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CHAPTER 22

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FORAGE QUALITY, EVOLUTION, AND PLANT BREEDING

Plant breeding is man-directed evolution. Plant breeders manipulate the genetic resources of a species, i.e., its germplasm, to produce plants that are of increased value to humanity. The same analogy applies to animal improvement programs. All of our major food crops and all of our domestic animals and their respective breeds, strains, or cultivars were developed by this process. Although humans have successfully manipulated the genetic resources of plants and animals for several thousand years, the science of genetics and breeding was not developed until this century.

Breeding work on most forage crops did not began until the 1930's and initial work was focused on developing strains that had good establishment capability, persistence, high forage yields, and had good insect and disease resistance. These are essential attributes of forages (Burton, 1986). This initial breeding work resulted in the development of grasses such as 'Coastal' bermudagrass (*Cynodon dactylon* L.), 'Lincoln' bromegrass (*Bromus inermis* Leyss.), and 'Kentucky 31' tall fescue (*Festuca arundinacea* Schreb.). Limited animal evaluation was involved in the development of these cultivars.

Breeding for improved forage quality was not an important research objective of most forage programs until the last 25 yr. Kneebone (1960) published a review of grass breeding and did not discuss breeding for improved forage quality. However, some earlier reviews on grass breeding including the extensive review of Hanson and Carnahan (1956) included minor sections on breeding for improved forage quality. It was not until the pioneering research of Dr. Glenn Burton and his associates at Tifton, GA demonstrated the economic value of improved digestibility in bermudagrass that breeding for forage quality became a major research objective of some grass breeding programs (Burton, 1972a; Chapman et al., 1972).

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Genes that are available for plant breeders to manipulate using conventional breeding methods are those that a species has accumulated during its evolutionary history. In contrast to traits such as seed production and rhizomatous spread, positive forage quality traits such as high digestibility may not be advantageous to a species. Any trait that discourages excessive utilization of their herbage could be advantageous to forage plants. Even breeding for high digestibility is breeding to remove the effects of factors that inhibit digestibility. Anti-quality factors such as alkaloid content, hydrocyanic acid precursors, and the presence of endophytes and their associated deleterious effects appear to enhance the evolutionary fitness of a herbaceous species. It is likely that herbivory by insects was more important than consumption by ruminants in this evolutionary process (Jones, 1981; Molyneux and Ralphs, 1992). Breeding for improved forage quality can be viewed as changing plants to reduce their fitness to compete in the "wild" but increasing their fitness for use in agriculture.

There are many facets to breeding for improved forage quality. A recent study utilized the Dephi survey technique to attempt to rank forage quality breeding objectives in terms of their importance for grasses and legumes utilized by livestock for meat, milk, and wool production (Wheeler and Corbett, 1989). In this procedure, repeated surveys are used to arrive at a consensus. Improved digestibility was the most important criterion on each of the four lists while high comminution was ranked second in all lists except legumes for wool where it was ranked third. High comminution relates to physico-chemical characteristics conducive to high rate of passage or high outflow rate from the rumen, promoting higher intake. For improving livestock gains, high non-structural carbohydrate content also was an important breeding objective. For improving wool production, high S-amino acid content of forage protein was ranked two or three. Protein content was in the middle of the list of 11 factors ranked. High relative palatability, high lipid content, and erect growth were ranked as least important. It was generally considered that mineral content and anti-quality constituents should be monitored rather than making them specific breeding objectives.

Although genetic and breeding research on forage quality has been conducted for over 50 yr and numerous papers have been written on the topic, only a limited number of cultivars with improved forage quality have been released for use in commercial agriculture. Cultivars with improved forage quality have not been developed for most forage species. The objectives of this report are to review the progress that has been achieved by breeding for forage quality, assess the potential for future genetic gains in forage quality, and identify breeding strategies and procedures, both conventional and molecular, that should be the most effective in achieving breeding objectives.

PLANT BREEDING AND TRANSFORMATION

Until very recently, the only genes that were available to a breeder for improving a species in a conventional breeding program were the genes that were in the plants of a species or its close relatives. Genes can be moved between plants of closely related species with varying degrees of difficulty.

Moving genes between unrelated species is not possible using conventional breeding methods. Molecular genetic approaches have and are making it possible to clone genes from virtually any living organism and insert the cloned gene into another organism including forage plants. The transformed plants express the cloned genes and produce the gene products of the inserted gene. Molecular genetics and transformation procedures give plant breeders the potential to use genes from any organism to improve a plant species.

Conventional Plant Breeding Procedures

Conventional plant breeding involves manipulating the genes of a species so that desired genes are packaged together in the same plant and as many deleterious genes as possible are excluded. The two main components of the plant breeding process are selection and hybridization. Selection of the plants to be mated is the critical component of the breeding process. The other component, hybridization or mating, can usually be done in a routine manner although for some species, the procedures are tedious and require a high degree of skill (Barnes, 1980; Burson, 1980; Hovin, 1980; Taylor, 1980). Breeding systems have been developed and continue to be developed that can be used to improve virtually all forage species. Recent reviews have described the relative theoretical and practical efficiencies of these systems (Hanna and Bashaw, 1987; Vogel and Pedersen, 1993). In brief, forage breeders have an array of breeding procedures that they can use to improve forage species. The critical problem involved in improving forage quality is having an effective and consistent selection procedure. A breeder must be able to differentiate and rank plants before breeding progress can be achieved.

Genetic studies are usually conducted before plant breeders initiate long-term breeding projects to obtain information on the inheritance of the specific traits that the breeder wants to improve. It is necessary to determine if the trait(s) is controlled by only a few genes that are expressed in a qualitative manner or if they are controlled by many genes and are expressed in a quantitative manner. Eye color in humans is a trait that is controlled by a few genes and is inherited in a qualitative manner while adult height and weight are controlled by many genes and are inherited in a quantitative manner. Qualitative traits such as eye color usually are not affected by environmental factors while quantitatively inherited traits are influenced by environmental factors. Breeders also often attempt to determine if genetic variation for quantitatively inherited traits is due to additive or non-additive genetic effects. Additive genetic effects are due to the accumulative effects of genes that are expressed in an additive manner while non-additive effects are those in which gene action results in heterosis. After breeders have determined the existence of genetic variation for a trait, they need to know the stability of the expression of those differences over environments.

