Achievements and Perspectives in the Breeding of Tropical Grasses and Legumes

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ACHIEVEMENTS AND PERSPECTIVES IN THE BREEDING OF TROPICAL GRASSES AND LEGUMES

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Abstract

Pasture and forage plant breeding is complicated by the perennial nature of the plants, the diversity of environments in which improved cultivars will be used, and the complex criteria of merit involved, criteria that necessarily include some measure of impact on the efficiency of animal production. While pasture plant breeding in the temperate zone is a demonstrably productive activity, the record of success for the tropical species -- "success" measured by release and adoption of bred cultivars -- is less convincing, in spite of four decades of activity in numerous public sector breeding programs and a large published literature. The difference is at least partly owing to the less developed state of pasture research in general in the tropics. More specifically, the reasons for the lack of success of tropical pasture plant breeding can be classified as: i) inadequate understanding of the socioeconomic environment in which the bred cultivars are to be used, ii) inadequate level and stability of institutional support, and iii) inherent biological obstacles. It appears that in most cases the biological obstacles, while sometimes formidable, are the least constraining to success. Until responsibility for tropical pasture plant breeding is assumed by the private sector (as it largely has been in the temperate zone) the single factor that would most improve chances of success (or at least avoid many of the failures) is intimate contact and constant communication between the public sector plant breeder and the seed industry that is the vehicle for diffusion of his new bred cultivars.

Keywords: Plant breeding, genetics, tropical forage, cultivar, release, adoption

Introduction

Temperate pasture plant breeding is demonstrably productive and actively pursued in both public and private institutions. Although a complex and costly, long-term endeavor, it has led to numerous successful commercial cultivars of the established temperate forage grass and legume species (Wijk et al., 1993; Humpherys, 1999).

Much question and debate, however, still surround the topic of forage plant breeding in the tropics (Cameron, 1983). This is particularly so if "success" is taken to mean not just the formal release and naming of new a bred cultivar, but release and adoption. By this more rigorous definition, the record of success of tropical forage plant breeding is frankly dubious, in spite of recent optimistic assessments (e.g. Cameron, 1997).

The differences between tropical and temperate forage breeding arises in large part from the vast difference in the level of development between temperate and tropical pasture research: many authors have pointed out over the years that tropical forage breeding is "in its infancy" (e.g.

Bray, 1975; Hacker & Jank, 1998), in spite of the four decades of activity that are reflected in a voluminous published literature.

The objectives of this paper are: 1) to attempt to identify the reasons for the relative lack of success of tropical forage plant breeding, and 2) to suggest some criteria for judging the potential of future breeding programs so as to improve the success record.

Examples from the numerous documented breeding programs will be considered to illustrate important points. The paper deals mainly with the truly low-land, tropical grasses and legumes, those used for sown, improved pastures rather than those used primarily for harvested forage.

A brief summary of the status of tropical pasture research

Sustained, scientific research on tropical grasses and legumes began early last century in the European colonies, especially in Australia (Eyles et al., 1985) and British East Africa (Boonman, 1993), and also in Hawaii and Puerto Rico. Agricultural research in the European colonies in tropical Africa and Asia was oriented towards plantation and export crops, so the early focus on grasses and legumes was in relation to their role as green manures and for soil conservation in permanent plantations or in rotation with annual cropping, more than as pasture plants for livestock production.

In order to restore soil fertility in the cropping cycle, agropastoral or ley farming systems developed directly from earlier systems of natural fallow in response to increasing pressure on agricultural land owing to population growth. Ruminant livestock production was an obvious means of maintaining some cash flow on mixed farms during the ley portion of rotations and it was soon established that grazing was not incompatible with regeneration of soil fertility for subsequent cropping (Boonman, 1993). In the Australian tropics, there was less interest in plantation crops or agropastoral systems, and the focus from the early years was on permanent pastures sown to improved perennial grasses and legumes (Eyles et al., 1985).

The valuable tropical grasses are the evolutionary result of the grass/large ruminant herbivore ecosystems, mostly in Africa (Clayton, 1983), and hence these grasses have acquired many attributes (high growth rate, protected growing points, underground reserves) that confer survival to heavy, close grazing. With their C_4 photosynthesis, they have an inherently higher growth rate than the C_3 legumes, which are further burdened with the energy cost of rhizobial N_2 fixation. Among the legumes, growth forms that can compensate for this inherently lower photosynthetic rate and that also can withstand the heavy grazing to which tropical grasslands are subject, simply have not arisen. If they had, they would have been recognized by graziers as valued components of natural tropical grasslands. They would have been domesticated, as were the valued temperate forage legumes: e.g. white clover (*Trifolium repens*) and alfalfa (*Medicago sativa*).

