



CHAPTER 15

Breeding for Increased Forage Quality

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Figure 1. A spaced-plant nursery of meadow brome grass ready for harvesting samples at a uniform leafy growth stage. Each 5x5 group of plants is a subset from which the best single plant will be selected.

Forage crops have a large number of benefits to society, including ecosystem services such as soil and water conservation, wildlife habitat and diversification of the agricultural landscape. However, their principal function can only be realized when they are processed through livestock to produce meat, milk or other animal products. This is an inherently inefficient process, because much of the energy that is locked up in forage plants is lost during the conversion of forage to animal products. These losses occur in the form of manure, urine, metabolic inefficiencies and processing losses. Since the 1960s, plant breeders have been working to reduce the losses associated with manure and urine, largely by selecting plants and varieties with improved forage quality.

How do we breed forage crops?

Genetic variation is the foundation of forage breeding. Plants vary — they are not all the same, even though they might look the same to the naked eye. Some of this variation is due to effects of the environment (imagine a nice

bluegrass, ryegrass or fescue lawn, then imagine what it would look like if you quit mowing it — that's an environmental or management effect). Other variation among plants is genetic, due to the direct effects of genes and proteins in the plant. We plant breeders are often criticized for using highly idealized and uniform growing conditions for our breeding nurseries, but that's exactly how we work to reduce environmental effects. Our goal is to maximize the genetic differences among plants and minimize the environmental differences. This allows us to increase heritability of plant traits. Most plant traits are controlled by many genes with small effects and the environment can easily mask the effects of these genes.

Most plant breeding is done in spaced-plant nurseries in which individual plants can be observed and harvested. Nurseries are kept uniform by using constant growing conditions and management and by grouping plants into subsets that are more uniform, allowing us to choose the best plants within each subset. After making numerous observations and measurements, including field and laboratory

traits, we choose the best plants, perhaps only 10–20 plants out of several thousand, dig them up and transplant them to an isolated crossing block. Once the plants are crossed, the first generation of progeny becomes a candidate variety that can be used to establish a new selection nursery and can be evaluated for possible release to the public as a named variety.

Once a candidate variety has been tested in field trials at several locations and for several years, a decision is made regarding its performance relative to existing varieties. If it has demonstrated superior performance for one or more traits, it moves into seed multiplication and release. Seed multiplication generally requires three generations from the breeder's seed to certified seed. The breeder generally has only 100–500 g of initial seed and a small portion of that is used to establish a Breeder Seed block, which will generate 50–100 kg of Breeder's Seed. That seed is then turned over to a company or foundation seed organization for two more generations of increase: Foundation Seed and Certified Seed. Seed of most forage varieties is produced in specialized locations with environmental conditions that promote good seed production and easy harvesting and processing. A good seed producer, combined with a good environment and a good variety, is capable of increasing seed by 500–1000x in one generation.

What is forage quality?

To a livestock producer, forage quality is simply the animal-production potential of a forage. Because animal production is a function of both intake and digestibility, forage quality is also a function of these two characteristics. Increase either intake or digestibility of forages and the animal will consume more available energy that can be converted to animal products.

To a plant breeder, the answer to this question is more complicated, mainly because plant breeding is a numbers game. The more plants we evaluate, the faster we can make progress toward improved varieties. Thus, plant breeders need to be able to measure forage quality in a high-throughput manner (rapidly and cheaply). For example, a plant-breeding program heavily focused on improving forage quality of a cool-season grass or legume will typically process between 20,000–25,000 forage samples per year. Using current technologies, this involves harvesting samples, drying under uniform conditions, grinding to a uniform particle size, scanning samples using near infrared spectroscopy (NIRS) and selecting the best plants from the NIRS data.

To operate on such a scale requires the use of surrogate traits to predict forage quality of individual plants and



Figure 2. Many breeders use other species as competitors in their selection nurseries, illustrated with alfalfa plants undergoing selection in a fine-fescue sod. Photo by Heathcliffe Riday.

breeding lines. Such a trait must have several fundamental characteristics: a high correlation with animal performance, a highly repeatable laboratory estimation method, stability or repeatability in the field (e.g. consistency), and a moderate to high heritability. The last criterion provides the plant breeder with assurance that this trait can actually be improved by breeding. *In vitro* digestibility, measured in a test tube using rumen microbes, is by far the most common trait that has been used to improve forage quality. Other traits that have been used by plant breeders include: crude protein, neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin, and water-soluble carbohydrates (WSC).

Breeding for quality: decisions and logistics

Numerous decisions must be made in the process of developing new varieties with increased forage quality. The first of these is the central objective — do we wish to improve intake potential or digestibility or (the Holy Grail) both? Typically, the input for this decision would originate from discussions and collaborations between plant breeders and animal scientists, an absolutely essential partnership in this venture. Plant breeders know how to grow, evaluate, and manipulate plants, but they must rely on counsel and advice from animal scientists to predict the best traits for evaluation, selection and breeding.