A few basic equations can be used to express many of the concepts involved in plant breeding (Allard, 1964; Falconer, 1981). Assuming selection is conducted on an individual plant basis, the heritability estimate (h_x^2) for a trait "x" (Equation 1) is the ratio of the additive genetic variation (σ_{ax}^2) for that trait divided by the phenotypic variance (σ_P^2) (Falconer, 1981). Except

for a few forage species for which it is possible to produce commercial F_1 hybrids, forage breeders have to utilize additive genetic variation. Additive genetic variation is used as the numerator in Equation 1 to provide an estimate of heritability in the narrow sense. Plant breeders and geneticists use various mating and evaluation strategies to obtain estimates of the additive genetic and phenotypic variance (Hallauer and Miranda, 1981). Narrow sense heritability estimates are used to predict gain from selection and also provide an estimate of the proportion of the total variation for a trait that can be attributable to genetic differences among individuals or families. Heritability estimates can range from 1.0 for a trait such as eye color that is not affected by environment to less than 0.10 for traits that are highly influenced by environment variables.

$$h_x^2 = \sigma_{ax}^2 / \sigma_P^2 \qquad [1]$$

$$G_x = i\, h_x\, \sigma_{ax} \qquad [2]$$

$$CG_x = i\, h_y\, r_{xy}\, \sigma_{ax} \qquad [3]$$

Gain from selection for a trait is the gain that is achieved by selecting individuals for that trait and intermating the selected plants to produce their progeny. The mean difference between the progeny of selected and unselected plants is the realized gain from selection. The expected or predicted gain from selection (G_x) for trait "x" is the product of the standardized selection differential (i), the square root of the heritability of the trait (h_x), and the square root of the additive genetic variation (σ_{ax}) (Equation 2). The standardized selection differential is simply the proportion of selected plants expressed in units of standard deviations from the mean. The genetic gain that can be achieved in a single breeding cycle is dependent upon the relative magnitude of the factors in Equation 2.

Selection for one trait can have an effect on another trait if the traits are genetically correlated. The expected correlated response (CG_x) for trait "x" if selection is practiced for trait "y" is given in Equation 3. The genetic correlation is (r_{xy}). If the genetic correlation is large and the heritability for trait y is also large, then substantial gains from selection can be achieved for a particular trait by indirect selection for the correlated trait. Indirect selection can be as effective as direct selection if h_y is 25% larger than h_x and the genetic correlation is 0.8 or larger. Correlated responses to selection can be important in breeding for improved digestibility in terms of selection criteria.

The stability of a trait over environments is important because it will influence the area of adaptation of an improved cultivar. Breeders can obtain estimates of the genotype x environment interactions by growing cultivars or experimental strains in an array of environments. Variance component analyses and regression procedures are used to determine the relative magnitude of genetic, environment, and genotype x environment interaction

(GxE) effects. If genetic effects are significant and GxE effects are non-significant for a specific trait even though environment effects are large, then the trait is stable over environments. If GxE effects are larger than genotypic effects, it may be necessary for breeders to develop cultivars for specific environments.

Molecular Genetics and Plant Transformation

Improving plants via molecular genetics involves isolating and cloning a gene from any source that regulates a specific metabolic activity and inserting that gene along with necessary promoter sequences into the DNA of the target organism. Many of the genes that have been cloned for herbicide, insect, and disease resistance are from microorganisms and produce enzymes that degrade herbicides, metabolites that are toxic to insects, or inhibit virus replication (Goodman et al., 1987; Gasser and Fraley, 1989). Genes that can block the expression of specific metabolic pathways also can be developed and cloned (Verma et al., 1987). Since many of the factors that reduce forage quality are substances that inhibit digestibility or are toxic, development of anti-sense genes that block the expression of specific metabolites would be a highly feasible approach (Iiyama et al., 1993). Anti-sense RNA for the messenger RNA for polygalacturonase in tomato fruits has been successfully utilized (Gasser and Fraley, 1989). Genes or anti-sense genes that regulate the production of plant metabolites such as lignin (Bailey, 1991) or plant development (Poethig, 1990) appear to be logical targets for developing improved forage plants via genetic transformation.

Methods of incorporating cloned, foreign DNA into the DNA of plant cells currently can be accomplished by using *Agrobacterium tumefaciens* (currently only with legumes and other dicots), micro-injection, polyethylene glycol, electroporation, particle guns or other mechanical means (Gasser and Fraley, 1989; Kaeppler et al., 1992; Hodges et al., 1993). These DNA transformation procedures must be used in cell or protoplast culture systems that are capable of being regenerated into intact plants. Prior to initiation of a molecular transformation program, it is first necessary to develop an appropriate cell or protoplast culture system for each specific species. These systems are often the most variable part of the entire process (Hodges et al., 1993). In a recent review of genetic transformation of forage crops, Hodges et al. (1993) indicated that, to date, alfalfa (*Medicago sativa L.*), white clover (*Trifolium repens* L.), birdsfoot trefoil (*Lotus corniculatus* L.), orchardgrass (*Dactylis glomerata* L.), and tall fescue (*Festuca arundinaceae* Screb.) have been transformed with foreign DNA. There undoubtedly will be other forage species transformed in the near future. The critical problems in genetic transformation of forage plants are determining what traits to alter, developing the appropriate cloned genes, and the development of improved transformation procedures for monocots. Methods for determining if transformed forage plants are safe when fed to livestock and are ecologically safe also need to be developed and utilized. Forage breeders do not need to develop plants that have the potential of becoming super-weeds.

GENETIC MODIFICATION OF QUALITY AND ANTI-QUALITY TRAITS

Forage Digestibility

Plant breeders must be able to screen large numbers of plants for the traits undergoing selection. Breeding for improved digestibility first became feasible when reliable, repeatable, *in vitro* dry matter (DM) digestibility methods were developed. The nylon bag *in situ* procedure enabled Burton et al. (1967) to select Coastcross-1 bermuda grass from an array of bermudagrass plants. However, the development of the two-stage *in vitro* procedure by Tilley and Terry (1963) was the critical development that allowed breeders to screen large numbers of plants for differences in digestibility (see Chapters 15 and 16). Subsequent developments including the use of cellulase enzymes to replace rumen fluid (Gabrielsen et al., 1988; Casler and Sleper, 1991) and the development of near infrared reflectance spectroscopy (NIRS) (see Chapter 10) have given breeders the capability to rapidly screen large numbers of samples. For plant breeders, the two-stage Tilley and Terry procedure (1963) remains the standard on which other *in vitro* DM digestibility methods are calibrated.

Direct Selection for Digestibility

Genetic variability for forage digestibility has been found for virtually every forage species for which a well designed and conducted trial has been completed. Some of the genetic differences are due to single gene effects while in other instances, differences in digestibility are due to the action of numerous genes, i.e., differences in digestibility are inherited in a quantitative manner. Many forage species are complex polyploids and can have up to seven or more sets of basic genomes (Hanson and Carnahan, 1956). A trait that may be simply inherited in a diploid may appear to be inherited in a quantitative manner in a hexaploid or octaploid species simply because of the number of genes segregating.

