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Breeding Grasses for the Future

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Breeding Grasses for the Future

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ABSTRACT

Plant breeding, including grass breeding, involves taking a raw product, plant germplasm, and improving or adding value to that germplasm by manipulating its genetic composition. The value added to the germplasm has a cost. It usually costs in excess of $100 000/yr to maintain a viable, ongoing grass breeding program. The output of a grass breeding program, i.e., the released cultivars and germplasm, should have an economic value in excess of the cost of the breeding program. Grass breeding programs have produced products such as 'Coastal' bermudagrass [Cynodon dactylon (L.) Pers.] where the economic value has greatly exceeded the input cost. Grass breeders have the opportunity to make additional major contributions to the welfare and benefit of future generations of humanity if research goals are carefully delineated and innovative, cost-effective breeding methods are used.

Plant breeders take a raw product, plant germplasm, and by genetic manipulations produce products such as cultivars that are of increased value to humanity. Hence, plant breeding can be described as human-directed evolution. The process is analogous to manufacturing in which raw materials are transformed into items that are of increased value by the manufacturing process. In each instance, value is added to the raw material by the breeding or manufacturing process. This improved value fulfills specific needs of humanity. Cultivars and other products of plant breeding must fulfill specific needs of society if they are to have any value.

The value that is added to germplasm in the breeding process occurs in incremental steps. A superior grass genotype or plant growing on the plains of Africa has value only to the owner of the cow (Bos taurus) that may graze it once or twice a year or to a wild herbivore. Although it has intrinsic value, its economic value is limited. If this plant is collected, increased, evaluated, used as a source of desirable genes in a breeding program, production tested, increased and released as a cultivar that is planted on millions of acres, its...
value is greatly multiplied. This procedure was basically used in the development of ‘Coastal’ bermudagrass [Cynodon dactylon (L.) Pers.] that is planted on millions of acres in the southern USA and that has added billions of dollars to the economy of this and other countries (see Chapter 3 in this book). Similar examples could be given for many other grasses. Each step in this breeding procedure (Fig. 7-1) adds value to the germplasm. As in the example above, uncollected germplasm has little economic value; it has value to humanity only after it has been collected and its attributes are known.

Each step in the development of an improved cultivar adds value, but the value added has a cost just as in manufacturing. Each step requires trained personnel, equipment, and facilities. In many grass breeding programs, the breeders may be involved in all aspects of cultivar development that are illustrated in Fig. 7-1. Although each step in the breeding procedure adds benefits and has a cost, the value added does not directly benefit humanity nor is there any return on the “investment” until an improved cultivar is released and used.

GERMPLASM
↓
$↓
↓
COLLECTION
↓
$↓
↓
EVALUATION
↓
$↓
↓
ENHANCEMENT
↓
$↓
↓
BREEDING
↓
$↓
↓
PRODUCTION TESTING
↓
$↓
↓
CULTIVAR INCREASE AND RELEASE
↓
$↓
↓
UTILIZATION

Fig. 7-1. Steps in the development and release of a forage or turf cultivar.
Grass breeders have developed cultivars that have greatly benefitted humanity and for which the economic value of the cultivar has greatly exceeded the development cost (see Chapters 2, 3, 4, and 5 in this book). The future of grass breeding depends upon the capability of grass breeders to continue to develop products or cultivars whose value greatly exceeds the investment cost. In general, it costs a minimum of $100,000/yr to maintain an ongoing grass breeding program. Since most turf and forage grasses are perennials that require extended periods for breeding and evaluation, a minimum period of 10 yr is usually required to develop a new cultivar. Thus, a new grass cultivar may represent an investment in excess of one million dollars. Its value to society and the public institution or private firm that developed it must exceed this cost. We recognize that public breeding programs also involve the training of professionals and the publication of research results that add to the information pool, but the economic impact of these products is difficult to assess. In this report, we will identify breeding objectives and appropriate breeding procedures for turf and forage grasses that in our opinion can have substantial economic impact. We have not attempted a comprehensive review of the literature, but rather have chosen specific papers that we have used to illustrate a point. We will also discuss selection, evaluation, and breeding methods that in our opinion have the most potential for making significant gains by breeding.

**FUTURE BREEDING OBJECTIVES WITH POTENTIAL ECONOMIC IMPACT**

Turf and forage grass breeders attempt to improve one or more plant attributes in their breeding programs. The principal attributes and the potential benefits that can be obtained by improving these attributes are as follows.