By the time that formal, academic pasture research was established, the valuable forage and pasture plants had already been adopted into domestication by farmers and graziers: These plants, by their special attributes, had in effect "forced themselves ... upon farmers" (Boonman, 1993). Early researchers logically focused attention on the widely recognized useful species -- those that farmers actually used. In the temperate zones, an array of grasses and at least two valuable legumes -- white clover and alfalfa -- came under study. They had already domesticated prior to the initiation of formal research. In the tropics, a number of grasses, almost all African, were in use prior to the research station agrostologists (Boonman, 1993; Clayton, 1983). These are still the useful commercial tropical forage plants. Clayton (1983) suggests that "it is likely that all useful species are already known to the herdsman", and that "we need not look for reservoirs of unrealized potential [genetic] resources among the rarer species." Hence, for the temperate forage grasses and legumes and the tropical grasses, the species focus of the new research programs was rather clearly defined from the beginning.

On the other hand, it is generally recognized that no legume comparable to white clover or alfalfa was available to early pasture researchers in the tropics as none had been brought into domestication by farmers and graziers. The striking contrast between the status of forage grasses and legumes for the tropics is illustrated by comparing the respective chapters on genetic resources of tropical forages -- "Tropical Legumes" (Williams, 1983) and "Tropical Grasses" (Clayton, 1983) -- that appear in a CSIRO publication. While Clayton could focus his discussion on 45 grass species (in an 8-page chapter), Williams' "focus" (in his 21-page article) embraces a total of 3,800 legume species in 228 genera that "need to be evaluated" for their possible forage potential.

Early Europeans colonists in the tropics sought to recreate the ryegrass/white clover model in the tropics. Researchers were not always optimistic regarding the eventual success of this model (e.g. Whyte, 1962), but beginning in the 1960's, in northern Australia, a major campaign was launched (Hutton, 1970) to develop tropical legumes for permanent, grass/legume, tropical pastures. Much of the early tropical pasture legume breeding was aimed at domestication of a "tropical white clover", i.e. a perennial, persistent, high quality legume that would form stable associations in permanent grass/legume pastures (Hutton, 1965).

The merits of permanent, grass/legume tropical pastures became something of a dogma among tropical pasture researchers and the "Australian pasture legume school" was subsequently adopted in tropical Latin America. Pasture research in the American and Australian tropics has had a remarkably strong focus on discovering and domesticating novel legume species (e.g. Hutton, 1970). Plant breeding was invoked more than once in this attempt.

To breed, or not to breed? (Cameron, 1983)

Forage crops are different from food crops in that they have no intrinsic value except as transformed into animal product. Hence, the economic importance of a particular species depends upon the attributes of alternative species. Constraints to animal production owing to deficiencies in forage plants can often be rectified by changing species. Hence, plant breeding, which implies a necessary commitment to <u>a species</u>, is inherently risky, unless and until the status of the species is well established by long-term successful use and extensive assessment of the possible alternative species. This mostly is the case for temperate species. It is decidedly <u>not</u> the case for most of the tropical forage species, which are under active study for suitability for particular environments and production systems. The tentativeness of species selection is extreme when it comes to the tropical legumes.

D.F. Cameron's paper considered the relative productivity of introduction, evaluation and selection vs. plant breeding in developing useful new pasture plant cultivars. The only relevant basis from which to formulate predictions for the future was the historical record, not very promising in 1979 for the tropical species, with only one example of a bred cultivar (*Macroptilium atropurpureum* cv. Siratro) that could be counted as a success.

The moderate, brief success achieved by cv. Siratro (between its release in 1960 (Hutton, 1962) and before it succumbed finally to rust (caused by *Uromyces appendiculatus*) in the late 1970's) was invoked often to justified subsequent breeding activity in tropical forages, both in Australia, and, indirectly by example, in other tropical countries in the developing world. Here was a case of a commercial cultivar having been bred from "wild" germplasm accessions of a species with no previous history of domestication or commercial use. If it could be done in *M. atropurpureum*, why not in *Centrosema* or *Stylosanthes*, or any of the other tropical species?

With the clarity of hindsight, it appears that the initial success of the *M. atropurpureum* breeding program that led to the release of Siratro sustained a severely distorted optimism among tropical pasture researchers, both in Australia and elsewhere, regarding the potential of tropical pasture plant breeding as a productive activity in the domestication and improvement of wild species.

Shortly after Cameron presented his paper, others in tropical Australia were also having second thoughts about the efficacy, in the short term, of tropical pasture plant breeding and regarding the magnitude of the potential difficulties involved. E.F. Henzell, then Division Chief, wrote a thoughtful introductory section to the 1981 Annual Report of CSIRO's Division of Tropical Crops and Pastures (DTCP) (Henzell, 1981), where he points out that caution is necessary in launching long-term, expensive plant breeding projects. These thoughts were apparently prompted in large part by the disappointment in the Division at failing to produce a replacement for cv. Siratro in the wake of 20 years of additional plant breeding efforts invested in *M. atropurpureum*.