Single genes that can significantly change forage digestibility are the brown midrib genes in maize, sorghum, and sudangrass (Barnes et al., 1971; Fritz et al., 1981). These genes are recessive, are expressed only in the homozygous state, and produce altered lignins (Kuc and Nelson, 1964; Gee et al., 1968). The brown midrib mutants of corn, sorghum, and sudangrass are almost 10 percentage units higher in *in vitro* DM disappearance (IVDMD) than their normal counterparts at similar stages of maturity. To date, no brown midrib strains or hybrids of these crops have been released for commercial use even though the nutritional advantage of these lines has been documented (Colenbrander et al., 1973; Lush et al., 1984), primarily because forage yield is lower (7 to 29%) than for normal lines (Lee and Brewbaker, 1984). From our perspective, increasing the forage yield of brown midrib maize and sorghum lines to improve economic returns ha^{-1} would be the most effective and efficient use of breeding resources to improve these plants as forage crops. Brown midrib mutants have not been found in polyploid forage species, probably because of the improbability of the recessive mutation being

found in the homozygous state in each of the genomes comprising a polyploid species.

Genes that control leaf surfaces and other anatomical features can affect forage digestibility. The recessive gene, *tr*, in pearl millet (*Pennisetum americanum* (L.) Leeke) removes tricomes from the leaves, leaving the leaves with a smooth waxy surface (Burton et al., 1977). This gene affects forage utilization by livestock by increasing palatability but causes a reduction in digestibility of intact leaves. It also increases the plants susceptibility to leaf rusts but reduces transpiration which aids in drought tolerance (Burton et al., 1977). In sorghum (*Sorghum bicolor* (L.) Moench), the bloom (a whitish, waxy covering) on the leaves can be removed by a single recessive gene. Green intact leaf sections of three bloomless sorghums were 22% more digestible than bloom covered green leaves of their normal isogenic lines but when dried and ground, bloom-covered leaves were slightly higher (14 g kg^{-1}) in IVDMD (Cummins and Dobson, 1972). Based on these results, breeding for altered leaf surface of forage species needs to be justified by improved animal performance.

Single loci can affect forage digestibility by altering leaf to stem ratios. The dwarf (d_2) gene of pearl millet shortens stem internodes (Burton et al., 1969). When evaluated in comparative feeding and grazing trials with isogenic tall counterparts, the dwarf gene reduced internode length by 25 to 43% which increased percentage of leaf by 20%, increased forage digestibility by more than 10%, and decreased forage yield by 30%. When fed to animals as hay, the hay from dwarf lines increased average daily gains by 20%. However, when grazed, pastures seeded to the dwarf plants had reduced carrying capacity (15%) but produced equivalent gains per hectare (467 vs 480 kg ha^{-1}) as the tall counterpart (Burton et al., 1969). It is likely that internodes could be shortened in other forage species with similar effects. Results on the quantitative inheritance of IVDMD indicate that it should be possible to improve IVDMD without decreasing forage yield (see following section) so breeding for shortened internodes may not be the most effective method of increasing animal productivity per unit of land.

Genetic differences among plants of a forage species appear to be inherited in a quantitative manner for most forage species with the exception of the few major genes described in the above sections. Genetic variation for *in vitro* digestibility has been reported for perennial ryegrass (*Lolium perenne* L.), orchardgrass (*Dactylis glomerata* L.), bermudagrass (*Cynodon dactylon* (L.) Pers.), smooth bromegrass (*Bromus inermis* Leyss.), crested wheatgrass (*Agropyron* spp.), intermediate wheatgrass (*Thinopyrum intermedium* (Host) Barkw. and D.R. Dewey), switchgrass (*Panicum virgatumi* L.), indiangrass (*Sorghastrum nutans* (L.) Nash), maize (*Zea mays* L.), forage sorghums, alfalfa (*Medicago sativa* L.), and other species (Cooper, 1962; Gill et al., 1967; Roth et al., 1970; Burton and Monson, 1972; Coulman and Knowles, 1974; Vogel et al., 1981a,b; Pedersen et al., 1982; Lamb et al., 1984; Vogel et al., 1986, 1993b; Deinum and Struik, 1989; Marten, 1989; Hopkins et al., 1993).

In most of the forages that have been evaluated for genetic variation in IVDMD, the phenotypic range in digestibility has been as large as 100 g kg^{-1} and the heritabilities are usually 0.3 or larger. These results clearly indicate

that it should be feasible to improve the digestibility of most forage crops if adequate sampling and laboratory protocols are followed and efficient breeding systems are utilized. Although genetic studies indicate that it should be feasible to develop cultivars with improved digestibility for almost every forage species, to date, only a limited number of forage cultivars with improved digestibility as validated in animal trials have been released.

Dr. Glenn Burton and his colleagues at Tifton, GA have been extremely successful in developing bermudagrasses with improved forage digestibility and increased yield. These improvements have been obtained by developing F_1 hybrid bermudagrasses that, although sterile, can be vegetatively propagated on a large scale. It is only necessary to identify a single superior plant to have a new cultivar. Coastcross-1 bermudagrass, a sterile F1 interspecific hybrid, was the first pasture grass bred for improved forage quality. It does not yield any more than Coastal bermudagrass, but in grazing trials and in feeding trials with pelleted hay it produced up to 30% higher average daily gains and up to 50% more live weight gain ha^{-1} (Burton et al., 1967; Burton, 1972a; Chapman et al., 1972). Averaged over grazing seasons, it was 60 g kg^{-1} higher in digestibility than Coastal (Table 1).

Table 1. Improvements in bermudagrass digestibility, yield, and beef production per hectare.+

Cultivar	IVDMD	Available herbage	ADG	Gain ha^{-1}
	g kg^{-1}	kg ha^{-1}	kg	kg ha^{-1}
Coastal	542	2900	0.48	498
Coastcross-1[1]	606	2280	0.72	746
Coastal	565	930	0.59	713
Tifton 78[2]	574	1190	0.68	985
Tifton 78	571	2450	0.65	789
Tifton 85[3]	594	2750	0.67	1156

+ADG = average daily gain; available herbage = mean herbage available for grazing in pastures during trials.

[1]Chapman et al. (1972). Animal gains averaged over stocking rates. Grazing season was 168 d.

[2]Hill et al. (1993). Grazing season was 168 d for 3 yr.

[3]Hill et al. (1994). Grazing season was 168 d. IVDMD values were based on esophageal samples. Trial was conducted from 1989-1991.

