GENE MANIPULATION IN PLANT IMPROVEMENT

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Edited by

J. P. Gustafson

USDA—ARS
University of Missouri
Columbia, Missouri

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The editor would like to dedicate his effort in the preparation of this publication to the memory of Ronald Walsh McLean

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J. P. Gustafson

May 7, 1984
Columbia, Missouri

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PLANT BREEDING 1910-1984

Glenn W. Burton

USDA, ARS
Coastal Plain Experiment Station
Tifton, Ga.

The title of my assignment suggests that I should say something about the history of plant breeding from 1910 to 1984. Why no earlier than 1910? Perhaps it is because by 1910 we were beginning to apply Mendel's classical genetic papers, recognizing the gene and its role in plant breeding. Certainly plant breeding did not start in 1910.

We have good reason to date the beginning of plant breeding with the beginning of agriculture. It started when the women gathering food for their families recognized variation and "selected" seeds from the best plants for the next generation. Larger seeds or fruits and yield must have been top objectives. What a "break-through" was the discovery of a plant that did not shatter its seeds - that held its fruits to facilitate harvest.

The contribution of plant breeding to mankind since 1910 has been great. More than half of the phenominal increase in agricultural production can be credited to plant breeding. Those of us fortunate enough to be called geneticists or plant breeders can point with pride to the achievements of our profession. The papers we will hear at this symposium will help to explain our progress. The thousands of papers on gene manipulation, a few of which will be quoted, will impress us and particularly our administrators. They may help us to increase the efficiency of our craft (plant breeding). But if plant improvement is the ultimate goal of plant breeding, we must continually ask how can this new fragment of information help us to reach our goal?

Lest we become so enamoured with our sophisticated manipulation of the molecular components of the gene that we think all else is naught, let us compare the wild progenitors of our crop plants with the best we have today. Most of the change was made by the primitive plant breeders. They know no genetics and had none of the tools that most of us "must have" today. They had the same five senses that you and I possess and they used them. They knew their plants, probably better than most of us know ours. They realized, perhaps instinctively, that whatever controlled the characteristics of their crops was maleble, capable of change. Perhaps most important, they recognized the power of selection when applied to characters they could see in their plants. The change, the progress the primitive plant breeders made was at the molecular level. We now know that it had to be, thanks to research in the area of molecular biology. The selection, the screening, however, was made at the plant level. Every significant advance in yield, for example, must have involved many changes in the DNA sequences present in the plant. Interesting as this may be for you and me, the significant contribution of the early plant breeders for them and for us was that they changed a few weedy species into crops that efficiently feed mankind.

Instead of trying to trace the history of plant breeding and duplicating things that Dr. Duvick will no doubt cover in his address, permit me to share with you 50 years of plant improvement by a geneticist born in 1910. He grew up on a rented farm in Southwest Nebraska where he had learned the importance of yield and the toll that drought could take before he was 12. He had won the blue ribbon at the county fair with his collection of native grasses and had learned how to select seed corn while still in high school.

In the summer of 1931, while an agronomy major at the University of Nebraska, he served as "agronomist" at the small branch experiment station at Alliance, Nebraska. Taking notes and harvesting Coit Suneson's wheat, <u>Triticum</u> ssp., and H. M. Tysdal's alfalfa, <u>Medicago</u> spp., gave him his first taste of plant breeding.

It was F. D. Keim, head of Nebraska's Agronomy department, who sent him to Rutgers University in 1932 to earn his M.Sc. and Ph.D. degress while working half-time in Howard Sprague's Crops deparment. Under the inspiring leadership of Howard Sprague, he helped with the breeding of corn, <u>Zea mays</u>, small grains and alfalfa, the teaching, the state-wide testing, the seed certification program and the turf research carried on in the Crops department.

In 1934, for his Ph.D. thesis, he became an alfalfa breeder crossing the Hairy Peruvian variety with winterhardy types in an effort to combine their superior traits. The inheritance of flower color and a number of quantitative characters produced his thesis and a 350-page New Jersey bulletin, one of his first publications (Burton, 1937).

He also cut and weighed spaced plants of a wide based population of alfalfa in a modified plant to row breeding method that led to the development of the variety Atlantic.

His training at Rutgers included completing 5 courses in chemistry, 3 in math, 3 in botany, 2 in plant pathology, and enough additional courses for a major in crops and minors in plant physiology and soils. Equally important he says were the experience and inspiration provided by Howard Sprague for 4 1/2 years.