Cv. Siratro was to prove a unique success, which was not repeated over the subsequent decades in Australia in spite of DTCP's employing as many as eight plant breeders at one time (Eyles et al., 1985), working on a range of tropical grasses and legumes, including *Setaria sphacelata*, *Cenchrus ciliaris*, *Chloris gayana*; *Digitaria eriantha, Leucaena leucocephala,* and several species of *Stylosanthes*, *Centrosema*, and *Desmodium*, among others, and despite the formal naming and release of a series of bred cultivars.

In tropical America, as in Australia, plant breeding was at first seen as the solution to the perceived shortcomings of "promising" new plants. At least one Brazilian state (Rio de Janeiro) funded *Centrosema pubescens* breeding from as early as the mid 1960's (Serpa, 1966), and the Brazilian national research organization, EMBRAPA, included tropical pasture plant breeding essentially from its founding (Porzecanski et al., 1979; Porzecanski, 1982).

The development of tropical pasture plants at the International Center for Tropical Agriculture (CIAT) began in a Beef Production Systems Program, which, between 1977 and 1979, evolved into the Tropical Pastures Program. The Australian school on the importance of tropical pasture legumes, and pasture plant breeding was adopted from the earliest years of forage research at CIAT. As a reflection of the preponderant importance given to legumes, the Program's 1977 Annual Report lists only 154 accessions of forage grasses in a total of 3,400 accessions. Even today, grasses represent only about 10% of forage germplasm holdings at CIAT (ca. 2,000 grasses in ca. 20,000 total accessions). Tropical legume plant breeding (selecting in hybrid *Centrosema* progenies) was being carried out by a CIAT forage agronomist formed in the Australian school (Dr. Bert Grof) as early as 1972 when he arrived in Colombia (Grof, 1982).

Subsequent CIAT breeding programs in *S. capitata*, *S. guianensis* (Cameron et al., 1984; Miles & Grof, 1997), *Centrosema* (Miles et al., 1990), *Leucaena* (Hutton, 1984), were more or less active during the late 1970's and throughout the 1980's. While *P. maximum* breeding activity is reported as early as 1977 (CIAT, 1978), this was a relatively minor project. Not until 1988 was serious grass breeding initiated at CIAT, as well as at EMBRAPA Beef Cattle (Campo Grande, MS) when the current *Brachiaria* genetics and breeding programs began.

Current status of bred cultivars

Nearly two decades after Cameron posed his Shakespearean question, he wrote another, rather more optimistic, assessment of tropical forage plant breeding (Cameron, 1997). Analyzing the Australian record (probably a best case scenario for tropical forage breeding) he presents a table of bred forage cultivars released between 1961 and 1995 for "northern Australia". As evidence of the recent success of tropical forage plant breeding he could now point to 11 (actually 12) bred cultivars released since 1980. Eliminating three cultivars of *Medicago sativa* (not really a tropical species), the current status of the nine remaining bred cultivars is summarized in Table 1. Only six of the nine belong to species (or genera) with a sufficient market share ($\geq$ 3% of total Australian sales of grass or legume seed, respectively) to warrant a separate listing in an inventory of the Australian tropical forage seed market (Loch & Ferguson, 1999): one *Sorghum* spp. hybrid, two cultivars of *Chloris gayana*, two cultivars of *Setaria sphacelata*, and a *Stylosanthes scabra*) Except for the hybrid sorghum cv. Silk, which rated a separate listing owing to its respectable 15% of total forage grass seed sales), it is not possible to determine the proportion of seed sales attributable to the bred cultivars. Again, except for cv. Silk, seed sales of the bred cultivars is not likely very large. Only cv. Cavalcade achieves a rating as high as "medium importance" in a comprehensive listing of tropical forage grass and legume cultivars compiled recently by Loch & Ferguson (1999). Even this is perhaps an exaggeration, given that seed sales for all *Centrosema* cultivars did not achieve even 3% of Australian forage legume seed sales. Four cultivars (*Stylosanthes scabra* cv. Siran; *M. atropurpureum* cv. Aztec; *Chloris gayana* cv. Finecut and cv. Topcut) are recent releases whose success could not be assessed yet in 1999. Not a single bred cultivar appears for five of the six species (or genera) that make up 80% of legume seed sales (*Lablab purpureus*, *Vigna unguiculata*, *Aeschynomene* spp. *Chamaecrista rotundifolia*, and *Neonotonia wightii*), nor for seven listed species or genera (*Cenchrus ciliaris*, *Axonopus affinis*, *Panicum coloratum*, *Panicum maximum*, *Brachiaria* spp., *Pennisetum clandestinum*, and *Bothriochloa*/*Dichanthium* spp.) that make up 59% of grass seed sales. One of the bred grass cultivars (*Digitaria eriantha* cv. Apollo) is rated by Loch & Ferguson as "Released but did not become commercially available".