Breeding work on improving both IVDMD and forage yield of bermudagrasses has continued at Tifton over the past 20 yr since the release of Coastcross-1. The development of 'Tifton 78' demonstrated that it is feasible to improve both yield and IVDMD in bermudagrass (Burton and Monson, 1988; Hill et al., 1993). Tifton 78 is a 'Tifton 44' x 'Callie' F_1 hybrid

and is taller and spreads more rapidly than Coastal. It also is higher yielding and was 10 g kg^{-1} higher in IVDMD than Coastal averaged over 3 yr in a grazing trial (Table 1). Tifton 78 can be stocked heavier than Coastal. Steers grazing Tifton 78 had significantly higher average daily gains than steers grazing Coastal. The combination of higher stocking rates and higher average daily gains results in significant improvements in total beef production per hectare (Table 1). 'Tifton 85' is the latest bermudagrass cultivar that has been released by the USDA-ARS program at Tifton (Burton et al., 1993) and it represents a remarkable breeding achievement. In a small plot trial conducted during 1989 to 1991, the IVDMD (g kg^{-1}) and annual DM yield (Mg ha^{-1}), respectively, of bermudagrass cultivars were as follows: Coastal (502, 11), Tifton 44 (513, 10.4), Tifton 78 (557, 11.3), Tifton 85 (573, 14.7) (Hill et al., 1994). In a grazing trial conducted during the same period at Tifton, Tifton 85 produced over 1000 kg ha^{-1} of gain when grazed by beef yearlings because of its high yield and high IVDMD (Table 1).

The development of Tifton 78 and particularly Tifton 85 are conclusive proof that it is possible to significantly improve both DM yields and forage digestibility by breeding. It should be noted that the improvements in both forage yield and digestibility were achieved by direct selection for both traits. The biochemical basis for the improved forage quality of the high IVDMD bermudagrasses has not been determined. It also needs to be noted that it took 20 yr to develop, test, and release Tifton 85 from the time Coastcross-1 was released.

Most of the forage species used in the temperate areas of the world are sexual, cross-pollinated perennial species. The first cultivar of a sexual, perennial species that was bred for improved digestibility was 'Trailblazer' switchgrass (*Panicum virgatum* L.) (Vogel et al., 1991). A series of experiments was conducted during the development and evaluation of Trailblazer. These experiments demonstrated that the IVDMD of switchgrass was improved by breeding by using a form of modified mass selection with selected plants polycrossed in isolation (Vogel et al., 1981b) and that the IVDMD of switchgrass plants sampled at panicle emergence was an excellent predictor of the IVDMD of their progeny in pastures throughout the grazing season (Tables 2 and 3) (Gabrielsen et al., 1990). A small improvement in IVDMD (3 to 4 percentage units) significantly improved animal performance (17 to 24%) as measured by both average daily gains and beef production per hectare in a replicated grazing study conducted for 3 yr (Table 3) (Anderson et al., 1988). Differences in animal performance were not due to differences in selectivity but to intrinsic differences in quality (Ward et al., 1989). Additional research demonstrated that changes in forage digestibility were achieved by increasing the extent of cell wall digestibility and not by changing the cell wall to cell solubles ratio or the rate of cell wall digestibility (Moore et al., 1993). The improvement in IVDMD was accompanied by correlated changes in the molar ratio of ferulic acid and p-coumaric acid, demonstrating that these components of plant cell walls were heritable and genetically correlated with IVDMD (Gabrielsen et al., 1990).

Table 2. Forage yields and IVDMD of switchgrass and intermediate wheatgrass strains in small plot trials in eastern Nebraska.

Species/strain	Forage yield	IVDMD
	kg ha^{-1}	g kg^{-1}
Switchgrass (1978-1980)[1]		
Pathfinder	9184	542
Trailblazer	9632	582
SE	NS	8
Intermediate wheatgrass (1986-1987)[2]		
Oahe	6720	604
Slate	6720	597
Manska	7168	616
SE	224	6

[1]From Vogel et al., 1984.
[2]From Moore et al., 1994.
[3]NS = not significantly different.

Table 3. Performance of beef yearlings grazing switchgrass and intermediate wheatgrass strains in eastern Nebraska and gross returns per acre.

Species/strain	ADG[3]	Gain ha^{-1}	$/ha[4]
	kg	kg	
Switchgrass (1982-1983, 1985)[1]			
Pathfinder	0.58	283	437
Trailblazer	0.73	350	540
SE	0.07	13	
Intermediate wheatgrass (1989-1990)[2]			
Oahe	1.05	256	395
Slate	1.05	260	400
Manska	1.22	298	459
SE	0.05	20	

[1] From Anderson et al., 1988.
[2] From Moore et al., 1994.
[3] ADG = average daily gain.
[4] Based on a price of $1.54 kg^{-1}

Two cool-season grasses with improved digestibility have been released recently. 'Badger' bromegrass was released in 1992 (Casler, 1992) by the Wisconsin Agricultural Experiment Station. It averages 10 to 30 g kg^{-1} higher in IVDMD than 'Rebound' smooth bromegrass and when grazed by ewes and lambs (*Ovis aries*) in a replicated trial in 1985, produced 11% higher daily gains (Casler, 1992). 'Manska' intermediate wheatgrass was developed by Dr. John Berdahl, USDA-ARS geneticist at Mandan, ND, by reselection in several sources of the unreleased strain 'Mandan 759' for agronomic traits (Berdahl et al., 1993). In a series of trials over several environments, it consistently had high IVDMD (Berdahl et al., 1993; Vogel et al., 1993b). It was included in a replicated grazing trial at Mead, NE along with the two cultivars, and another experimental strain (NE TI 1) that had been bred for high yield and high IVDMD in the USDA-ARS program at Nebraska (Moore et al, 1994). In the grazing trial, beef yearlings grazing Manska produced over 14% more gain per hectare than yearlings grazing the two most widely used cultivars, Oahe and Slate (Tables 2 and 3) (Vogel and Moore, 1993; Moore et al., 1994). Although NE TI 1 had similar yields and IVDMD values as Manska, gains of cattle grazing it were only slightly higher than for cattle grazing Slate and Oahe.

An alfalfa cultivar with improved IVDMD also has been developed whose improvement in digestibility has been validated in animal trials (Emile et al., 1993). The experimental cultivar, '632P', was compared to the cultivar, 'Europe', in a feeding trial with lactating dairy cows in which first or second cut alfalfa was fed. The intake was larger for 632P than for 'Europe' and the cows fed 632P produced more milk than cows fed 'Europe'.

Table 4. Dry matter digestibility and milk production from Holstein cows fed hays of two alfalfa strains differing in *in vitro* organic matter digestibility (from Emile et al., 1993).

	Alfalfa strain	
Trait	6328P	Europe
In vitro digestibility, g kg^{-1}	677	627
Dry matter intake, kg d^{-1}	18	16.1
Milk production, kg d^{-1}	22.5	21.1

The limited numbers of cultivars specifically bred and released to date for improved forage digestibility demonstrate that forage digestibility of warm- and cool-season grasses and legumes can be developed by direct selection for IVDMD. The predictions of Howarth and Goplen (1983) "that the in vitro digestion technique does not have much potential for improving the digestibility of cool season forages" has been proven to be false.

