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EVALUATION OF APPROACHES TO BREEDING FORAGES

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ABSTRACT

The approach to forage breeding will vary, depending on such factors as the environment in which the forage must grow, the germplasm available, the class of livestock it must feed, the rescources of the breeder, and his interests. Each forage breeder must develop the approach that will be best for him and will finally produce a forage that will improve the efficiency of the livestock industry. To do this, the breeder must try to improve one or more of the following forage characteristics: adaptation, dependability, pest resistance, stress tolerance, quality, and yield. This will require better screens for most of their traits than those presently available. These he must develop alone or with the help of specialists such as entomologists and plant pathologists. Commercial propagation methods will influence the breeding approach chosen. If the improved cultivar can be propagated vegetatively on the farm, we believe the approach that we used to improve bermudagrass, *Cynodon dactylon*, will be the best. For seed-propagated species, the breeder will probably choose one of the approaches described in this paper: developing synthetics, F_1 hybrids or apomictic cultivars, or improving populations that may become cultivars by mass selection or recurrent restricted phenotypic selection.

KEYWORDS

Mass selection, recurrent restricted phenotypic selection, cytoplasmic male-sterility, synthetic cultivars, apomixis, self-incompatability.

INTRODUCTION

The approaches to breeding forages are many. The molecular geneticist will study the DNA of the speies to be improved. The cytologist may look at genome relationships in wide crosses. The geneticist may make an understanding of the inheritance of quality his first objective. Cultivar creation may be of secondary importance as the university plant breeder tries to develop better breeding methods. The commercial breeder may have as his only concern the development of a better cultivar. Increasing the yield and improving the quality of an adapted forage will be the final objectives for each of them.

The approach that will best realise these objectives will be influenced by a number of factors. The environments in which the forage must grow, the class of livestock it must feed, the forages that must be improved, and the resources of the breeders, are four of them. Developing F_1 hybrids that may be best for areas where rainfall and soil fertility are good will not be the best approach for the arid range. Breeding forages for milking cows will place greater emphasis on quality than breeding for beef cattle. The reproductive habits of the forage and its weaknesses will determine the breeding method that may be used. The breeder with limited resources may be forced to develop synthetics rather than hybrids. Certainly the end product must satisfy the needs of the livestock industry at a cost that it can afford.

The remainder of this paper will present information that can help the forage breeder choose the best approach for him.

CHOICE OF SPECIES

The choice of the species to be improved is extremely important. Most species with forage potential may have been evaluated. Certainly the breeder will need to know all that is known about them. Questions about a forage for which he would like answers include: How good is it now?, What are its desirable traits and its weaknesses?, Are corrective genes available?, How difficult will it be to transfer them?, How good could it be? Research designed to answer some of these questions may be a profitable prelude to an extensive breeding programme.

FORAGE BREEDING OBJECTIVES

Dependability must be one of the major objectives of the forage breeder. Increasing the tolerance of forages to stresses such as drought and cold will improve their dependability. A forage that is killed by mismanagement or adverse weather will force its user to sell his animals at a loss or pay too much for replacement feeds.

Increasing land costs and alternate high income uses for land make high yield potential and high photosynthetic capacities important objectives for the forage breeder. Increased efficiency in the use of all growth factors (water, CO_2, light, temperature, and plant nutrients) must also be sought to make forages economically competitive with alternate crops.

Cultivar increase, distribution, and propagation must always be a major concern of the forage breeder. A forage that cannot be successfully and economically propagated on the farm will be of little value to the livestock industry.

Improving forage quality (digestibility, intake and/or animal utilisation) will usually improve the yield of animal product. Coastcross-1 bermudagrass, bred to be 12% more digestible than Coastal bermuda, gave 30% higher average daily gains (ADGs) and liveweight gain per acre (LWG/A) when grazed or fed as hay or pellets (Burton *et al.*, 1967).

Breeding varieties resistant to pests, such as diseases, insects, and weeds, will improve the dependability, yield, and quality of a forage species.

PREPARATION

Improving a species to satisfy these objectives efficiently requires a knowledge of its cytology and its mode of reproduction. Techniques for selfing, crossing, and screening must be found. If such information is not available, research must be designed to produce it as soon as possible.