Forage plant breeding has been in progress in tropical America for nearly as long as in Australia, and the various projects are well documented, as they have generated a voluminous published literature. (*Stylosanthes*: Cameron et al., 1984; Miles & Grof, 1997; *Centrosema*: Miles et al., 1990; *Andropogon*: Miles & Grof, 1990; *Brachiaria*: Miles & Valle, 1996; *P. maximum*: Savidan et al., 1989). In spite of a large and active international market for tropical forage seed (e.g. 80,000 t of *Brachiaria* seed commercialized annually in Brazil (Santos Filho, 1996; Souza, 1999)), the author is aware of only two, minor, bred cultivars of tropical forage species that are currently listed by seed companies. Both are grasses: *Andropogon gayanus* cv. Baeti and *P. maximum* cv. IAC Centenário.

This anomalous situation begs an explanation: the question Cameron posed in 1979 is perhaps even more relevant in 2001 than in 1979 owing to all of the apparently unproductive breeding activity in the intervening two decades. Based on the historical record, even the recent past, there seems little basis for optimism regarding the relevance of tropical forage breeding.

Perhaps the issue will be resolved soon, though not by researchers. Public research funding for tropical pastures research, including plant breeding, has declined steadily over the past 10-15 years, and the research groups formerly devoted to tropical pasture cultivar development are being disbanding. Private companies are not at present involved in tropical forage plant breeding. Nor, if history is any guide to the future, are they likely to become involved, except perhaps in a few very special cases. Plant breeders are, by nature, optimists. Reluctant as we tropical forage plant breeders seem to be to face a pessimistic reality, it does appear that funding agencies are paying attention -- and taking action.

Why Has There Not Been Greater Success In Tropical Pasture Plant Breeding?

The reasons for so much mostly unproductive activity in tropical pasture plant breeding are complex; they differ in time, among countries, and among programs. The reasons for failure seem to fit into three general categories: i) inadequate assessment of target environment, in socioeconomic terms; ii) inadequate institutional base; iii) true biological obstacles.

Inadequate assessment of socioeconomic target environment. A forage breeding project is a major commitment of human and material resources over many years. In deciding whether to embark on a breeding program and to commit these resources, the plant breeder needs to assess honestly the probability of achieving his breeding objectives. Just as important is an honest assessment of whether or not there is a real need for the product(s) of the proposed breeding activities, assuming the breeding objectives are in fact achieved. This is nothing more than marketing research, albeit on a 15- to 20-yr time horizon. It requires, at the least, access to detailed knowledge of the production system in which the bred lines are proposed to be adopted and profitably used. This assessment of market is evidently not commonly done with sufficient rigor.

1 - <u>Choice of species.</u> Forage plants, unlike most other crops, have no intrinsic value, except as transformed to animal product. Hence, species are largely replaceable. The launch of a plant breeding project, unlike a program of germplasm collection and evaluation, is a long-term commitment of resources to <u>a species</u>, so the most fundamental decision the forage breeder must make is the choice of the species that warrants the resource commitment. Much tropical forage breeding has been invested in species, which in hindsight appear inappropriate: undomesticated, unused, or very minor species (for example, essentially all the tropical pasture legumes). Many breeding programs were optimistically designed to rectify perceived problems of persistence in legumes that are not used, but that appeared "promising" on a limited experimental or commercial basis. All the *Stylosanthes* breeding in Latin America (*S. guianensis* and *S. capitata*) fall into this class, as well as *Centrosema virginianum*, and *Desmodium* spp. in Australia. In only one case (*M. atropurpureum*) was a commercially useful product developed by plant breeding in a previously non-commercial species, and at that, the single cultivar produced (cv. Siratro) had a relatively modest and short life, before essentially disappearing from the market. Siratro was not replaced with a better cultivar, in spite of several decades of additional plant breeding. *M.*

atropurpureum has essentially returned to its pre-Siratro status of one more "promising" tropical pasture legume.

There are fundamental difficulties with launching a breeding program in an undomesticated species. It is probably very common that the species is not commercialized owing to attributes totally unrelated to the defects that the researcher perceives as the obstacles to adoption. Lack of commercial use on an extensive scale makes it essentially impossible to make a realistic assessment of cultivar defects or to establish realistic breeding objectives. Which isn't to say that much genetic gain for chosen traits cannot be made in undomesticated species. In fact, genetic gain may be easier to achieve in undomesticated, "wild" species than in more developed agricultural species. Clearly genetic gain has been achieved in many entirely unsuccessful breeding projects (anthracnose resistance in *Stylosanthes*; seed yield in *Stylosanthes*; persistence in *C. virginianum*, etc. etc.). It's just that when the "improved" lines are finally available after years of expense and dedicated effort, no one is really interested, and commercial adoption is minor and short-lived at best.