**Establishment**

Rapid and reliable establishment is critical to the economic culture of turf and forage grasses. Seedling establishment can be improved by either improving the establishment capability of the plants by breeding or by modifying the environment with cultural practices. The primary causes of poor establishment are the related factors of moisture stress and weed competition. Breeding for improved seedling vigor can result in seedlings that develop rapidly and that are effective competitors with weeds for available moisture. Factors that affect seedling vigor are seed size, seed quality, germination rate, emergence rate, relative growth rates, and other physiological processes (McKell, 1972). In virtually all the studies that have been done to date, seed size or weight has been an important component of seedling establishment capability (Asay & Johnson, 1987; Voight et al., 1987). For example, in sand bluestem [Andropogon gerardii var. Paucipilus (Nash) Fern.], 50% of the genetic variability for seedling weight 8 wk after emergence was due to differences in seed size, while the remainder of the genetic variability was due to
other factors (Glewen & Vogel, 1984). Many physiological processes are involved in seedling establishment. Seedling weight at a fixed time following seeding is a simple method of quantifying the end result of these processes and making selections (Asay & Johnson, 1987; Voight et al., 1987). Selections for seedling size or weight are inexpensive and effective methods of improving vigor. In most forage and turfgrasses, improvements in establishment capability by breeding for seedling vigor will require long-term breeding efforts. Most forage and turfgrasses are perennials and their main competitors at establishment are annual weeds, many of which excel in seedling vigor.

Breeding for mechanisms that permit effective weed control can be an effective method of improving establishment capability. Atrazine [2-chloro-4-ethylamino-6-isopropylamino-1,3,5-triazine] can be used as a preemergence herbicide for the establishment of big bluestem [Andropogon gerardii Vitman] and switchgrass (Panicum virgatum L.) (Martin et al., 1982). Preemergence atrazine applications can reduce the seeding rate needed for the establishment of satisfactory stands of these grasses with a net savings in cost of seed of $35 to $148/ha (Table 7-1), and can result in increased forage production in the establishment year with a net value of more than $220/ha (Table 7-2). Big bluestem and switchgrass are the only two forage grasses

Table 7-1. Seeding rates and costs for establishing big bluestem and switchgrass with preemergence atrazine application (2.2 kg ha\(^{-1}\)).

<table>
<thead>
<tr>
<th>Seeding rate</th>
<th>Stand</th>
<th>Seeding rate</th>
<th>Cost</th>
<th>Stand</th>
<th>Seeding rate</th>
<th>Cost</th>
</tr>
</thead>
<tbody>
<tr>
<td>seed m(^{-2})</td>
<td>%</td>
<td>kg ha(^{-1})</td>
<td>$ ha(^{-1})</td>
<td>%</td>
<td>kg ha(^{-1})</td>
<td>$ ha(^{-1})</td>
</tr>
<tr>
<td>215</td>
<td>66</td>
<td>3.4</td>
<td>75</td>
<td>69</td>
<td>6.7</td>
<td>147</td>
</tr>
<tr>
<td>325</td>
<td>71</td>
<td>5.0</td>
<td>110</td>
<td>65</td>
<td>10.1</td>
<td>220</td>
</tr>
<tr>
<td>430</td>
<td>70</td>
<td>6.7</td>
<td>147</td>
<td>78</td>
<td>13.4</td>
<td>295</td>
</tr>
<tr>
<td>F value</td>
<td>NS</td>
<td></td>
<td></td>
<td>NS</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

† Data except for costs are from Vogel (1987).
‡ Seed costs estimated at $22 kg\(^{-1}\) ($10 lb\(^{-1}\)) for both grasses.

Table 7-2. Effect of preemergence atrazine applications on yield and net return of big bluestem and switchgrass at Mead, NE. Forage yields are from Martin et al. (1982).

<table>
<thead>
<tr>
<th>Grass</th>
<th>Atrazine kg ha(^{-1})</th>
<th>Yr 1</th>
<th>Yr 2</th>
<th>Yr 1</th>
<th>Yr 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mg ha(^{-1})</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Big bluestem</td>
<td>0</td>
<td>0.8</td>
<td>7.1</td>
<td>40</td>
<td>355</td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>7.2</td>
<td>9.1</td>
<td>340</td>
<td>455</td>
</tr>
<tr>
<td>Switchgrass</td>
<td>0</td>
<td>0</td>
<td>9.0</td>
<td>0</td>
<td>450</td>
</tr>
<tr>
<td></td>
<td>2.2</td>
<td>5.4</td>
<td>11.3</td>
<td>250</td>
<td>565</td>
</tr>
</tbody>
</table>

† Years 1 and 2 are the year of establishment and the year following establishment, respectively.
‡ Based on a hay value of $50 Mg\(^{-1}\) and an atrazine cost of $20 ha\(^{-1}\).
for which a preemergence herbicide is labeled for use. The atrazine tolerance of these grasses has a potential value in excess of 100 million dollars because of the reduced seeding costs and increased establishment-year forage yields that can be achieved if atrazine is used as a preemergence herbicide. Breeding for herbicide tolerance in other grasses by using either conventional or "genetic engineering" techniques could have a similar impact. Breeding for herbicide tolerance may result in greater improvement in establishment than breeding for seedling vigor or seed size.