The success of any plant breeding programme depends largely on the genetic diversity of the germplasm available. All introductions should be evaluated as potential parents in a breeding programme. The best introductions, after their superiority has been established, may be named and released as new cultivars without genetic improvement. Many named subtropical forage cultivars such as Pangola grass, *Digitaria decumbens*, were developed in this way.

Large scale propagation methods will influence the materials chosen and the approaches taken. Annuals and perennial bunch grasses are usually propagated by seeds. Good seeding habits for such forages will become a major breeding objective. Progeny tests will be required. Population drift will be a major concern if the seed for a cross pollinating cultivar must be produced outside the area of use.

For species such as pangola grass and bermudagrass, *Cynodon dactylon,* that are propagated vegetatively on a commercial basis, the plant breeding approach can be quite different. Here the plant breeder needs to develop only one superior plant. The long, laborious task of progeny testing can be eliminated. Heterosis, disease resistance, and other desirable traits found in the superior plant will be maintained. Wide crosses to combine the desired traits of different species or genera can be attempted with the assurance that good hybrids can find commercial use, even though sterile. Sterile cultivars are easier to control than those producing seeds. Vegetative propagation facilitates the identification of new cultivars and puts them within reach of small land holders, who have more labour than money.

EFFICIENT SCREENS

The success of any forage breeding approach will depend upon the efficiency of the screen. For resistance to an insect pest, an entomologist should be involved in developing and improving the screen. To improve forage quality, the animal nutritionist should be challenged to improve the best screen available. An effective screen for yield must allow every spaced plant to express its yield potential in a uniform environment. Soil heterogeneity effects on space plantings can be reduced by selecting a uniform field, growing a uniform cover crop such as soybeans the previous year, and fumigating with methyl bromide before planting. Stressing uniformity in every operation from the planting of the seed to the final selection of the better plants is essential.

PLANT BREEDING METHODS

Vegetatively propagated hybrids

For bermudagrass, we believe breeding for vegetative propagation is the preferred approach. We used this technique to breed Coastal bermuda that yields about twice as much as the common bermuda and has been planted on some 10 million acres. It is the best of 5000 spaced plants from a cross between a unique common and an excellent introduction from South Africa. Tested first with 146 selections in replicated plots for three years and later in numerous other tests for the important objectives described earlier, it ranked first when named and released to the public.

To increase the quality of Coastal bermudagrass, we crossed it with a highly digestible introduction from Kenya and selected from many F_1 hybrids the Coastcross-1 previously described.

To increase its winterhardiness, our approach was to cross Coastal with a winter hardy common bermudagrass from Indiana. The best of these F_1, named Midland, occupies more than one million acres in Oklahoma. For greater winter hardiness and yield, we selected Tifton 44 from several thousand F_1 of a cross between Coastal and a winter hardy common bermuda found in Berlin, Germany. Rust immune Tifton 44 crossed with the rust and cold susceptible Callie produced Tifton 78 with the good traits of both parents that in a three-year grazing test produced 36% more live weight gains per acre and 13% better average daily gains than Coastal.

Synthetics

Many of the improved forages that have been developed in the world have been synthetics. Ecotypes (often from old pastures), introductions and selected clones developed in the breeding programme are evaluated and several of the better ones are combined to make a synthetic that is better than varieties generally grown. If tested in the Syn 1, such synthetics may exhibit significant heterosis that will largely disappear in advanced generations. If the time required for increase will not permit the synthetic to reach the farm before Syn 3, the synthetic should be evaluated at Syn 3, not Syn 1.

To avoid drift and loss of important traits, the clones of perennials are often retained and increase is not permitted beyond a specified generation. Certification that makes the blending of the parent clones — the S_1 — breeders stock, and increases through foundation, registered, and certified classes with certified seed only from fields planted to registered seed will usually limit drift and loss of important traits in the parent clones.