His farm experience and the training he had received in Nebraska and Rutgers stood him in good stead when he arrived at the Coastal Plain Experiment Station, Tifton, GA, April 30, 1936. The seventh professional person, a USDA agent later entitled "geneticist", his assignment was large--his job description was brief--he was to develop better grasses for the South. His first summer was spent with the help of a day laborer, fencing 5 acres of pasture land, installing an irrigation system and building a fieldhouse, in addition to acquainting himself with the species he was to breed.

With the exception of sorghum, *Sorghum bicolor*, nothing was known about the breeding behavior of the other species to be improved. The limited genetic improvement with cold season forage grasses had emphasized pasture type. The breeding method used called strain building consisted of pooling together low growing types (often selected in old pastures) that could persist under close grazing. The young geneticist recognized the importance of persistence and tolerance of close defoliation, but he believed that "improvement" should increase yield. His experience in New Jersey had convinced him that farmers interest in new varieties was proportional to the yield increase that might result from their use. He has continued to believe that forage crop improvement must increase yield of forage, or the meat and milk the forage will produce. With this conviction, much of his time has been spent measuring the yield of potential varieties that his program has developed.

His experience with hybrid corn, *Zea mays*, had convinced him that the best way to increase yield was to discover a means of putting the F_1 hybrid on the farm. His studies of bermudagrass, *Cynodon dactylon*, in 1936 convinced him that it was cross pollinated, highly heterozygous and that it could spread fast enough with stolons and rhizomes to permit vegetative propagation. The logical strategy for improvement seemed to be the development of an outstanding F_1 hybrid plant that could be propagated vegetatively on the farm. Therefore, in 1937, Tift bermuda (selected in a Tift County cotton patch) and two excellent 1936 introductions from South Africa were interplanted in isolation so they could intermate (Burton, 1954). The few seeds produced when these plants were selfed and the appearnace of their selfed progeny proved that most of the 5000 spaced plants from this intermating effort were F_1 hybrids. Many notes on rate of spread, disease resistance, seed head formation and vigor were used in the fall of 1937 to select 147 hybrids. Forage yields of a triplicated planting of these hybrids in 4-inch clay pots in the greenhouse in the 1937-38 winter failed to correlate with later field performance and proved a waste of time. The procedure, however, did supply excellent potted plants to be set one each, in the center of triplicated 4 x 24 foot plots in the spring of 1939. Five-foot alleys between the plots kept clean and weed controlled with a lot of hoeing by high school boys, enabled most of the clones to cover the 4 x 24 foot plots by the end of the season. Many notes, including rate of spread, forage yield, seed head protection, compatability with annual lespedeza, *Lespedeza striata*, and disease resistance taken on this planting pointed to five hybrids good enough to be included in large replicated plots with and without crimson clover, *Trifolium incarnatum*, and with rates of 4-8-4 fertilizer up to 1000 lb/A.

In June, 1942, a plot of hybrid number 35 growing beside common bermudagrass was obviously producing about twice as much forage but was producing no seed. A national pasture specialist, when he learned that vegetative propagation on the farm was planned, asked, "Who ever heard of planting a pasture grass vegetatively?" and went on to say, "I'd throw it away if it were mine". In 1943, in response to an urgent request from L. L. Patten, prominent Georgia farmer, hybrid 35 was named "Coastal" for the station where it was developed and released (Burton, 1954). In 1943, bermudagrass was still the South's worst weed and Mr. Patten's neighbors thought he had lost his mind. It took another 15 years of numerous well replicated experiments, with and without the help of other scientists to ascertain fertilizer and management requirements and develop planting methods, certification procedures, and proof of the excellence of Coastal bermudagrass. Tests and demonstrations by others across the South led to the planting of 10,000,000 acres of Coastal bermudagrass that is performing as well today as it did 40 years ago.

The excellent combination of genes carried by Coastal bermudagrass has made it a logical parent in future breeding efforts with bermudagrass. Out of several hundred F_1 hybrids with a winterhardy common bermudagrass from Indiana screened for yield, cold tolerance, etc., came one superior plant named Midland (Harlan and Burton, 1954). More winterhardy than Coastal, it has been planted on more than a million acres north of the Coastal Belt.