Persistence

Breeding for persistence is a worthwhile objective since the annual cost of establishment and the subsequent loss of production and use equals the establishment costs divided by N, where N is the number of years the stand persists. Grass breeders traditionally have selected for persistence by first making selections among species for adaptation to the target environment and cultural conditions (Hanson & Carnahan, 1956). Because of the large number of grasses that were available, it was usually easier to select at the species level for a particular ecological niche than to attempt to change the adaptability of a species by breeding. Breeders found adapted germplasm in either native species or in introduced species from areas that were approximate climatic analogues of the target environment. They have subsequently conducted breeding work to improve disease and insect resistance because of the effect these factors have on persistence. Increased knowledge of the physiological processes that affect persistence has enabled breeders to devise screening procedures that can aid in selecting for persistence. However, there are no short cuts in breeding for persistence; extended testing in realistic stress situations is required.

Disease and Insect Resistance

Diseases affect turf and forage grass persistence, quality, yield, and utilization. Turfgrass diseases directly affect every homeowner in the USA who has a lawn. Control of turf diseases is a multi-million dollar a year business that helps to support a growing proliferation of lawn and garden stores and professional turf maintenance services. Diseases of forage grasses also affect everyone, except strict vegetarians, by their effect on forage yields and quality which directly affect animal production of meat and milk. Grass breeders have made significant improvements in the disease tolerance and resistance of turf and forage grasses. Virtually every improved 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 turf and forage grasses. Genetic sources of resistance have been reported for almost every disease of economically important cool-season grasses (Braverman, 1986). A similar situation probably exists in warm-season grasses. Breeding for disease resistance should be an integral part of every grass breeding program. In the perennial grass breeding program at Lincoln, NE, we con-
tinually apply selection pressure for disease resistance, generation after generation. More structured programs may be needed for severe disease problems, in which case a plant pathologist should be an integral part of the breeding team. When new, disease-resistant cultivars are developed, breeders need to document the economic benefits to homeowners or forage producers in terms that a layman can readily understand.

Insects also have a major impact on turf and forage grasses. In Lincoln, homeowners have to spend from $30 to $50 per year for insect control if they want to have an acceptable bluegrass (*Poa pratensis* L.) lawn. Damage by other insects such as the *Labops* spp. on wheatgrasses also can produce tremendous economic losses (Campbell et al., 1984). Genetic sources for insect tolerance or resistance have been identified for important turf and forage insect pests (Stimman & Taliaferro, 1969; Asay et al., 1983; Campbell et al., 1984). Recent reports (Funk et al., 1983; Johnson et al., 1985; Clay et al., 1985) demonstrate that fescue (*Festuca* spp.) and ryegrass (*Lolium* spp.) endophytes (*Acremonium* spp.) confer broad-spectrum insect resistance to grasses they infest. These endophytes will reduce the economic losses to turf insects by billions of dollars per year once they have been incorporated into fescue, ryegrass, and possibly other grasses that are widely used for turf. Breeding for insect resistance can have significant economic benefit and the use of resistant cultivars is ecologically more desirable than using insecticides for insect control.

**Seed Yield**

Considerable effort has been and is being expended to improve the seed yield of forage and turf grasses. Except for specific instances where poor seed yields are preventing the use of an otherwise valuable grass, we do not believe that this effort is warranted. Seed yields for grasses are lower than for grain crops, but the number of hectares of forage crops for use as pastures or harvested forage that can be seeded from each seed production hectare is often greater for grasses than for grain crops (Table 7–3). At present prices, the per hectare value of the seed produced on most grass seed fields is greater than the per hectare value of seed produced from certified grain crops, and

<table>
<thead>
<tr>
<th>Crop</th>
<th>Seed yield</th>
<th>Production field or pasture</th>
<th>Seed yield/ seeding rate ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Seed yield</td>
<td>Value</td>
<td>Seeding rate</td>
</tr>
<tr>
<td>Tall fescue</td>
<td>600</td>
<td>1320</td>
<td>12</td>
</tr>
<tr>
<td>Switchgrass</td>
<td>400</td>
<td>7040</td>
<td>3.5</td>
</tr>
<tr>
<td>Wheat</td>
<td>2700</td>
<td>520</td>
<td>67</td>
</tr>
<tr>
<td>Soybean</td>
<td>2700</td>
<td>832</td>
<td>67</td>
</tr>
</tbody>
</table>