In addition, the results of the animal evaluation trials in which the improved cultivars were compared with standard cultivars demonstrate that small changes in IVDMD can have significant economic impact on the profitability of livestock production systems. Since management costs will be identical among similarly yielding cultivars of a species except for possible

differences in seed costs, genetic improvements in digestibility that lead to improved gains can be considered to be 100% profit. The economic value of a percentage unit (1% or 10 g kg^{-1}) improvement in digestibility will vary with the productive potential of a unit of land and the market value of livestock products. Trailblazer and Manska both were evaluated in eastern Nebraska and they were similar in forage yield to the check cultivars to which they were compared. If the market value of beef yearlings is assumed to be \$1.54 kg^{-1}, then in regions that have the forage production potential of eastern Nebraska, a percentage unit improvement in IVDMD as determined in small plot trials has an economic value of \$25 ha^{-1} (Tables 2 and 3) (Vogel and Moore, 1993).

Indirect Selection for Digestibility

Forage digestibility also can be improved by indirect selection for other traits. Improvements in forage digestibility have been achieved by selecting for changes in maturity (lateness), palatability, and cell wall composition or fractions.

Late maturing cultivars may not differ in digestibility from early maturing strains of the same species if sampled at the same physiological stage of development, but will be higher in digestibility on specific dates during the pre-flowering growing season because of their slower rate of development. In pearl millet, late maturing, near-isogenic populations had higher forage yields, higher digestibility, better seasonal distribution of forage yield, and were more persistent than their earlier maturing counterparts (Burton et al., 1968). 'Tiflate' pearl millet is a late maturing cultivar that was released because of its improved performance that is largely attributable to its late maturity (Burton, 1972b). It is photoperiod-sensitive and requires a short day for flowering. It will not set seed in the continental USA, but will produce abundant seed in the tropics.

'Morpa' weeping lovegrass (*Eragrosits curvula* (Schrad.) Nees) was developed from plants of a plant introduction that survived the winter at Woodward, OK (Voight, 1971). The surviving plants were probably all the same genotype because of their uniformity and because Morpa is an obligate apomixix (produces seed by asexual reproduction). Morpa was selected for improved palatability in palatability trials. In a subsequent grazing trial, cattle grazing Morpa had 12% higher gains than cattle grazing common weeping lovegrass (Voight et al., 1970). Later research indicated that Morpa had higher forage digestibility than common lovegrass (Voight, 1975) and was also 6 to 8 d later in maturity (Voight, 1971). It is likely that the improved palatability and digestibility of Morpa was due to its later maturity.

In the USDA-ARS switchgrass breeding program at Nebraska, a single cycle of selection for high IVDMD and high forage yield in 'Cave-in-rock' switchgrass improved forage digestibility about a percentage unit. In subsequent evaluations, the high IVDMD Cycle 1 selection population was about 2 d later in maturity than the base population which was the original cultivar (Hopkins, 1993; K. P. Vogel, personal communication). Gabrielsen et al. (1990) reported that in switchgrass, IVDMD declined from 2.7 to 3.5 g kg^{-1} d^{-1} prior to flowering in a 3 yr study (Figure 1). In the evaluation trials

of Cave-in-rock lines, the plants in plots were staged for maturity using the system of Moore et al. (1991) prior to harvest. After IVDMD was adjusted to a common maturity stage by regression procedures, there were no differences between the Cycle 1 stain selected for high IVDMD and the original population. The differences in IVDMD were apparently achieved by indirect selection for maturity. In the development of Trailblazer switchgrass, all plants were sampled at a common maturity stage so IVDMD per se was improved.

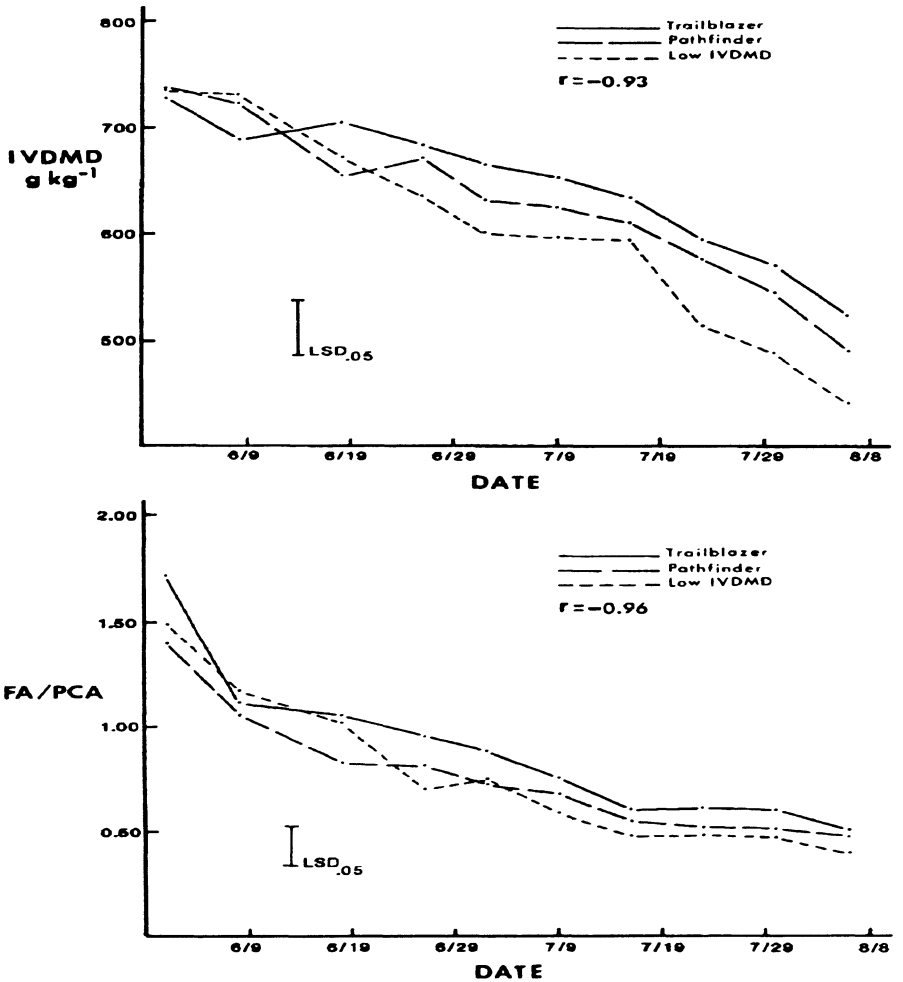

Figure 1. In vitro dry matter digestibility (IVDMD) and ferulic/*p*-coumaric acid (FA/PCA) ratio in grazed switchgrass forage of three different stains during 1984. Correlation coefficients (r) are for linear (IVDMD) and quadratic (FA/PCA) regressions with maturity, respectively, analyzed across strains. The LSD is for comparisons of strains. (From Gabrielsen et al., 1990).