The choice of starting germplasm is also critical. This begins with a definition of the target region for production of the new variety. Once that geographic region is defined, the breeder will assemble germplasm from existing varieties, plant introductions from outside the region and from existing breeding lines, to create populations of plants for evaluation.

The evaluation of forage plants for quality has become

highly streamlined with improved methods and technologies. Plant breeders have the luxury of selecting the best plants from nearly any population for nearly any forage-quality trait in their toolbox. The standard method consists of germinating seeds in the greenhouse during winter and transplanting seedlings to a field nursery as early as possible in spring. These are generally what we call ‘spaced-plant nurseries’ that consist of thousands of plants, spaced a regular distance apart in bare soil (Fig. 1). Sometimes, the bare soil is planted to a morphologically distinct species (e.g. fine fescues for an alfalfa nursery) to provide some level of competition to the plants (Fig. 2).

Once the plants are established and growing uniformly, they can be sampled when their growth stage is representative of the target use for the variety. For example, if the variety is intended for hay or silage production when 50% of the production will come at first harvest, the breeder probably will delay the first quality evaluation until spring of the next year, when the plants are at this growth stage. Alternatively, if the variety is intended for pasture or grazing, sampling for forage-quality measurement can begin during a regrowth period of the establishment year. Three key research findings, validated on several species, reaffirm the validity of these methods:

- ▶ Forage quality measured on widely spaced plants without competition is highly correlated with forage quality measured on sward plots with competition. While the absolute values will be different the ranking of different genotypes generally does not vary. This is sweet frosting on the cake for a plant breeder.
- ▶ Forage quality of leaves and stems are highly correlated with each other within a harvest and both leaves and stems tend to be highly correlated across harvests. These principles allow the plant breeder to select the best plants based on one or two harvests within a single year, rather than many over many years, speeding up the breeding process.
- ▶ If a forage-quality trait has moderate to high heritability, the progeny of superior plants will breed sufficiently true that an increase in forage quality will be realized not only at the location where the breeding took place, but at all locations throughout the region of adaptation for the variety (Fig. 3). This principle allows the plant breeder to focus selection and breeding efforts for forage-quality traits at a single location, greatly simplifying the program and maximizing gain per unit cost.

Breeders must take absolute care in harvesting and processing samples to ensure uniform treatment, so that as much of the variability that is measured is due to genetic differences and not to other factors that could have been controlled. This involves the use of sophisticated planting designs, sampling schemes and statistical analyses to help control the high levels of environmental variation that occur for most forage-quality traits. For example, because nearly all forage quality traits vary diurnally, changing by as much as 25% within each day’s photosynthetic cycle, we use a simple rule in our breeding program: selection must be made within genotypes that are harvested within 30 minutes of each other. This is where some of the statistical methods come into play, using numbers and computers to account for the diurnal variation that occurs when it takes us 8–10 hours to harvest 2000 samples for forage-quality analysis.

The next step is currently the biggest bottleneck in breeding for increased forage quality. We currently process samples by grinding and scanning with NIRS, then use predictive equations from the scans to predict digestibility, protein, NDF or whatever trait we want to use for selection. In Europe, advancements in NIRS optics have allowed breeders to install NIRS units on a Haldrup harvester and they use these to routinely scan harvested samples from plots. This technology has yet to be adapted to large-scale spaced-plantings of 2000–5000 plants. Rather, we are currently testing a hand-held NIRS unit to scan individual intact leaves to predict forage-quality traits on thousands of plants. If this method is successful, it will reduce the cost per sample by over 50%, eliminating thousands of person-hours of grinding and scanning during the winter.