† Average yields and current prices in principal areas of production are listed. Grass stands were assumed to persist for 10 yr.
the cost of establishing pastures or other forage crops is less than that of grain fields when amortized over years (Table 7-3). Grass seed costs are currently high because of the Conservation Reserve Program, but even if they were half of their present price, grass seed production would still be economical for growers. Since seed is not the principal product of these grasses and since seed yields of most grasses are adequate in general, it does not seem reasonable to routinely breed for improved seed yields. There are instances, however, in which breeding for seed yield can improve the use of a grass; for example, the development of cultivars with reduced seed shattering in reed canarygrass [*Phalaris arundinacea* L.] (R.R. Kalton, 1987, personal communication), and the discovery of a mutant in eastern gamagrass [*Tripsacum dactyloides* (L.) L.] that increases seed yield 20- to 25-fold (Dewald & Dayton, 1985). In each of these examples, a specific problem that was limiting seed yield was solved and was worth the breeding effort expended.

### Forage Yield

Improving forage yield has always been one of the principal objectives of grass breeders. Recent reports document that forage yields can be significantly improved by breeding with substantial economic benefits (Table 7-4). Burton (1982, 1985) improved forage yield of bahiagrass (*Paspalum notatum* Fluegge) by direct selection for yield using Restricted Recurrent Phenotypic Selection. Nelson et al. (1985) improved forage yield of tall fescue (*Festuca arundinacea* Schreb.) by selection for leaf area expansion rate. These breeding efforts were successful because the breeders either selected directly for yield or for a trait that was correlated with yield, and they used recurrent selection methods that effectively exploited the additive genetic variability for the selected traits within the species. It should be possible to improve the yield of most forage grasses by using well-designed recurrent selection methods. Breeding for yield remains a valid research objective.

<table>
<thead>
<tr>
<th>Population</th>
<th>Forage yield</th>
<th>Gain/cycle</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>kg ha⁻¹</td>
<td>$ ha⁻¹</td>
</tr>
<tr>
<td>Bahiagrass (Burton, 1985)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pensacola commercial</td>
<td>5273</td>
<td>264</td>
</tr>
<tr>
<td>Pensacola RRPS Cycle 9</td>
<td>9241</td>
<td>462</td>
</tr>
<tr>
<td>Tall fescue† (Nelson et al., 1985)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Leaf area expansion C0</td>
<td>5130</td>
<td>256</td>
</tr>
<tr>
<td>High leaf area expansion C4</td>
<td>6274</td>
<td>314</td>
</tr>
</tbody>
</table>

† Yields are from references indicated. Hay value = $50 Mg⁻¹.
‡ Mt. Vernon data.
Forage Quality

Forage quality can be improved by breeding for enhanced positive quality factors such as digestibility or for reduced negative factors such as alkaloids (Burton, 1981; see Chapter 6 in this book). Significant gains have been made in improving digestibility that have resulted in improved animal performance (Anderson et al., 1988; Chapman et al., 1972). Reduction in the levels of undesirable alkaloids either by direct selection (Marten et al., 1976) or by eliminating endophytic fungi that are associated with undesirable alkaloids from the forage (Hoveland et al., 1983) has also resulted in significantly improved animal performance. Other examples could be given for both positive and negative quality factors. It should be possible to improve the forage quality of virtually every grass by using appropriate breeding procedures since genetic variability has been reported for both positive and negative quality factors in virtually every grass that has been studied (Burton, 1981). In addition, it should be possible to simultaneously improve both forage yield and quality since the correlations between these traits in most studies are either low or nonsignificant. In those instances when correlations have been negative, the correlation coefficients have been low. If a breeder must make a choice between breeding for yield or quality, he/she should select quality. Increased quality results in increased net return to a livestock producer and does not require any additional investment. Increased yield can increase net return but the producer must buy or raise additional livestock to use the additional forage.

Turf Quality

Turf quality is often an aesthetic criterion that is difficult to quantify and weigh in economic terms in a breeding program. It can be rated or ranked, but the rating is dependent upon the personal preference and skill of the person doing the ranking. Turf quality factors such as color, leaf size, leaf texture, tiller density, wear tolerance, absence of disease and insect damage are all under genetic control. Turf breeders have improved turf quality and we are confident that they will continue to do so since quality greatly influences acceptability.