Synthetics among annuals are usually stabilised and perform much as a cultivar. A broad gene base is desirable with one or more important characteristics well-established. Tiflate pearl millet is a very late maturing synthetic developed from 54 introductions from Nigeria and Burkina Faso (Upper Volta) that bred true for short-day photoperiod sensitivity (Burton and Powell, 1968). Three generations of incresing a mixture of the seed of four introductions of this highly cross-pollinated species produced the breeders seed for Tiflate pearl millet. Usually synthetics become stabilised and may be sources of germplasm for developing a new synthetic. They are rarely altered by intentional selection but may drift as they are increased for several generations in a new environment.

Developing synthetics from breeding material provides an inexpensive and effective method for making the products of a breeding programme available to farmers, breeders, or other users. Certainly the components must be good seed producers and should be highly cross-pollinated. Synthetics that concentrate in heterozygous germplasm a desirable trait such as short-day-photoperiod sensitivity store germplasm in a useful form for the plant breeder.

Mass selection

Mass selection is the oldest plant breeding method. It was used by the primitive plant breeders 10 000 years ago as they gradually created cultivated crops from their weedy progenitors. In mass selection, open-pollinated seed from the better plants in a population is mixed together to plant the next cycle. Selection is based on the performance of the phenotype. The plants in the population must be fertile, cross pollinated, and must produce seed. The measured performance of the phenotype and its progeny must be correlated and the selections must be intermated to build up the frequency of the genes controlling the traits being selected.

Mass selection is one of the most effective methods of improving traits with high heritability such as disease resistance. Progress then will be controlled largely by the efficiency of the screen. Because heritability for forage yield on a single plant basis is usually low, improvement of forage yield by mass selection will be slow unless heritability can be improved.

Recurrent restricted phenotypic selection

Recurrent restricted phenotypic selection (RRPS) is mass selection modified by eight restrictions to make it four times more efficient than mass selection (Burton, 1974). The research that was designed to increase the forage yield of *Pensacola bahiagrass*, a cross pollinated diploid, and that led to the development of RRPS was begun in 1960. A special study showed a correlation of only +0.4 between the yields of spaced plants and their clonally established plots in a replicated clipping test. In the beginning, actual green yields of the spaced plants over a two-year period were used for plant selection. Throughout the 25-year study, the population size per cycle has been limited to 1000 spaced plants. The top yielding five plants in a 5 x 5 (25) plant grid were selected, making 200 plants to be intermated for the next cycle. Grid selection helped to reduce soil heterogeneity effects and increased the heritability values for forage yield. During the past 25 years, other procedures have been modified to improve the precision of the screen for yield and the intermating system.

Today eight restrictions complete one cycle of RRPS per year and increase the mean yield of the space planted population more than 16% per cycle through Cycle nine (Burton, 1985). Plants started from polycrossed seed in December transplanted to two-inch pots in late January, and space planted in the field in mid-April are heading ready to select for the RRPS polycross by mid-July. Visual selection of the five better plants in grids of 25 brings together in the polycross the top 200 plants out of a population of 1000. Three culms (ready to flower) harvested from each of the 200 selections placed in containers of water and grouped together under a paper tent less than three feet in diameter are intermated by agitating the tent each morning to make the RRPS polycross. Green plant yields taken in July (after the polycross is made) and in late October plus winter survival and spring vigour data mark the poorest 35 of the 200 polycrossed progenies so they can be discarded before the April space planting. Six plants from each of the 165 remaining progenies are space planted at random for the next cycle.

In plots established from seed, Cycle nine over a three-year period, has produced 47% more forage than the Pensacola bahiagrass check with which we started in 1960. Cycle nine, scheduled for release as Tifton 9 in 1987, should maintain its superiority for a number of successive generations. RRPS is continuing to increase forage yields of Pensacola bahiagrass about 16% per cycle through Cycle 11. RRPS with slight modification should be a very effective method for increasing the yield of tall fescue, *Festuca arundinacea*, and many other cross-pollinated forage species. It should also be an excellent method for enhancing germplasm.

Developing seed propagated F_1 hybrids

Heterosis or hybrid vigour is the increase in quantitative characters such as yield or height observed in an F_1 hybrid compared with the mean of its parents. The best F_1 hybrids may yield 20 to 50 percent more forage than open-pollinated cultivars. Such hybrids usually exhibit greater stress tolerance and use growth factors more efficiently. Because increasing yield is usually one of the major objectives of the forage breeder, he can well afford to ask and try to answer, how can we put the F_1 hybrid on the farm? A brief description of several approaches that answer this question follow.