Out of 385 F_1 hybrids between Coastal and a highly digestible but cold susceptible plant of *C. nlemfuensis* screened first on sand dune soil but finally tested in grazing and feeding trials came Coastcross-1 (Burton, 1972). Sterile and with only above ground stolons, Coastcross-1 compared with Coastal is 12% more digestible and when grazed gives 30 to 40% better average daily gains (ADG) and liveweight gains per acre (LWG/A). Cuba is using a half million acres of Coastcross-1 to produce milk because it has produced more milk without supplement than other grasses tested. Its lack of winterhardiness has restricted it to Florida and the tropics.

Tifton 44, released in 1978, is the best of several thousand F_1s between Coastal and a winterhardy bermudagrass from Berlin, Germany (Burton and Monson, 1978). It combines the desirable traits of Coastal with extra quality and enough more winterhardiness to grow dependably 100 miles farther north. Its extra cold hardy genes makes Tifton 44 a better gene pool than Coastal for further breeding purposes.

Tifton 78-22 is an F_1 hybrid between Tifton 44 and Callie that combines most of the desirable traits of both parents with added hybrid vigor. The dominant genes for immunity to rust from Coastal are making Tifton 78-22 immune to this disease. Callie is very susceptible to rust.

Most golf courses and many football fields, athletic fields, and lawns across the South and in the tropics around the world are planted to Tifgreen, Tifway, and Tifdwarf bermudagrass, sterile *C. dactylon* x *C. transvaalensis* F_1 hybrids (Burton, 1982). Added to their excellent turf qualities is their failure to produce the pollen that brings pain to asthma and hay fever sufferers. They are also excellent for the sod production used to plant today's "instant turf" because their rhizomes left in the sod-field soil after stripping reestablishes the turf without planting.

Tifway II, released in 1981, and Tifgreen II, released in 1983, are M_1 radiation induced mutants of Tifway and Tifgreen created in 1971 by exposing dormant rhizome sections to gamma rays (Burton, 1982). Repeated tests have shown them superior to their normal parents in several important traits especially under low cost maintenance.

Breeding elephant grass, *Pennisetum purpureum*, during his first 10 years at Tifton, the young geneticist crossed a very leafy dwarf he had selected with a tall type to produce F_1 hybrids from which Merkeron, a tall type was selected. Merkeron, propagated in the tropics from stem cuttings and used as a green chop forage for milk cows, was also kept living in a grass nursery at Tifton. The interest in biomass production motivated research to prove that Merkeron could produce up to 40 metric tons per ha in one growing season at Tifton. The improved quality of the short Tifleaf 1 pearl millet suggested that short leafy elephant grass should be evaluated with cattle. The dwarf elephant grasses were gone but the dwarf genes preserved in Merkeron were not. Selfing Merkeron has produced a number of dwarfs currently being tested with livestock.

Breeding a disease resistant sudangrass, Sorghum bicolor, was one of the challenges suggested for the young geneticist in 1936. Enroute from Bartley, Nebraska to Tifton in April, 1936, the young geneticist stopped at the Hays Kansas Experiment Station and obtained from D. A. Savage, seeds of Leoti sorghum, Sorghum bicolor, his most disease resistant variety. In the summer of 1936, the disease resistant Leoti sorghum was crossed with susceptible sudangrass. The F_1 grown in the winter in a section of a little horticultural greenhouse, produced enough seed to plant 35,000 F_2 plants in 1937. Six of these plants were as free of disease as Leoti sorghum but they were also coarse-stemmed. The resistant plants crossed again to sudangrass gave F_1s increased in the winter and 30,000 F_2s planted in 1938. One of these F_2s with fine stems was as resistant as Leoti. When selfed progeny of this plant bred true for disease resistance and fine stems, it was increased and became Tift sudan (Burton, 1950).

Tift sudan had a high content of the HCN glucoside. The development of low HCN lines of sudangrass in Wisconsin and the discovery of greater disease resistance in other sorghums motivated a breeding effort directed toward combining low HCN, maximum disease resistance and a uniform seed coat color in one variety. Eleven years of crossing and testing were spent transferring the genes responsible for these traits into one variety. No attempt was made to measure yield. When the goal was achieved in Georgia 337 sudangrass and yield was measured, it yielded less than the commercial sorghum sudangrass hybrids and never was accepted by farmers (Burton, 1964). Georgia 337 has been useful germplasm for some sorghum breeders and may have been used as a parent in one commercial sorghum-sudangrass hybrid.