Turf Maintenance Costs

Turf requires mowing, fertilization, and weed, disease, and insect control, and in many areas of the country, irrigation. All of these practices contribute to turf maintenance costs. Cockerham and Gilbeault (1985) have reported that for a hypothetical city of 170,000 located in a major urban area of the USA, there are 2500 ha of turf of which about 1400 ha are accounted for by the lawns of approximately 45,000 homes. Homeowners will each spend more than $200 a year to maintain their lawns (Cockerham & Gilbeault, 1985). The remaining turf is for apartments, parks, churches, golf courses, cemeteries, businesses, and industrial sites. Development of turf-
grasses with disease and insect resistance, slow growth rate that reduces the number of mowings, and reduced fertilizer requirements can reduce maintenance costs. If improved turf cultivars were developed that could reduce maintenance costs by 25%, the savings to home-owners alone in this hypothetical city would be in excess of 2.2 million dollars a year. A city of this size, such as Lincoln, NE could probably afford to have its own turf breeding program because of the potential savings such a program could provide its citizens.

In the western half of the USA where it is necessary to irrigate lawns, improving the water-use efficiency of turfgrasses can also greatly reduce maintenance costs and also the cost of maintaining extensive water systems. The city of Thornton, CO (population 57,000), a suburb of Denver, has spent 52 million dollars to buy farms and their water rights from an area near Fort Collins with the intention of piping this water 80 km south to Thornton (Flanery, 1987). The city of Denver and its suburbs are proposing to build a $500 million dam on the South Platte River to meet the area’s future water needs (Flanery, 1987). There is substantial genetic variability among turfgrasses for water-use efficiency as measured by evapotranspiration rates (Beard, 1985; Shearman, 1986). It is reasonable to assume that developing grasses that require less water to maintain a functional and attractive turf could save cities and their citizens substantial amounts of money, particularly in the arid and semiarid western states. These states and even individual cities should consider funding or increasing the funding of turfgrass breeding programs.

**IMPROVED METHODS FOR SELECTION AND EVALUATION**

Selection is the component of the breeding process that usually determines the success or failure of a program. The other major component of the process, mating the selected plants, usually is done in a routine manner. Selection of the plants to be mated is the critical component of the breeding process.

**Selection for Physiological Traits**

Breeders can improve a quantitatively inherited trait such as yield by either direct selection for the trait or by indirect selection for component physiological processes. Plant physiologists have identified and described physiological processes such as photosynthetic rate, light interception ability, respiration, photosynthate partitioning, evapotranspiration rate, and others that determine traits such as yield. Instrumentation has been developed that enables breeders to measure and select directly for these physiological processes. In general, breeding for physiological processes is expensive and time consuming, and it has not been as successful as direct selection for the trait itself (Asay & Johnson, 1983; Kube et al., 1989). Breeding for physiological traits has not been as successful as direct selection because usually only one or two
physiological parameters have been measured and used to make selections while numerous processes are involved in a complex trait such as yield. The lack of success can also be explained by examining equations for predicting gain from selection (Falconer, 1981).

\[ G_x = i \ h_x \ \sigma_{ax} \]  

\[ CG_x = i \ h_y \ r_{xy} \ \sigma_{ax} \]  

\[ CG_x = G_x \text{ if } [(h_y r_{xy})/h_x] > 1 \]

where \( G \) is the expected gain from selection for traits \( x \) or \( y \) (subscripts); \( CG_x \) is a correlated response in \( x \) due to selection for \( y \); \( i \) is the selection intensity; \( h \) is the square root of heritability, \( \sigma_a \) is the square root of additive genetic variability for trait \( x \) or \( y \) (subscripts) and \( r_{xy} \) is the genetic correlation between traits \( x \) and \( y \). Equation [1] gives the expected gain for direct selection for a trait such as yield \((x)\) while Eq. [2] gives the expected gain for a trait such as yield \((x)\) when selecting for another trait such as photosynthetic rate \((y)\). Comparing Eq. [1] and [2] as a ratio (Eq. [3]) indicates that indirect selection can be as effective as direct selection only if \( h_y \) for the physiological trait is at least 25% larger than that of \( h_x \) and the genetic correlation is 0.8 or larger. This usually does not occur and hence direct selection is more efficient. Physiological studies have been extremely helpful, however, by providing information that has enabled breeders to modify or alter the selection environment so as to provide maximum differentiation between genotypes. A practical example is the use of irrigation gradients to select for drought tolerance.

**Selection for Plant Composition**

The development of instruments and associated software and procedures for such methodology as near infrared reflectance spectroscopy (NIRS), high performance liquid chromatography (HPLC), gas chromatography, ion chromatography, and other procedures has greatly expanded the capability of both turf and forage grass breeders to select for specific plant composition and constituents. The objectives of turf and forage breeders are often diametrically opposite. For example, turf breeders may want high fiber content because it improves wear tolerance (Shearman & Beard, 1975) while forage breeders want low fiber content because it is associated with improved digestibility. It is probably true that regardless of the specific plant constituent a breeder wants to measure and select for or against, analytical equipment is now available for the necessary analyses. These analyses, however, are not cheap because the equipment is expensive to purchase, maintain, and operate.