It is fascinating to contemplate the reasons why so much competent plant breeding effort was expended over so many years on tropical legumes which, even now, represent a miniscule proportion of a minor component of the forage seed market. Undoubtedly the perceived problems were with the legumes -- mainly, but not only, their notorious lack of persistence under grazing. Experiment station study of expanding germplasm collections revealed the apparent cause(s) of legume failure, and breeding objectives were chosen accordingly (see next section). Significant genetic variation for these attributes of interest was readily documented, and breeding programs launched. In most cases, significant genetic gains were documented. Yet, even when the resulting cultivar was released, adoption of the "improved legume cultivar" almost always was disappointing. Tropical pasture legume breeding efforts over the years are an interesting case of optimism, generally encouraged by the demonstrable genetic progress measured in the breeders' nurseries.

The choice to work with an undomesticated species makes realistic decision of need to breed difficult to impossible owing to insufficient information from realistic, commercial production situations. Can the desired goal be achieved by simply changing plant species and substituting a more suitable species -- unlike most crops, this is always an option with forages. Can intra-specific germplasm collection rather than plant breeding achieve the desired genotype? Is there a non-genetic solution to the problem (e.g. relocating commercial seed production sites, rather than breeding for more refined environmental response for flowering and seed set)?

2 - Choice of breeding objectives. The general objectives of forage plant breeding have been amply documented (e.g. Bray & Hutton, 1976) and analyzed (Bray, 1975). The critical importance of clear objectives to eventual success has been stressed by many authors (e.g. Bray, 1975; Bray & Hutton, 1976; Miles et al., 1990; Miles & Grof, 1997; Cameron, 1983). Decisions on breeding objectives often seem clear from the perspective of the experiment station. Bray (1975) asks whose responsibility it is to set breeding objectives. He considers several academic disciplines (plant breeder or pasture agronomist), but does not even mention consulting with grazier or seedsman. For example, the reasons for poor legume persistence often appeared obvious to researchers: e.g. disease susceptibility (*Stylosanthes* spp: Cameron et al., 1984; *Centrosema* spp.: Hutton, 1983; 1985a); low yield (*C. pubescens*: Miles et al., 1990; *Stylosanthes capitata*: Hutton & Grof, 1993); N_2 fixation/*Rhizobium* compatibility (*Centrosema pubescens*: Miles et al., 1990) low seed production (*S. guianensis*: Cameron et al., 1984; *C. macrocarpum*, *C.*

acutifolium: Miles et al., 1990; *C. virginianum*: Clements & Thomson, 1983); poor rooting/stoloniferous habit (*C. pubescens*: Hutton, 1983;1985a); low basal branching (*S. guianensis*: Grof et al., 1970); poor winter survival (*C. virginianum*: Clements & Ludlow, 1977; *S. guianensis*: Cameron et al., 1984; Brolmann, 1979); acid soil tolerance (*C. pubescence*: Hutton, 1983;1985a); broad edaphic adaptation (*S. guianensis*: Cameron et al., 1984); environmental stress tolerance (e.g. drought in *S. guianensis*: Brolmann 1980; flood tolerance in *Stylosanthes*: Brolmann, 1978); insect resistance (*Stegasta bosquella* in *S. guianensis*: Cameron et al., 1984; *Caloptilia* sp. in *S. capitata*: Lenné & Calderon, 1984); seedling regeneration in pastures (*S. guianensis*: McIvor et al., 1979, *M. atropurpureum*: Jones & Jones, 1978).

Again, and with hindsight much clearer than foresight, we can conclude that breeding objectives often have been poorly chosen, at least in cases where achievement of breeding goals does not result in a successful commercial cultivar. A case close at hand is that of the *S. guianensis* breeding project begun at CIAT in 1980 (Miles & Grof, 1997). The stated objectives were to combine high anthracnose resistance with improved seed yield. Good disease resistance was achieved, though it still is not clear if this was resistance only to anthracnose or also to another severe wilting/dieback disease (CIAT, 1995). Persistence of selected lines in agronomic small plots in a high disease pressure environment (Carimagua, eastern Colombian Llanos) was excellent. Seed yield in selected lines was two to three times higher than for highly resistant germplasm accessions. Yet, despite excellent disease resistance in selected lines, persistence in grazed pastures was very poor. Improved seed yields were still insufficient to induce interest in the private seed industry. After minor on-farm testing, the "improved" lines have essentially been shelved.

A large part of the explanation for inappropriate (at least in hindsight) choice of species and breeding objectives seems to lie in the isolation that exists between academic, public sector plant breeders and the forage seed industry that must promote the new cultivars and make a profit on sales of their seed.

3 - <u>Failure to foresee critical importance of key attributes</u>: Lack of persistence under grazing, particularly of legumes, has constrained adoption of bred lines (e.g. *S. guianensis* and *Centrosema* breeding programs at CIAT).