Since heritability for heading date is usually large (0.80 or larger) for most species and heritability for IVDMD is low (0.3 or less), a rapid way to improve digestibility during the growing season is to simply select for late maturity. Potential gain will be limited by winter survival problems for plants that mature too late.

Plants can vary in digestibility due to differences in maturity, leaf to stem ratios, fertile to sterile tiller ratio, digestibility of plant parts, cell wall percentage of each component, and digestibility of cell walls (Casler, 1986; Buxton and Marten, 1989; Carpenter and Casler, 1990; and see Chapters 3, 4, and 18). These factors all can be considered to be components of whole plant digestibility and successful selection for any single factor will improve whole plant digestibility. In some instances, selection for a single component trait can result in greater initial gains than direct selection for IVDMD as demonstrated by Carpenter and Casler (1990) in smooth bromegrass. However, IVDMD is the only criterion that integrates all components of digestibility. If there is genetic variation for any component of digestibility in a species, the digestibility of its forage can likely be improved by breeding for improved IVDMD. If a breeder attempts to improve digestibility by selecting for one of its components such as acid detergent lignin, the potential gain is limited by the genetic variation for that trait alone.

Stability of Digestibility

Environmental factors including heat, drought, and light intensity can affect the digestibility of forage (Buxton and Casler, 1993). Genotype x environment interaction studies have been completed on crested wheatgrass (Lamb et al., 1984), intermediate wheatgrass (Vogel et al., 1986, 1993b), switchgrass (Hopkins, 1993; Hopkins et al., 1994), bromegrass (Casler et al., 1994), and timothy (McElroy and Christie, 1986). In each of these studies, IVDMD was more stable over environments than forage yield. In the crested wheatgrass and intermediate wheatgrass studies, GxE interaction effects for IVDMD were not significant. In the switchgrass study, 20 elite switchgrass strains were evaluated in Nebraska, Iowa, and Indiana. Although there were significant differences among strains for forage yield at individual locations, over locations the strains did not differ because of large GxE interaction effects. In contrast, GxE interaction effects were either small or not significant for IVDMD and there were significant differences among strains over environments. In the timothy GxE trials that were conducted in Canada, the GxE effects for IVDMD were significant but the variance component for the GxE effect was only 0.10 the size of the genetic variance for IVDMD. Based on a series of experiments in Wisconsin, South Dakota, and Canada, Casler et al. (1994) indicated that GxE effects for digestibility are relatively unimportant in that region for smooth bromegrass. In brief, forage digestibility is relatively stable over environments which means that strains should rank the same in digestibility over years and locations in which they are adapted.

Altering Plant Digestibility Via Molecular Genetics

Research is in progress to modify plant cell walls via molecular genetics including isolating and cloning genes regulating lignin synthesis (McIntyre et al., 1993a, b). The cloned genes are being utilized in anti-sense RNA and ribozyme technology to alter the lignification process. Transformed plants with altered lignin composition or structural changes will undoubtedly be developed. These transformed plants will require extensive evaluation by both animal scientists and agronomists to document any superiority and also to document their safety for use by livestock in specific environments.

Digestibility Summary

Although an effective method of evaluating forages for improved IVDMD has been available for over 25 yr and numerous studies have documented the existence of genetic variation for IVDMD, only a few forage cultivars have been developed and released with improved digestibility. Why the lack of breeding progress for improved digestibility? There are several possible reasons. Some breeding programs have placed emphasis on traits other than digestibility because they did not recognize the economic value of breeding for improved digestibility or believed other traits were more important. In some instances, breeders have used inappropriate selection criteria or methods or have simply misinterpreted their results and have come to the erroneous conclusion that it is not feasible to improve forage digestibility in specific species. In addition, there has been a lack of commitment to animal evaluation trials to validate the results of the laboratory and small plot research. Even when there has been animal evaluation, the results have sometimes been misinterpreted.

As an example, Kamstra et al. (1973) reported the results of an evaluation trial in which they compared the progeny of smooth bromegrass clones differing in digestibility. In a genetic study, the progeny of bromegrass clones were evaluated for differences in IVDMD. Plants whose progeny differed significantly in IVDMD were identified. These plants were used to produce 2-clone synthetics which then were tested in sward trials along with the cultivar 'Sac'. The hay from the trial was fed to wether lambs. In the spaced-planted breeders progeny test, the high IVDMD synthetic, SD1, was 5 percentage units higher in IVDMD than the low IVDMD synthetic, SD2 (Table 5). Plots in the sward trial were 0.135 ha with 4 replicates. There were no differences among the high and low IVDMD synthetics for IVDMD or *in vivo* digestibility for hay from the sward plots although both were higher in IVDMD and in *in vivo* digestibility than Sac. The *in vivo* digestibility and IVDMD values were similar except the *in vivo* values were 30 to 40 g kg^{-1} larger. Kamstra et al. (1973) expressed concern about the failure to obtain expected differences in IVDMD and *in vivo* digestibility in the sward trial and questioned the applicability of results from breeder's nurseries to field situations. They noted that the average daily gains ranked in the order predicted by the progeny test (Table 5) but failed to grasp the significance of these data. The average daily gains were the best estimate of forage quality

that they had available and these data clearly showed that selection for IVDMD resulted in improved animal performance. To get enough hay for the feeding trial, they had to have large plots and it is likely that their failure to detect differences in IVDMD were due to sampling errors. Since the sheep ate most of the hay produced per plot, the sampling errors were likely negated. The point is that animal performance is the best measure of forage quality.

Table 5. Digestibility and daily gains of wether lambs fed hays of two experimental smooth bromegrass strains and the cultivar 'Sac' (from Kamstra et al., 1973).

Test and trait	Sac	SD1	SD2
Breeder progeny test			
IVDMD, g kg^{-1}		642[a]	587[b]
Hay from sward trial			
IVDMD, g kg^{-1}	628[b]	656[a]	668[a]
In vivo lamb trial			
Hay digestibility, g kg^{-1}	590	625	627
Hay intake, kg/d^{-1}	0.77	0.82	0.88
Daily gain, kg	0.025[b]	0.062[a]	0.047[b]

[a,b]Means with a different superscript letter differ significantly at the 0.05 level of probability.