Improving the seed set and ergot, Claviceps microcephala, resistance of dallisgrass, Paspalum dilatatum, by breeding offered some new problems. The striking uniformity of selections, introductions and their progeny indicated that it was an obligate apomict. Crossing it on two other Paspalum species produced vigorous ergot resistant F_1 hybrids but they were highly sterile and the occasional seed produced gave rise to apomictic offspring (Burton, 1943). Their bunchgrass growth habit and performance under close clipping made their farm-use with vegetative planting impracticable.

Irradiating seeds of dallisgrass to break apomixis produced mutants in the M_1 generation (Burton and Jackson, 1962). None of these were as good as the dallisgrass parent and when they gave rise to uniform progeny, it was apparent that apomixis had not been broken.

A 40-chromosome introduction (common dallisgrass has 50 chromosomes) proved superior to common dallis in clipped plots and gave good results when grazed. It too was apomictic, was susceptible to ergot and set seed poorly. When it was attacked by chinch bugs, plans to release it were dropped and dallisgrass breeding was discontinued. Much was learned but attempts to improve dallisgrass by breeding had failed.

Breeding projects designed to improve several other species were dropped when their obligate apomixis and/or lack of adaptation made it seem advisable.

Pearl millet, Pennisetum americanum, a robust annual bunchgrass proved to be an ideal species for genetic and breeding method studies. Called cattail millet and used as a summer grazing crop in the South in 1936, it was drought tolerant and well adapted to infertile sandy soils. Its sexual reproduction and protogynous flowering habit facilitated crossing without emasculation and selfing by enclosing heads in paper bags. Its 7 pairs of large chromosomes and its many heritable traits made it well suited for cytogenetic studies.

Starr pearl millet, the first product of the breeding effort with this species was a synthetic variety produced by blending together several lines with similar traits (Hein, 1958). Its increased leafiness and its later maturity enabled it to yield up to 25% more than the cattail millet check it replaced.

The heterosis observed when certain inbred lines were crossed indicated that yields could be materially increased if F_1 hybrids could be put on the farm. The attrition of the weaker seedlings in plantings at the normal seeding rate suggested that 100% hybrid seed would not be required to obtain a 100% hybrid yield. It was reasoned that a mixture of 4 compatable inbred lines flowering at the same time would produce seed 75% of which would be a mixture of the 6 possible single crosses and 25% would be selfs and sibs. A six-year clipping yield trial planted to various inbred hybrid seed mixtures proved that a 50% hybrid seed mixture planted at the normal rate would yield as well as 100% hybrid seed (Burton, 1948).

For this chance hybrid breeding procedure to succeed, four inbred lines that would produce high yielding hybrids in all possible combinations were needed. Numerous clipping trials of diallels involving different inbred lines were required to isolate 4 inbreds that met these requirements. Seed harvested from a field planted to a mixture of equal numbers of pure live seeds of these 4 inbreds - Tift 13, 18, 23, and 26 contained 75% of hybrids and

25% of selfs and sibs. When compared in repeated clipping trials, this chance hybrid seed yielded as well as the double cross involving the same inbreds and outyielded the cattail check by 50%. Named Gahi 1 (short for Georgia hybrid) it was released in 1962 (Burton, 1962). The USDA National Foundation seed program increased the 4 inbreds in isolation and prepared the foundation seed mixture. Only seed grown from foundation seed under state certification could be called Gahi pearl millet, a restriction required due to loss of vigor in the next generation. For many years, Gahi 1 was the leading pearl millet variety grown in the South.

To facilitate seed production, Gahi 2 was produced by substituting dwarf lines for tall lines. These dwarfs, selected from selfed progenies of exotic material, different from each other so that hybrids between any two of them would be tall. This helped the tall hybrids to eliminate the dwarf selfs and sibs in the plantings grown from Gahi 2. The discovery of cytoplasmic male sterility (cms) in pearl millet and the failure of Gahi 2 to yield as well as Gahi 1 prevented its release to the public as an improved variety.

The chance hybrid plant breeding method used to increase pearl millet forage yields was later shown to be an effective method for increasing yields of sudangrass (Burton et al., 1954).