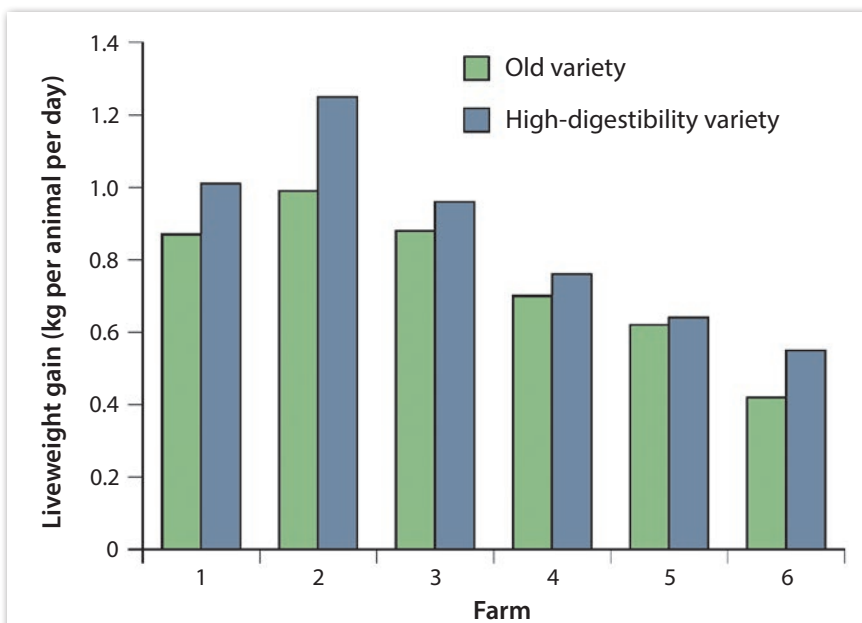


Figure 3. Consistent superiority of an improved perennial ryegrass variety compared to an older variety when evaluated on six working beef farms in the UK (Walters 1984).

Table 1. Reducing alkaloid levels in reed canarygrass has a significant positive impact on animal weight gains and health (Marten et al. 1976; 1981).

Variety	Lamb gains <i>g/animal/day</i>	Steer gains <i>g/animal/day</i>	Diarrhea incidence %
High alkaloids	51	140	20
Low alkaloids	108	330	1

Benefits of increased quality

Most of the documented benefits from tried-and-true varieties with improved quality originate in the warm-season grasses. This is partly because the low inherent quality of warm-season grasses makes it easier to make improvements and to measure those improvements, and partly due to the fact that some of the early and longest-running efforts were initiated on warm-season grasses.

Even so, new varieties with improved quality have been documented and adopted in several cool-season forage species, including alfalfa, perennial ryegrass, Italian ryegrass, smooth bromegrass, orchardgrass, tall fescue and intermediate wheatgrass. Generally, a 1% increase in digestibility has resulted in a 3.2% increase in average daily weight gains of heifers or steers. Having these numbers to present is a direct result of collaborations between plant breeders and animal scientists, again pointing out the critical nature of these partnerships.

Many plants have chemical compounds called alkaloids, which inhibit intake and cause numerous health issues with livestock. Reed canarygrass has several naturally occurring alkaloids, several of which have been removed by plant breeders, screening and searching for those plants that contain beneficial alkaloids, but not the highly toxic alkaloids. These activities resulted in transformation of a highly toxic grass to one that is highly valued in rotational grazing systems (Table 1).

Pitfalls of increased quality


There are limits to which forage quality can be increased without having negative consequences on yield, survival and stress tolerance of forage plants. A very prominent example of this is the brown-midrib traits of maize, sorghum and pearl millet. This trait was first discovered about 100 years ago in a maize nursery. During that time, brown-midrib populations have undergone many generations of breeding and selection, with especially intensive efforts since the early 1970s. Despite these efforts, there seems to be a forage-yield ceiling on even the best brown-midrib lines that are consistently penalized by 5–10%. The brown-midrib trait arises from mutations to genes that help synthesize lignin, a key component to building plant cell walls, which are especially significant and prominent in stems. These immovable yield reductions point to lignin as having a key and unalterable role in the basic metabolism of forage plant

growth and development.

Early work on genetically modified (GMO) forage crops resulted in similar types of plants that were largely stunted and very low in vigor. However, recent advances in understanding exactly how lignin is created in plants, and the individual role of each enzyme and gene, have led to solutions to this problem. Recent results have indicated that individual genes can be targeted for “down-regulation” to reduce their activity and, hence, reduce lignin content of forages without sacrificing forage yield or vigor. There are still many significant barriers to legal de-regulation, commercial release and public acceptance of varieties created by these technologies. Low-lignin alfalfa, created by GMO technologies, has been sufficiently tested that it will likely move into the public arena for de-regulation and release in the near future.

Even traditional efforts to breed for increased forage quality can be associated with some significant pitfalls. Forage plants selected for increased digestibility are typically lower in lignin content, often the principle mechanism for increasing quality by breeding and genetics. In many cases, these materials have suffered from increased insect predation, because lignin is a key component in a plant’s inherent resistance to chewing and boring insects. Increased susceptibility to winter injury has also been reported in some cases. In many cases, breeders have solved these problems with additional selection efforts for agronomic traits, but some of these problems have persisted for many generations of selection, severely complicating the breeding process.

Conclusion

With concerted and dedicated efforts, breeders can improve forage-quality traits of forage crops. Results from livestock trials are sufficiently numerous and consistent that we have a high degree of confidence in the relevance of increases in forage digestibility and its impact on animal performance. Continued progress will be dependent on continued funding for forage breeding research and on breeders’ innovative and imaginative approaches to solving barriers such as yield drag associated with increased quality. 

References available online at www.farmwest.com

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