Attempting to breed forages for improved forage quality without conducting animal evaluation trials can lead to erroneous conclusions. In the USDA-ARS grass breeding program at the University of Nebraska, three grazing trials have been conducted to evaluate strains differing in IVDMD. In a switchgrass trial (Anderson et al., 1988), results were as expected, i.e., the strain with the highest IVDMD produced the highest average daily gains. In an intermediate wheatgrass trial (Berdahl et al., 1993; Moore et al., 1994), one of the high IVDMD experimental strains, 'Manska', produced the animal performance expected while another one, 'NE TI 1', did not. In a crested wheatgrass trial, the cultivar that had the highest IVDMD in small plots, 'Ruff', produced lower daily gains than the cultivar 'Nordan' in some years (Vogel et al., 1993a). Again, the point is that genetic gains in improving digestibility need to be validated in animal trials.

Improved Rate of Passage

Improving the rate of passage of forage or the ease of comminution has been suggested as a means of improving forage quality (Wheeler and Corbett, 1989; Mertens, 1993). However, it is clear from Mertens (1993) recent review that factors which affect rate of passage are not completely understood and that laboratory tests that could be used on large numbers of breeder

samples are not available. Wheeler and Corbett (1989) suggested that it would be desirable to develop techniques that could be used to measure ease of comminution such as energy required to pulverize forage samples, tensile strength, and shear strength. It will be necessary to establish the relationships between such measurements and rate of passage before they should be used in breeding programs. In addition, the relationship between rate of passage traits and other nutritional characteristics need to be determined. Grass breeders have finite resources. At the present time, investing those resources to improve digestibility would likely produce greater economic gains than breeding for improved rate of passage.

Protein Concentration and Quality

The proteins in forages primarily are enzymes that are involved in metabolic processes such as photosynthesis and respiration. Genetic variation for protein content has been found in forage plants but the genetic variation is less than the genetic variation for IVDMD and the GxE interaction variances are larger (Vogel et al., 1981a, 1986, 1993b; Lamb et al., 1984). Since the proteins in forages are involved in metabolic activities and are not storage proteins, it is probably not feasible to make major changes in protein quality or protein composition of forage plants by breeding and still have viable, vigorous plants. Small changes in protein concentration may be feasible. It is unlikely that changes in protein quality are feasible using conventional breeding approaches. Attempts are in progress to insert genes in forage plants that would result in improved protein quality. These include inserting chicken ovalbumin genes into alfalfa (Schroeder et al., 1991). Expression of these and other genes in forages may result in production of proteins for which there is no sink or storage site. This may affect the normal metabolism and vigor of forage plants.

Minerals

Mineral imbalances in forages can lead to nutritional diseases in livestock utilizing this forage. The major problem involving minerals is grass tetany caused by Mg and Ca deficiencies in C3 forage species. Most of the genetics and breeding research on minerals in forages has been on Ca, Mg, and K concentrations, which are the principal minerals involved in the grass tetany syndrome. Significant genetic differences in concentrations of these minerals have been found in all cool-season species evaluated to date including tall fescue, ryegrass, crested wheatgrass, reed canarygrass (*Phlaris arundinaceae* L.), and orchardgrass (Sleper et al., 1989). In general, the heritabilities for Mg and Ca are higher than those for K and their concentration is more stable over environments than is K concentration. Heritability estimates and genetic variances indicate that it should be possible to alter the mineral concentration of forages by breeding (Sleper et al., 1989).

Mass selection was successfully used by Hides and Thomas (1981) to increase the Mg concentration of annual ryegrass in three cycles of divergent selection. After the three cycles of selection, the high Mg population was

35% higher in Mg concentration than the control population while the low Mg population was 24% lower in Mg concentration than the control population. A tall fescue cultivar, 'Martin', has been released with increased Mg concentration (D. A. Sleper, personal communication). Crested wheatgrass cultivars that differ significantly in Mg concentration and the grass tetany potential ratio (K/(Ca + Mg) meq basis) also have been reported (Vogel et al., 1989b, 1993a). The incidence of grass tetany is usually not a production problem when this ratio is 2.2 or less (Kemp and t'Hart, 1957; Butler, 1963).

Animal evaluation trials have been conducted on ryegrass and crested wheatgrass cultivars differing in mineral concentrations. Mosely and Baker (1991) reported that when grazed by lactating ewes, a cultivar of Italian ryegrass bred for high Mg content, Bb 2067, resulted in significantly lower incidences of grass tetany than a control cultivar, 'RvP'. In the control pastures, the incidence of grass tetany was 21% in the first 10 d but was only 2 to 5% in the Bb 2067 pastures. Ewes grazing Bb 2067 also maintained Mg levels in their blood serum while Mg levels in the ewes grazing the control pastures dropped 35%. In a crested wheatgrass grazing trial, beef yearlings grazing the cultivar, 'Nordan', had 5% higher serum Mg levels than steers grazing the cultivar, 'Ruff' (Vogel et al., 1993a). These differences were associated with a less desirable K/(Ca + Mg) ratio for Ruff than for Nordan (2.6 vs 2.3) (Vogel et al., 1993a). In the crested wheatgrass trial, both cultivars had similar Mg concentrations in their forage but Ruff had higher K concentrations.

Based on previous genetic and breeding studies, it should be possible to alter mineral concentrations of most C3 forages by breeding. Since Mg and Ca concentrations are more heritable and more stable over environments than K concentrations, emphasis should be placed on breeding to increase Mg and Ca concentration in the forage. It may not be feasible to develop forages that will totally eliminate the risk of losses due to grass tetany under all environmental conditions, but it should be possible to develop forages that will reduce the incidence of grass tetany by breeding for increased Mg and Ca concentrations.

Diseases and Endophytes

Foliar Diseases

Burton (1981) reported that *Colletotrichum graminicola* (Ces.) G.W. Wils., which killed an estimated 10% of sudangrass leaves at Tifton, GA in the summer of 1952, increased lignin content of the leaves by 20%. Rust caused by *Puccinia sugstriata* Wll. & Barth var. *indica* on pearl millet made the forage highly unpalatable to livestock (Burton, 1981). Gross et al. (1975) reported that IVDMD of smooth bromegrass plants inoculated with either *Drechslera bromi* (Died.) Shoem. or *Rhynchosporium secalis* (Oud.) Davis was lower compared to uninoculated plants. Linear regression analyses showed that a 1% increase in disease-induced lesions resulted in a 0.04% decrease in IVDMD. Karn and Krupinsky (1983) reported that intermediate wheatgrass plants affected with leaf diseases had lower in vitro organic matter digestibility

(7.5 percentage units) and higher NDF contents than healthy plants in field and greenhouse studies. These and other reports clearly document that foliar diseases of forage plants that kill or damage plant tissue reduce the digestibility and palatability of forage plants.

Almost every improved forage cultivar on the market today is superior in disease resistance to common strains or earlier cultivars. Additional genetic gains in disease resistance can be made for virtually every forage crop. Genetic sources of resistance have been reported for almost every disease of important cool-season forage grasses (Braverman, 1986). A similar situation probably exists for warm-season grasses and legumes. In addition to the genetic gains for disease resistance that can be achieved by conventional breeding methods, it is likely that plants with improved resistance to specific diseases will be developed by transforming plants with specific genes. Improved disease resistance may be among the first uses of molecular genetics in forage plant improvement. In general, improvements in disease resistance will likely result in improved forage digestibility.