If vegetative propagation is practicable, the F_1 hybrid can be bred and put on the farm easily as already described for bermudagrass. Most forages must be propagated with seeds and for those that are highly cross pollinated, developing the first-generation chance hybrid may be the best approach. The highly successful Gahi-1 pearl millet, similar to Cattail but capable of yielding up to 50% more forage is a good example (Burton and Powell, 1968). Gahi-1 seed was harvested from fields planted to a mixture of equal quantities of pure live seeds of four carefully selected inbreds that gave high yielding hybrids in all combinations. For many years, the National Foundation Seed Project increased the four inbreds and prepared the seed mixture used by commercial seedsmen to produce certified Gahi-1 pearl millet seed. Because the second generation yielded much less, only the first generation could be called Gahi-1.

Experimental self-incompatability hybrids produced in a seed field planted to alternate strips of selected self-incompatable cross-compatable clones of Pensacola bahiagrass and bermudagrass have been developed (Burton and Hart, 1967). Although the hybrids exhibited good hybrid vigour, and hybrid seed could be obtained from seed fields for many years by simply harvesting all seed produced, they have not reached the farm. Low bermudagrass seed yields and the high cost of planting the bahiagrass seed fields are responsible. Developing vegetatively propagated hybrids for bermudagrass and RRPS for Pensacola bahiagrass are better breeding methods for these species.

Cytoplasmic male-sterility offers one of the most practical mechanisms for producing F_1 hybrid seed of sexual species. Because forage hybrids, produced on cytoplasmic male-sterile stocks, need not have their fertility restored, the forage breeder need only be concerned with the search for male lines that will give the best hybrids when crossed with the male-sterile parent. Producing male sterile forage hybrids will improve their quality by retaining photosynthate in the forage that might otherwise be transferred to the seed. It will also minimise their weed potential.

Most of the highly successful sorghum-sudangrass hybrids have been produced by crossing selected sudangrass males on the cytoplasmic male-sterile grain sorghum lines used to produce grain hybrids.

Apomixis defined as vegetative reproduction through the seed may be used to put the F_1 hybrid on the farm. However, it must occur naturally in the forage being improved and sexual plants must be found or created if apomictic plants are to be improved.

Apomixis in the tetraploid obligate apomictic *Paspalum notatum* was broken by first creating induced tetraploids of the sexual diploid Pensacola bahiagrass. These sexual tetraploids, used as females, were crossed with obligate apomicts to release greater variability than previously observed in nature (Burton and Forbes, 1960). From this material, by selection and recombination, have come promising sexual and obligate apomictic plants.

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SYMPOSIUM DISCUSSION

Dr H.S. Easton, Grasslands Division, DSIR

What sort of seed production area can your industry stand for the 4-way hybrids or are you able to multiply up the four clones individually?

Burton

Those inbred lines were increased in Arizona under contract, in isolation. Our national foundation seed programme took the seed and mixed the 4 lines together in equal quantities and that was sold to the commercial seed producers. They were able to sell it only as certified seed.

Easton

Do you know whether the total area of seed fields required was greater or less than with for example a synthetic?

Burton

I can't tell you the total area. They probably produced 1 500 lb/acre of pearl millet seed.

Dr R. Burdon, Forest Research Institute

We are interested in the genetics basis of forest tree crops with regard to disease risk. What is the typical lifetime of the swards? What are the ploidy levels you are dealing with? Have you encountered problems of breakdown in disease resistance?

Burton

The 4-line hybrid is an annual so the sward lasts about three months. We have found immunity to rust in *Pennisetum amillety* and we transferred it in an extensive backcrossing programme.

Sir Otto Frankel, CSIRO

You open up so many choices to graziers they must have difficulty in selecting an appropriate cultivar. How do you help them?

Burton

We test the Bermuda grasses across the south. We have replicated grazing trials in which we have a good idea of what each one of those will do under certain circumstances.