The search for cms in pearl millet was rewarded in 1955 when an F_2 plant from a cross between inbred 556 and Tift 23 was sterile when selfed but fertile when crossed with Tift 23, our best inbred (Burton, 1958). Repeated generations of mating the sterile plants with Tift 23 soon produced Tift 23A, the first cms pearl millet inbred. The excellence of Tift 23, including seed yield and the heterotic ability it had demonstrated in the production of Gahi 1 suggested that a single cross based on Tift 23A could be superior to Gahi 1.

In 1961, K. O. Rachie, Rockefeller Foundation millet coordinator in India, reported that 27 million acres of pearl millet were grown in the most arid portion of India. He stated that it was grown primarily for its grain for human food because it could outyield other crops under those conditions. Beginning in 1962, Rachie led a coordinated millet improvement program that involved making and testing F_1 hybrids between Tift 23A and lines developed by Indian breeders. In February, 1965, Rachie reported that the Indian millet breeders and agreed to release HB1 hybrid millet, a cross between Tift 23A and D. S. Athwal's Bil 3B, because it had yielded 88% more grain than the best open pollinated checks from 11 to 31 degrees north (Burton, 1983). In 1965, India produced 3.5 million tons of pearl millet grain. In 1970, with the help of HB1, it produced 8 million tons.

The study of the inheritance of five dwarfs isolated from selfed progenies of exotic germplasm, revealed that one labeled $\underline{d}_2$ was superior to the others in several respects (Burton et al., 1969). Controlled by a single recessive gene, $\underline{d}_2$ reduced the internode length of tall lines enough to cut their height in half without reducing peduncle length, head exsertion, leaf number, and leaf or head size (Burton et al., 1969). Introduced into Tift 23A and B with frequent backcrosses, the $\underline{d}_2$ gene produced Tift 23DA and Tift 23DB (Burton, 1969). When F_1 hybrids involving Tift 23A and Tift 23DA yielded the same, the use of Tift 23DA to facilitate hybrid seed production was indicated.

In 1972, Gahi 3, the first forage single cross was released (Burton, 1977). Using Tift 23A or Tift 23DA as its female parent, Gahi 3 had as its male parent, Tift 186, an excellent inbred selected from a South African introduction (Burton, 1977). Compared with Gahi 1, Gahi 3 is leafier, more disease resistant, later maturing, and more productive. The absence of the dominant fertility-restoring R gene in Tift 186 makes Gahi 3 male sterile, a desirable trait in a forage grass. Most Gahi 3 seed is produced on Tift 23DA, but because Tift 186 is tall, Gahi 3 is also tall.

Tiflate pearl millet, a synthetic produced by blending together 54 short day introductions from West Africa, requires a short-day (12 hours or less) to initiate seed head primordia (Burton, 1972). As a consequence, it fails to mature seed before frost in most of the continental U.S. Tiflate compared with Gahi 3 produces more forage in the fall or when cut for silage and gives a better seasonal distribution of its forage when grazed.

Tifleaf 1, released in 1975, is an F_1 hybrid between Tift 23DA and Tift 383 (Burton, 1980). Because both parents are dwarfed with the $\underline{d}_2$ gene, Tifleaf 1 grows only half as tall as Gahi 3 and yields only about 80% as much dry matter. When grazed, however, it produces more ADG and LWG/A than Gahi 3, due to its much greater leafiness.

Bahiagrass, Paspalum notatum, a slow spreading perennial from South America is well adapted to the sandy soils of the deep South. Introductions available in the later '30s and early '40s all gave very uniform spaced progeny suggesting apomixis as their mode of reproduction. When a white stigma male-sterile mutant pollinated with pollen from a red stigma plant gave rise to many male-sterile white stigma plants with several red stigma hybrids carrying 60 chromosomes instead of the usual 40 its obligate apomixis was confirmed (Burton, 1948).

In 1941, county agent E. H. Finlayson described a bahiagrass growing wild near Pensacola, Florida, where the old Perdido docks had been located before they were destroyed by a hurricane

(Finlayson, 1941). A search for the origin of Pensacola bahiagrass led to the conclusion that it probably originated in northern Argentina and was brought to Pensacola, Florida in the digestive tracts of cattle shipped from Santa Fe, Argentina to Pensacola before the Perdido docks were destroyed (Burton, 1967). A space planting of this Pensacola bahiagrass grown at Tifton, Georgia showed it to be highly variable and to have smaller seeds, longer stolons, and greater frost tolerance than the South American introductions. It also set seed better and produced more seed than the tetraploid apomicts. Cytological studies found Pensacola bahiagrass to be a diploid (2n = 20) with regular meiosis and sexual reproduction (Burton, 1955).