Breeders usually need to be able to rank genotypes for a particular plant constituent, and precise analytical values are usually unnecessary if the rankings are adequate. It may be possible to reduce the analytical costs for breeder samples by modifying the procedures so that they adequately rank the sam-
Table 7-5. Performance of beef yearlings grazing switchgrass at Mead, NE in 1982, 1983, and 1985 (3-yr means).†

<table>
<thead>
<tr>
<th>Strain</th>
<th>IVDMD</th>
<th>Available forage</th>
<th>Animal gain</th>
<th>Gross return‡</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>%</td>
<td>kg ha⁻¹</td>
<td></td>
<td>$ ha⁻¹</td>
</tr>
<tr>
<td>Trailblazer</td>
<td>58.0</td>
<td>3420</td>
<td>351</td>
<td>463</td>
</tr>
<tr>
<td>Pathfinder</td>
<td>56.2</td>
<td>3380</td>
<td>284</td>
<td>374</td>
</tr>
<tr>
<td>Low-IVDMD</td>
<td>55.5</td>
<td>3160</td>
<td>299</td>
<td>394</td>
</tr>
</tbody>
</table>

† IVDMD%, available forage, and animal gain values are from Anderson et al. (1988).‡ Gain was valued at $1.32/kg ($0.60/lb).

A forage cultivar has value only when it is used. Laboratory analyses can be used to breed cultivars with improved quality, but the results of laboratory analyses will not convince a farmer or rancher to plant a cultivar with improved digestibility. Actual animal performance data are needed that quantify the genetic gains in economic terms. In small plots, the new switchgrass cv. Trailblazer had forage yields similar to the cv. Pathfinder, but it differed in digestibility by 3 to 4 percentage units (Vogel et al., 1981, 1984). In replicated pasture trials with yearling steers, cattle grazing Trailblazer had higher total gains/ha which resulted in $89/ha ($35/acre) greater net return for the Trailblazer pastures than for the Pathfinder pastures (Table 7-5). Foundation and certified seed of Trailblazer has sold out every year since its release and it is obvious that the pasture and not the small plot data are responsible for its demand.

Selection for Nebulous Attributes

Traits such as tolerance to grazing and wear tolerance in turf are difficult to define, evaluate, and quantify. The only way that traits such as tolerance
Multiple Trait Selection

Direct selection for a single trait usually will result in the maximum gain from selection. Multiple trait selection adds to the challenge because the desired traits may have low or negative genetic correlations with one another. In general, grass breeders have made limited use of formal selection indexes based on quantitative genetic theory but have instead relied on informal subjective indexes. We believe that the use of selection indexes based on quantitative theory in which traits are weighted by realistic economic values will result in improved breeding efficiency. Considerable work needs to be done in determining economic values of traits. For example, at the present time we do not know what a unit of forage yield is worth in economic terms in comparison to a unit of digestibility for any forage grass.

CONVENTIONAL BREEDING PROCEDURES

The breeding system that a breeder uses determines the rate of gain from breeding, its cost, and the potential gain that can be made. Conventional grass breeding systems use additive and nonadditive genetic variability in plants with both sexual and apomictic reproductive mechanisms to make genetic gains.

Additive Genetic Variability

Almost all forage and turf grasses are cross-pollinated by wind. They have small florets that are difficult to emasculate, and effective mechanisms for producing hybrids such as cytoplasmic male-sterility (cms) have not been developed for most of these grasses. Thus, breeders are largely limited to procedures that use additive genetic variability and that do not require any emasculation. Fortunately, there is substantial additive genetic variability for most traits in grasses, and breeding methods that do not require emasculation are some of the most efficient that are available. The expected gain from selection that can be made by using the breeding procedures or schemes that have been developed to date are described by Empig et al. (1972), Nguyen and Sleper (1983), and Hallauer and Miranda (1981). In grass breeding programs, most of the available breeding procedures can result in breeding progress if the following guidelines are followed.

1. A productive population that possesses substantial genetic variability for the desired traits is used as the base population.
2. An adequate effective population size is maintained. The rate of in-breeding for wind-pollinated genotypes in an isolation is $1/2N$ where $N$ is
the number of selected genotypes being polycrossed. If \( N = 100 \), the rate of inbreeding is 0.5\% per cycle which is negligible. We consider effective population sizes of 50 (rate of inbreeding of 1\% per cycle) to be the minimum population size to use in a long-term program. The number of selection units, i.e., families or plants, needed in the selection nursery is \( N \) divided by the selection percentage expressed as a decimal fraction.

