibilities. 39:27-37 (this issue).
- Hopkins, A.A., K.P. Vogel, and K.J. Moore. 1993. Predicted and realized gains from selection for in vitro dry matter digestibility and forage yield in switchgrass. Crop Sci. 33:253-258.
- Inoue, T., I.M. Brookes, A. John. T.N. Barry, and W.F. Hunt. 1993. Effect of physical resistance in perennial ryegrass leaves on feeding value for sheep. p. 570-571 In M.J. Baker et al. (eds) Proc. XVIII Intl. Grassl. Congr. 8-21 Feb. 1993. Palmerston North, NZ. NZ Grassl. Assoc., Palmerston North.
- Jung, H.G., and M.D. Casler. 1990. Lignin concentration and composition of divergent smooth brome grass genotypes. Crop Sci. 30: 980-985.
- Kephart, K.D., D.R. Buxton, and R.R. Hill, Jr. 1989. Morphology of alfalfa divergently selected for herbage lignin concentration. Crop Sci. 29:778-782.
- Khan, M.R.I., A. Ceriotti, L. Tabe, A. Aryan, W. McNabb, A. Moore, S. Craig, D. Spencer, and T.J.V. Higgins. 1996. Accumulation of a sulfur-rich seed albumin from sunflower in the leaves of transgenic subterranean clover (*Trifolium subterraneum* L.). Transgenic Res. 5:179-185.
- Lenssen, A.W., E.L. Sorensen, G.L. Posler, and D.L. Stuteville. 1991. Resistance to anthracnose protects forage quality of alfalfa. Crop Sci. 31:147-150.

- Mackinnon, B.W., H.S. Easton, T.N. Barry, and J.R. Sedcole. 1988. The effect of reduced leaf shear strength on the nutritive value of perennial ryegrass. *J. Agric. Sci. (Cambridge)* 111:469-474.
- Marten, G.C. 1989. Breeding forage grasses to maximize animal performance. p. 71-104. *In* D.A. Sleper et al. (ed) *Contributions from breeding forage and turf grasses*. CSSA Spec. Publ. 15. CSSA, Madison, WI.
- Marten, G.C., R.M. Jordan, and A.W. Hovin. 1976. Biological significance of reed canarygrass alkaloids and associated palatability variation to grazing sheep and cattle. *Agron. J.* 68:909-914.
- Mayland, H.F., and D.A. Sleper. 1993. Developing a tall fescue for reduced grass tetany risk. p. 1095-1096. *In* M.J. Baker et al. (eds) *Proc. XVIII Intl. Grassl. Congr.* 8-21 Feb. 1993. Palmerston North, NZ. NZ Grassl. Assoc., Palmerston North.
- McNabb, W.C., C. Higgins, L. Tabe, and T.J.V. Higgins. 1993. Transfer of genes encoding proteins with high nutritional value into pasture legumes. p. 1085-1086. *In* M.J. Baker et al. (eds) *Proc. XVIII Intl. Grassl. Congr.* 8-21 Feb. 1993. Palmerston North, NZ. NZ Grassl. Assoc., Palmerston North.
- Moseley, G., and D.H. Baker. 1991. The efficacy of a high magnesium grass cultivar in controlling hypomagnasaemia in grazing animals. *Grass Forage Sci.* 46:375-380.
- Munro, J.M.M., and D.A. Davies. 1989. Animal production evaluation of new herbage varieties. p. 1273-1274. *In* *Proc. XVI Intl. Grassl. Congr.* 4-11 Oct. 1989. Nice, France. The French Grassl. Soc., Lusignan.
- Munro, J.M.M., D.A. Davies, W.B. Evans, and R.V. Scurlock. 1992. Animal production evaluation of herbage varieties. 1. Comparison of Aurora with Frances, Talbot, and Melle perennial ryegrass when grown alone and with clover. *Grass Forage Sci.* 47:259-273.