Endophytes

Animal disorders caused by livestock feeding on endophyte (*Acremonium coenophialum* Morgan Jones and Gams)-infected fescue and ryegrass results in major economic losses in many temperate areas of the world. In the USA alone, over 95% of the 12 million plus hectares of tall fescue is endophyte-infected (Shelby and Dalrymple, 1987). Several reviews on the endophyte and the consequences of its association with tall fescue have been published recently (Studemann and Hoveland, 1988; Pedersen et al., 1990; Bacon, 1993; Clay, 1993; Hoveland, 1993; Schmidt and Osborn, 1993) and, consequently, we will address the problem only from the viewpoint of breeding tall fescue with improved forage quality.

Alkaloids produced in endophyte-infected plants produce three major types of animal disorders, fescue foot, bovine fat necrosis, and fescue toxicosis, when consumed by livestock. Endophyte-free tall fescue can be developed since the disease is only transmitted through the seed and breeding stock free of the endophyte can be obtained by using old seed or with seed treatments. However, endophyte-infected tall fescue has several important agronomic advantages over uninfected tall fescue (Pedersen et al., 1990). Endophyte infection improves seedling performance and survival, is associated with insect and nematode resistance, improves nitrogen assimilation, and improves seed set. Survival of infected fescue is probably higher than that of endophyte free fescue, especially in drought or heat-stressed environments.

Breeders would like to keep the desirable aspects of endophyte infection but eliminate the undesirable aspects. Evidence indicates that different associations of endophytes in different fescue genotypes results in different levels of alkaloids being produced (Siegel et al., 1987; Hill et al., 1991). The alkaloids that have been extracted from infected tall fescue differ in their toxicity to ruminants and insects (Siegel et al., 1987). It may be possible to develop endophyte-plant combinations that produce alkaloids that provide resistance to insects and nematodes but do not produce alkaloids that are

toxic to ruminants. This will require research on the genetics of the endophyte and its interaction with the host plant. Integrated research teams of biochemists and fungal and plant geneticists using molecular genetic approaches will be necessary to develop the desired endophyte and fescue or ryegrass combinations. At the present time, an inadequate knowledge base of the interactions and the genetics of the interacting organisms prevents breeders from solving the endophyte problem other than eliminating it from ryegrasses and fescues intended for use as forages.

Although endophyte-related problems of fescue and ryegrass have received the most attention, endophytes are known to occur on other species. White (1987) examined 100 genera of grasses using herbarium collections and found typical endophyte mycelium in 22 species of 9 genera demonstrating that endophytes are widespread in the Poaceae. Some of the species in which the mycellium were found included *Elymus canadensis* L., *E. virginicus* L., *Stipa robusta* (Vasey) Scrib., *Bromus anomalus* Rupr., and *Digitaria insularis* (L.) Mez. The widespread distribution of endophytes and the economic value or cost of their association with grasses will make research on improving the desirable aspects of this association increasingly important.

Anti-quality Compounds

Plant toxins provide a competitive advantage to plants that is usually directed at protecting the plant from predation by insects or diseases, and usually poisoning of ruminants or other livestock is a secondary result of this defensive mechanism (Jones, 1981; Molyneux and Ralphs, 1992). Plant toxins usually seem to be directed toward insects (Molyneux and Ralphs, 1992). As an example, dhurrin [(S)-p-hydroxymandelonitrile β-D-glucopyranoside] is a secondary metabolic product in *Sorghum* and *Sorghastrum* spp. and yields hydrocyanic acid (HCN) when hydrolyzed. It is produced at a metabolic "cost" to the plant. Woodhead and Bernays (1978) reported a positive correlation between the HCN released when sorghum plants were bitten by *Locusta migratoria* L and the unpalatability of individual plants to the locust. Phenolic acids liberated from phenolic esters by enzymes during feeding also had a contributing deterrent effect (Woodhead and Bernays, 1978).

The toxic and antinutrient compounds synthesized by legumes and other forages can be categorized as alkaloids, amino acids, cyanogens, isoflavone and coumestran estrogenic principles, nitro compounds, protease inhibitors, phytohemagglutenins, saponins, selenium compounds, and tannins (Smolenski et al., 1981). Genetic variation has been found in forage species for many of the anti-quality compounds and breeders have been successful in developing cultivars with low levels of the anti-quality compounds. The forage of these improved cultivars is generally safe for livestock utilization.

Success stories include the development of reed canarygrass cultivars with reduced levels of deleterious alkaloids (Marten et al., 1981; Kalton et al., 1989a,b) and the development of 'Blanco' blue lupine (Forbes et al., 1964) which lacks the poisonous alkaloid found in blue lupine (*Lupinus angustifolius* L.). Blanco also has white flowers which distinguishes it from the toxic, blue-flowered lupine. Low coumarin cultivars and germplasm of sweetclover have

been released (Goplen, 1981; Gorz et al., 1992). Sudangrasses with decreased potential for prussic acid poisoning have been developed and released (Haskins et al., 1990). In each of these species, the genetic changes were achieved by using genes from within the species or related species.

Breeding to reduce the bloat potential of forages such as alfalfa or white clover to date has been unsuccessful. The substances in these plants that cause bloat in ruminants have not been clearly determined although several substances including saponins and proteins and structural components such as chloroplast membranes have been implicated (Howarth et al., 1986). Breeders lack definitive selection criteria for bloat. Until the causes of bloat are clearly delineated, forage breeders will not be able to successfully address this problem.

The anti-quality compounds that are found in forages are the products of specific pathways that have been characterized in many species. Using molecular genetic approaches to blocking those pathways using anti-sense genes or other "blocking" genes appears to be a highly effective means of developing forages with reduced or zero levels of anti-quality compounds. Since most of these compounds are not necessary for growth or development, blocking their synthesis may not affect forage yield or other agronomic traits. Molecular genetic approaches may eliminate the need to screen extensive germplasm arrays using conventional breeding methods for genes that reduce anti-quality compounds in forages.

CONCLUSIONS

Breeding improved perennial forages with improved forage quality and forage yield requires long-term investments in sustained research. It has been clearly demonstrated in both cool and warm-season species that forage quality can be significantly improved by breeding if the breeder is committed to improving forage quality and works with cooperative teams of agronomists and animal scientists. However, to date, only a limited number of cultivars have been developed and released with improved forage quality. These cultivars have demonstrated that improvements in forage quality usually result in greater improvement in forage profitability than similar improvements in forage yield. Breeders have the selection methods and breeding tools to make significant improvements in the quality of all forage plants.

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