Simple lack of interest among graziers (and reflected by the seed industry) for an expensive, high risk technology like pasture legumes, a technology which has only a marginal potential benefit on the animal productivity, may be the primary reason for lack of commercial success of bred legumes.

An additional possible cause for lack of successful adoption of bred cultivars is simple economics of production, and particularly unfavorable shifts in the profitability of livestock production. Recent low beef prices (coupled with successive years of severe drought) have constrained adoption of most technological production inputs in recent years in Australia. Social and political instability and rural violence in Colombia have almost completely restricted all rural technology adoption. But, even where conditions for technology adoption are favorable, new pasture cultivars must compete with other possible investments and in the production enterprise. Return on investment in "improved" pasture plant cultivars, particularly legumes, is often judged to be unfavorable in comparison with other possible investments.

Inadequate institutional base. Plant breeding is conducted in both public and -- increasingly -- in private (commercial) institutions. To the author's knowledge, no private company is actively conducting tropical forage plant breeding, and efforts to date are confined to the public sector, in Australia and Brazil, principally, and at CIAT.

Another common general cause for failed forage breeding in tropical countries lies in the institutional base. Except for Australia and Brazil, no other country with a large tropical ruminant livestock industry has seriously engaged in pasture plant breeding. Minor plant breeding projects have been carried out in Cuba, but to the author's knowledge, these have not led to released cultivars, at least having a large economic impact. Even in Australia and Brazil (and at CIAT, a publicly funded international agricultural research institution) publicly funded agricultural research, and particularly tropical forages research, is not receiving sustained funding. It is impossible to conduct the long-term research necessary to develop successful breeding programs without equally long-term, stable financing. *Stylosanthes* breeding at CIAT, for instance, has been essentially discontinued over the past 12 years of declining budgets, partly owing to changing priorities, but also owing to lack of funding to support the project. Of the eight pasture plant breeders in the DTCP in 1969 (Eyles et al., 1985), only one remains engaged in tropical pasture plant breeding.

CIAT, which 20 years ago, had three international staff engaged in forage plant breeding, has had only one for the last 17, and with increasingly meager operational budget.

The private seed industry has not reached the level yet to support large breeding programs. This situation may change in the near future if the large multinational seed companies enter the tropical forage seed market, especially in Brazil. This seems increasingly likely as plant variety protection legislation is adopted in more Latin American countries. If private companies do, indeed, establish their own research and cultivar development operations it still remains to be seen whether private investment will improve or weaken stability of funding for tropical forage plant breeding.

Plant breeding, requires a diversity of specialized, professional support. Depending on breeding objectives, support in plant pathology, entomology, plant physiology, and increasingly biotechnology, will probably be productive. For forage plant breeding, all the animal-related disciplines -- animal nutrition, grazing management -- can be invaluable in assessment of breeding populations. The large, public-supported forage breeding programs in northern Australia, in Brazil, and at CIAT, all include multidisciplinary teams of researchers. However, at least in Australia and CIAT, these research teams have seriously eroded in recent years.

Political stability, reflected in stable government policies regarding agricultural sector goals, is the basis of financial stability in research support. In many countries of the developing tropical world, a degree of political stability adequate to see long-term plant breeding projects to successful conclusion simply does not exist.

Another component of successful cultivar development is an institutional mechanism for handling the new bred cultivar at the termination of the breeding program proper. This involves cultivar maintenance, seed multiplication, seed certification, promotion, and diffusion. In many tropical countries, these functions are handled by public entities and effectiveness is not always optimal. In Latin America, a vital and aggressive private forage seed industry is very effective in getting new lines -- if they are really useful -- from the public research institution to farmers. With the increasing internationalization of the tropical forage seed market, a useful cultivar developed anywhere can achieve quick diffusion and adoption through this private seed sector. A graphic case is the fate of a *Brachiaria brizantha* cultivar developed by the Colombian national program from a germplasm accession, and released in 1987. In the absence of a local seed industry, the new cultivar languished for several years with very minor public sector seed multiplication and promotion, but without any real, spontaneous adoption. The line has achieved considerable success after it reached the hands of a Brazilian company, and has been promoted by them in several countries in Latin America. However, it is unfortunate that the Colombian national research institution has received no formal recognition for developing this cultivar: the Brazilian company markets it under their own designation and promotional literature makes no mention of its true origin.

Biological obstacles. In the case of tropical forage plant breeding, the truly biological obstacles to developing successful new cultivars, while many, are relatively minor and mostly possible to overcome.