3. Recurrent selection procedures are used.

4. The selected traits are quantified with reasonable precision and environmental variation is adequately controlled.

The procedure that will give the best gains will be the one that uses the most additive genetic variability per cycle or per year. Restricted Recurrent Phenotypic Selection (Burton, 1974) has the potential to make the most gains per year of any breeding procedure if the trait can be adequately measured on an individual plant basis. However, the most efficient breeding procedure probably has not yet been developed.

**Nonadditive Genetic Variability**

Grass breeders in general have not capitalized on the nonadditive genetic variability that exists in forage grasses even though substantial heterosis for traits such as yield exists in many grasses. The inability to effectively emasculate large numbers of plants in seed production fields has limited grass breeders' ability to develop hybrids for commercial use. One breeder, Dr. Glenn Burton, has successfully produced hybrid cultivars by using a variety of techniques as summarized in a recent review (Burton, 1986). These techniques and their possible application to other grasses are as follows.

1. First-generation chance hybrids. Four inbred lines of pearl millet \([Pennisetum glaucum \text{ (L.) R. Br.}]\) that flowered at the same time were bulked and used to plant seed production fields. The seed harvested from the seed field contained 75\% hybrid seed of the six possible hybrids. Plots planted with this seed yielded as well as plots seeded with a mixture of the six controlled crosses because the more vigorous hybrids crowded out the less vigorous selfs and sibs (Burton, 1948). ‘Gahi 1’ pearl millet was released and used as a first generation hybrid until it was replaced by superior hybrids developed by using ems. This same procedure could be used for many other grasses. Since many grasses have high levels of self-incompatibility, lines based on sibs or families or even populations could be used in lieu of inbred lines.

2. Self-incompatibility hybrids. Many perennial grasses contain plants that are self-incompatible but that are cross-compatible with each other. If two plants are identified that produce superior \( F_1 \) hybrids, then the two plants can be vegetatively increased and transplanted into seed production fields. All the seed harvested from the field would be \( F_1 \)-hybrid seed assuming that proper isolation requirements were maintained. These seed fields could be maintained for many years for perennial grasses. Two bahiagrass hybrids were developed based on this procedure but were not successful because of the labor and cost of establishing seed production fields. Two recent developments should improve the economics of developing self-
incompatibility hybrids. Tissue culture techniques can improve the process of vegetatively increasing individual plants, and large scale increases of single plants are possible. Transplanting procedures have been mechanized to the extent that large commercial sugarbeet \textit{(Beta vulgaris L.)} fields are now being established with transplanted seedlings. Because of these developments, we believe that self-incompatibility hybrids of many perennial grasses could be commercially feasible.

3. Cytoplasmic male-sterile hybrids. Cytoplasmic male-sterility has been used to develop hybrids of many crops. Many desirable grasses are polyploids and in addition are self-incompatible which makes identifying and transferring maintainer and restorer genes into desirable germplasm difficult. Considerable effort by both public and private breeders has been expended to develop \textit{cms wheat \textit{(Triticum aestivum L.)}} hybrids with limited commercial success. It is doubtful that breeders of polyploid grasses could be successful in developing \textit{cms} hybrids since they will have fewer resources. Cytoplasmic male sterility may be a useful breeding procedure to produce hybrids for diploid grasses, however.

4. Apomictic hybrids. Many grasses including bahiagrass, buffelgrass \textit{(Cenchrus ciliaris L.)} and Kentucky bluegrass \textit{(Poa pratensis L.)} produce seed by apomictic mechanisms. Basic genetic studies in these grasses have provided breeders with information that allows them to make sexual crosses that produce \textit{F\textsubscript{1}} apomictic progeny \textit{(Hanna & Bashaw, 1987)}. Superior plants can be identified and once identified can be multiplied by direct seed production without any loss of vigor or change in genotype. Apomictic hybrids such as Coastal bermudagrass can also be vegetatively propagated for commercial use. Apomictic mechanisms are the most economical way to produce hybrids, and breeders should be vigilant to developments and plants that will enable them to use apomixis in their breeding programs. Hanna and Bashaw \textit{(1987)} in a recent review describe methods for identifying apomictic plants, mechanisms for using apomixis in breeding programs, and possible new developments that could expand the use of apomixis.

We believe another method that has potential for producing hybrids is the use of male gametocides. Hybrid wheat cultivars have been marketed that were produced by using male gametocides to effectively emasculate the lines used as females. It seems reasonable that some of the compounds that have been tested and proven effective as gametocides on wheat may also be effective as gametocides on forage grasses such as the wheatgrasses. Since many of these gametocides are proprietary compounds, the necessary research would have to be done in conjunction with the appropriate firms that have ownership of the compounds.