- Munro, J.M.M., and R.J.K. Walters. 1986. The feeding value of grass. p. 65-78. *In* J. Frame (ed) *Grazing. Occ. Symp.* 19. 5-7 Nov. 1985, Malvern, Worcestershire. British Grassl. Soc., Reading, Berkshire.
- Ni, W., N.L. Paiva, and R.A. Dixon. 1993. Reduced lignin in transgenic plants containing an engineered caffeic acid *O*-methyltransferase antisense gene. *Transgenic Res.* 3:120-126.
- Oram, R.N., H.E. Schroeder, and R.A. Culvenor. 1985. Domestication of *Phalaris aquatica* as a pasture grass. p. 220-221. *In* *Proc. XV Intl. Grassl. Congr.* Kyoto, Japan. 24-31 August. Japan. Soc. Grassl. Sci., Nishi-nasumo, Tochigi-ken, Japan.
- Rae, A.L., C.L. McIntyre, R.J. Jones, and J.M. Manners. 1996. Anti-sense suppression of the lignin biosynthetic enzyme, caffeic acid *O*-methyl transferase, improves forage digestibility. SYM-21-07. *In* *Combined Conference Abstracts*, Australian Soc. Plant Physiol., Canberra, 29 Sept. to 2 Oct. 1996.
- Surprenant, J., D.K. Barnes, R.H. Busch, and G.C. Marten. 1988. Bidirectional selection for neutral detergent fiber and yield in reed canarygrass. *Can. J. Plant Sci.* 68:705-712.
- Surprenant, J., R. Michaud, and G. Allard. 1990. Effect of one cycle of divergent phenotypic selection for crude protein, digestibility and digestible yield in timothy. *Can. J. Plant Sci.* 70:757-765.
- Tilley, J.M.A. and R.A. Terry. 1963. A two-stage technique for in vitro digestion of forage crops. *J. Br. Grassl. Soc.* 18:104-111.
- Undersander, D.J., W.T. Howard, and R.D. Shaver. 1993. Milk per acre spreadsheet for combining yield and quality into a single term. *J. Prod. Agric.* 6:231-235.
- Van Soest, P.J. 1994. *Nutritional ecology of the ruminant*. 2nd ed. Cornell Univ. Press, Ithaca, NY.
- Van Wijk, A.J.P., J.G. Boonman, and W. Rumball. 1993. Achievements and perspectives in the breeding of forage grasses and legumes. p. 379-383. *In* M.J. Baker et al. (eds) *Proc. XVIII Intl. Grassl. Congr.* 8-21 Feb. 1993. Palmerston North, NZ. NZ Grassl. Assoc., Palmerston North.
- Vaughn, D.L., D.R. Viands, and C.C. Lowe. 1990. Nutritive value and forage yield of alfalfa synthetics under three harvest-management systems. *Crop Sci.* 30:699-703.
- Vogel, K.P., B.C. Gabrielson, J.K. Ward, B.E. Anderson, H.F. Mayland, and R.A. Masters. 1993. Forage quality, mineral constituents, and performance of beef yearlings grazing two crested wheat-grasses. *Agron. J.* 85:584-590.
- Vogel, K.P., and D.A. Sleper. 1994. Alteration of plants via genetics and plant breeding. p. 891-921. *In* G.C. Fahey et al. (ed) *Forage quality, evaluation, and utilization*. ASA, Madison, WI.
- Walters, R.J.K. 1984. D-value: the significance of small differences on animal performance. p. 60-68. *In* *The Grass Ley Today*, *Proc 18th NIAB Crop Conference*. 12-13 Dec. 1984, Cambridge, UK. Natl Inst. Agric. Bot., Cambridge.
- Wolf, D.P., J.G. Coors, K.A. Albrecht, D.J. Undersander, and P.R. Carter. 1993. Forage quality of maize genotypes selected for extreme fiber concentrations. *Crop Sci.* 33:1353-1359.