1 - <u>Ignorance of basic biology of species</u>. Nearly all tropical forage plants are "new" to plant breeding, without a background of knowledge of their basic biology, genetics, reproductive mode, etc. Techniques so elemental as controlled crossing techniques often have to be worked out before breeding can progress. However, these obstacles are often exaggerated, and much useful and productive plant breeding can be achieved in the absence for example of detailed genetic knowledge of the plant. After all, all our crop plants were initially domesticated -- a monumental plant breeding achievement -- when our ancestors knew nothing more about genetics than their observation that offspring tended to resemble parents. After fully twelve years of *Brachiaria* breeding, we still lack a single genetic marker trait, or any detailed information on the genetic structure of natural germplasm or the inheritance of any important agronomic attribute. Another reason for considering plant breeding only for plants that are widely used in commercial agriculture is that many of the details of crop husbandry will be already known, though never in as great detail as for the established food crops.

One of the common justifications of tropical forage breeding, even where no successful commercial cultivar is produced, is the accumulation of knowledge of the plant species involved. Early breeding work with *Stylosanthes* in Australia and at CIAT generated publications on reproductive biology, genetics, marker traits, and improved breeding schemes (Cameron et al., 1984), and useful information on species relationships has been generated by *Centrosema* breeders in their attempts at interspecific hybridization (Miles et al., 1990).

2 - <u>Barriers to genetic exchange</u>: Fertility barriers of one sort or another are not uncommon in tropical forage breeding, owing to the wild nature of the species and inadequate knowledge of inter- or intraspecific variation. One of the major obstacles encountered in the *S. guianensis* breeding work in Australia was the common sterility in progeny of the wide crosses involved, which finally frustrated the efforts to combine the desired traits in fertile lines (Cameron et al., 1984; Cameron et al., 1997). Poor seed set on otherwise promising apomictic hybrid *Brachiaria* selections may be owing to the interspecific nature of the hybridization program (Miles & Valle, 1996; Valle & Miles, 1994).

Ploidy differences may cause difficulties in combining attributes, but these can usually be overcome by judicious use of colchicine, either to develop biotypes of identical ploidy (e.g. for *Brachiaria*: Swenne et al., 1981), or to restore fertility to sterile inter-ploidy hybrids (e.g. fertility of sterile triploid hybrids produced by crossing diploid pearl millet (*Pennisetum glaucum*) x tetraploid napiergrass (*Pennisetum purpureum*) is restored in the colchicine-induced hexaploid (Hanna, 1981; Hanna et al., 1984))

Apomixis is a common mode of reproduction in tropical forage grasses. If obligate, apomixis is an absolute barrier to genetic recombination as the maternal genotype is reproduced without modification in the progeny of apomicts (Asker & Jerling, 1992). However, apomixis seldom is absolute and once overcome as a barrier to genetic exchange, it can be a powerful breeding tool since heterozygous (and heterotic) genotypes can be fixed indefinitely. Apomixis probably delayed the initiation of plant breeding in *Brachiaria* for a decade until sexual material compatible with the natural polyploid apomicts was developed in Belgium (Ferguson, 1974; Swenne et al., 1981; Ndikumana, 1985). Compatible sexuality has been available in tetraploid guineagrass for more than two decades (Savidan, 1980), but plant breeding is still only incipient (Savidan et al., 1989; Hacker & Jank, 1998). In this case, not apomixis, but the availability of abundant natural variation, has lessened the urgency to initiate systematic hybridization programs.

3 - Inadequate germplasm base: While some tropical forage breeding programs have been launched from a limited genetic resources base (e.g. *M. atropurpureum* (Cameron, 1983); *C. virginianum* (Clements, 1989)), lack of adequate germplasm resources can be a serious obstacle to effective tropical forage plant breeding. Breeding programs are usually being conducted in a region where the species is not native, so special collecting missions must be organized to acquire the necessary genetic diversity. Lack of appropriate variation sets limits to the potential progress that can be achieved even under optimal conditions (e.g. Miles et al., 1990). It also poses the very real risk that subsequent germplasm introductions will be superior to the products of plant breeding from an inadequate germplasm base (Harlan, 1983).

Perhaps as important as access to genetic diversity, is an intimate knowledge of the resource at hand. Hence, thorough assessment of germplasm collections is required before parental material can confidently be selected for hybridization.

It is possible that even a large and comprehensive collection of germplasm of the species of interest still does not contain the desired expression of the required attributes. Persistence under grazing of most (all?) *Stylosanthes* and *Centrosema* species may be a case in point. Many years of evaluation of very large germplasm collections, followed by plant breeding projects have (so far) failed to produce genotypes that persist well in grass/legume pastures, at least under conditions of better moisture balance in tropical America (Miles & Grof, 1997; Miles & Lascano,1997).

Even where adequate attribute expression is not found among the available germplasm accessions, judicious use of recurrent selection may produce the required level. After two generations of selection on spittlebug resistance using rigorous artificial screening methodology, clones with resistance levels superior to the original "resistant" parental germplasm accessions are now routinely recovered in the sexual tetraploid *Brachiaria* breeding population developed at CIAT (Cardona et al., 1999; C. Cardona, G. Sotelo, and J.W. Miles, unpublished, 2000).