\textbf{Production of Grass Hybrids—Summary}

The methods that have the best potential for producing commercial grass hybrids are the use of self-incompatibility, apomixis, and gametocides. The potential increase in forage yields that could be achieved by the production of hybrid seed for use on farms definitely warrants the allocation of some breeding resources for this objective.
CELL CULTURE AND MOLECULAR GENETICS TECHNIQUES

Grass breeders to date have used conventional breeding techniques to develop new cultivars. New technologies are now becoming available for breeders to greatly expand their capabilities to solve specific breeding problems. These technologies which we will refer to as cell culture and molecular genetics techniques must be used in conjunction with conventional breeding methods because their sole use would not result in the development and use of commercial cultivars.

Tissue Culture

Techniques to culture individual plant cells and to regenerate plants from these cells have been developed for many grasses and probably can be developed for any grass by modifying the appropriate "recipes". Tissue culture gives breeders the capability to rapidly and efficiently multiply individual plants that should make commercial self-incompatible hybrids feasible if somaclonal variation can be controlled. It also enables breeders to select and apply mutagenic treatments at the cellular level (Chaleff, 1983; Schweiger et al., 1987). Cell culture can result in increased genetic variability because of somaclonal variants that can be induced by the culturing process. Cell culture permits the screening of millions of individual cells for specific traits that can be assayed at the cellular level such as resistance to specific toxins or herbicides, but it does not permit selection for many agronomically desired traits that must be investigated at the whole plant level. Mutants produced at the cellular level can be regenerated and evaluated at the whole plant level, however. Recombinant DNA work probably will be done primarily in cell culture or cell suspension systems. Techniques have been developed that permit mass culturing of cells or the culturing of individual cells (Schweiger et al., 1987). Cell culture systems and procedures will be valuable tools of present and future grass breeders.

Molecular Genetics

Molecular genetics techniques as applied to plant breeding will be used primarily to transfer traits between plants that cannot be crossed by conventional procedures (Goodman et al., 1987; Barton & Brill, 1983). The progressive complexity of the breeding procedures needed to transfer genes between organisms is shown in Table 7-6. In 1983, Barton and Brill (1983) proposed

<table>
<thead>
<tr>
<th>Organism to plant transfer</th>
<th>Techniques used</th>
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<tr>
<td>Plant to plant, within species</td>
<td>Conventional breeding</td>
</tr>
<tr>
<td>Plant to plant, between species, within genera, within family</td>
<td>Conventional breeding + TLC†</td>
</tr>
<tr>
<td>Plant to plant, between genera, within family or tribe</td>
<td>Conventional breeding + TLC</td>
</tr>
<tr>
<td>Any organism to a plant</td>
<td>Molecular genetics + tissue culture</td>
</tr>
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</table>

† TLC = Tender loving care.
that these techniques could be used to breed for insect and pest resistance, modification of seed proteins, N₂ fixation, improved photosynthesis rates, and improved stress tolerance. Goodman et al. (1987) reported that genes for herbicide and insect resistance have been transferred from bacteria into plants and that genes encoding the protein coat of tobacco mosaic virus had been inserted into tobacco (Nicotiana tabacum L.) and tomato (Lycopersicum esculentum Mill.) resulting in increased resistance to the virus. In addition to giving the breeder the capability of transferring genes from dissimilar organisms, molecular genetics techniques permit the transfer of specific genes rather than whole blocks of genes.

Specific molecular genetics approaches that offer promise for gene transfer in plants are: transfer of genes by plasmids, gene transfer by viruses, uptake or insertion of purified DNA, protoplast fusion, and Agrobacterium-mediated gene transfer (Goodman et al., 1987; Cocking & Davey, 1987). These and yet to be developed techniques will be used to transfer and manipulate genes in grasses. Undoubtedly, these procedures will be used in the development of grasses with tolerance to specific herbicides, insects, and diseases. We do not expect all grass breeders to become molecular geneticists, but we do consider it vital for all grass breeders to become knowledgeable in the area of molecular genetics. This knowledge will allow breeders to cooperate with molecular geneticists to solve specific problems with this new technology.

SUMMARY

There are tremendous opportunities for grass breeders to make extremely valuable contributions to humanity in the future. Grass breeders must carefully define their objectives and select those that will have the most impact on society. They must then use the most cost effective breeding methods to develop improved cultivars that meet these objectives. They also must document the added value of the results of their breeding work in economic terms and that documentation should be provided in layman’s terms in order to “sell” the improved cultivars to the consuming public.

REFERENCES


BREEDING GRASSES FOR THE FUTURE