When the sexual tetraploid necessary to break apomixis could not be found in the various introductions, Ian Forbes, Jr. was asked to try to create one by doubling the chromosome number in the sexual diploid, Pensacola bahiagrass. Among many plants from colchicine treated seed, Forbes found several plants or plant sectors with highly sterile heads (detected by chewing a few "seeds") that proved to be tetraploids (Forbes and Burton, 1957). Isolated from the diploids, they set seed reasonably well and when used as females were easily hybridized with the obligate apomicts. Extensive inheritance studies that followed indicated that in the autotetraploid bahiagrass, apomixis in most of the material was controlled by a recessive gene _a_ that must be homozygous (Burton and Forbes, 1960). This hypothesis could not explain the inheritance of apomixis in all of the material studied. The occurrence of only 1 apomictic plant in 36 F_2s required large populations to produce the two good apomictic hybrids Tifton 54 and Tifton 91 that have not been released to date.

The extreme variability in F_2 populations from sexual x apomictic introductions indicated that the natural apomicts were very heterozygous. Most of the F_2s were inferior to their apomictic parent. Attempts to develop a superior sexual tetraploid population by intermating the best plants, has been hampered by the occurrence through cycle 5 of a high percentage of inferior plants.

Most plants of Pensacola bahiagrass are largely self-sterile and cross-fertile (Burton, 1955). This discovery suggested that commercial F_1 hybrid seed could be produced by harvesting year after year all seed produced in a field planted to alternate strips of two self-sterile cross-fertile clones. Two such clones, whose F_1 hybrids yielded 17% more dry matter than the Pensacola check in clipping tests were sought and found by screening several diallels. A pilot seed production field planted vegetatively produced seed to plant in a pasture that gave 17% more LWG/A than Pensacola bahiagrass when grazed for 4 years. Two of these hybrids, Tifhi 1 (Hein, 1958) and Tifhi 2, were released but the hand labor required to establish the seed fields and the cold injury to one parent clone in a severe winter (discovered after their release) kept them from becoming important on the farm.

In 1961, a population improvement program was begun with Pensacola bahiagrass starting with a mixture of seed from 39 farms as a wide gene pool (WGP) and seed from an isolated planting of 75 F_1 plants of Tifhi 2, a 2-clone hybrid, as the narrow gene pool (NGP). The objectives were to increase the forage yield and improve the efficiency of mass selection. The beginning breeding procedure consisted of cutting and weighing 1000 spaced plants of each population and intermating the top 20% for the next cycle (Burton, 1974). At cycle 6 when the NGP and WGP populations yielded the same and were equally variable, they were combined (Burton, 1982). By cycle 8, the first-year-yield of the spaced plant population was still increasing at an annual rate of 16.4% and it still possessed enough variability to indicate continued progress. The breeding method at cycle 8 (improved each year) contained 8 restrictions that made it 4 times more efficient than ordinary mass selection. Called recurrent restricted phenotypic selection (RRPS), its success resulted from the improved screening and intermating systems imposed by the 8 restrictions. In replicated seeded plots clipped several times per year for 2 years, cycle 8 has yielded as much dry matter as the best 2 clone hybrid between plants selected from cycle 4 and has yielded 40% more than the Pensacola bahiagrass check.

Finally, permit me to record a few of my convictions about my profession, plant breeding.

Plant germplasm as expressed in higher plants is maleable and capable of significant response to selection pressure. Plant breeding is the profession charged with the responsibility of modifying the germplasm of a few species to better serve mankind. If plant breeding is to be held responsible for more than half of the increased production required to satisfy the food, fiber, wood, etc. needs of twice as many people in 40 years, the efficiency of its methodology must be improved. The time required per unit of advance must be reduced. I believe it deserves as much support and attention as genetic engineering which at best can only be a plant breeding tool.

The efficiency of backcrossing, an old reliable tool for gene transfer, was greatly increased when we learned how to grow four generations of pearl millet per year instead of one or two (Burton, 1983). Five generations per year, our present goal, will soon be realized.

The effective screening systems that Homer Wells has developed for resistance to rust and Piricularia leafspot in pearl millet are