4 - Long generation time: Tropical forage plants are mostly perennials and most have a generation time of not less than a full year. Breeding progress thus is inherently slower than for an annual crop where two or more generations can often be grown within a single calendar year. Many of the important attributes of perennial forage species (e.g. persistence) simply cannot be assessed in short time periods (Kretschmer, 1989). Seed dormancy can further delay generation turnover, though in vitro embryo rescue (e.g. for *Brachiaria*: Rodrigues-Otubo et al., 2000) may be implemented where justified to overcome this inconvenience.

5 - Complex criteria of merit: The combination of attributes required by successful tropical forage cultivar are complex (e.g. Bray, 1975). Ease of multiplication and establishment (seed yield and quality) are essential, although they have nothing directly to do with pasture productivity and animal performance. The established plants must survive and produce nutritious feed under very stressful conditions of plant-to-plant competition and periodic defoliation in the grazed pasture, over the entire annual and year-to-year range of weather conditions. Fundamentally, the final measure of merit is animal -- not plant -- performance, under all the variability inherent in different regimes of animal and pasture management.

6 - Difficulty/cost in measuring relevant attributes: The complexity of the criteria of merit in forage plants inevitably adds to the cost of conducting a forage breeding program where attributes need be measured on many individuals and families in the breeding populations. The simple factor of individual plant size for most forages demands large land area for testing, with all the attendant costs of preparation and maintenance of breeding nurseries and test plots, adding further to the cost of breeding.

A fundamental difficulty with forage plant breeding is assessing plant merit through animal performance. Many forage plant breeders and agronomists (e.g. Jones & Walker, 1983) have pointed out the fact that most genotypes in the forage breeding population are perforce discarded following agronomic assessment under very artificial conditions before any of them is put to the test by actual grazing animals. The environmental (non-genetic) differences between clipped, agronomic small plots or spaced plants and the grazed pasture (e.g. intra- and interspecific plant-to-plant competition; trampling; selective grazing) give rise to potential interaction with genotype that may entirely obviate, or even reverse, the positive effects of early agronomic selection (Bray, 1975; Kretschmer, 1989).

Forage plants must, at some stage, be grazed, and this requirement adds tremendously to the cost of the evaluation process in a plant breeding program. Realistic grazed plots must be large, individually fenced, and provided with watering and weighing facilities, all increasing the cost of experimentation. Add to these costs the necessity of multi-site, replicated trials continued over several years. Hence, the forage plant breeder needs to balance the constraints of cost with need for accuracy of assessment throughout the culling process, often on the basis of intuitive hunches and educated guesses, rather than hard data, about the magnitudes of genotype-by-evaluation-system interactions involved.

7 - Inadequate breeding methods: Breeding methods applied to tropical forages are generally adaptations of those developed for annual crop breeding -- e.g. phenotypic recurrent selection ("strain building") for outbreeders (mostly grasses), or pedigree selection for the inbreeders (mostly legumes). Pedigree selection may not be appropriate for genetically complex traits in species with long generation time, as is the case in nearly all tropical forage plant breeding programs. Special techniques to enhance the degree of genetic recombination in predominantly inbreeding species that are not amenable to easy hybridization have been proposed and actually implemented (e.g. *S. guianensis*: Miles, 1985; Cameron & Irwin, 1986). Special procedures are also needed for the apomictic polyploid grasses, which have no counterpart among annual crops, and some progress has been made in this area (Valle & Miles, 1994; Miles & Valle, 1996; Savidan, 2000; Valle & Miles, in press). Optimal exploitation of heterosis in polyploids will require special methods to maximize allelic diversity at relevant loci (Bingham, 1980). Rigorous theoretical or modeling studies are needed to arrive at schemes that are optimal both genetically and economically for the different species and different apomictic systems.

Disease resistance is a common objective in tropical forage breeding, and major resistance genes have been identified in the Australian stylo breeding programs (Cameron & Irwin, 1983; Irwin et al., 1984; Cameron et al., 1997). To develop stable resistance for perennial forages, reliance on a single gene, however effective, is probably ill advised. This is perhaps a situation where molecular marker technology would be useful to follow several disease resistance genes, simultaneously, in a backcrossing program. Most other attributes seem to be quantitatively inherited and are probably not readily amenable to marker technology, at least cost-effectively (Moreau et al., 2000; Bernardo, 1999).

8 - Inadequate testing/premature release: Some tropical forage breeding programs have failed to produce successful commercial cultivars owing to testing that, in hindsight, was inadequate (in space or time), or to unforeseen shifts in the biological environment in which the cultivar was to function. It is still unclear whether the failure of a *S. capitata* breeding program initiated in Colombia and closed in Brazil (Hutton & Grof, 1993) was owing to inadequate testing, or to shifts in pathogen populations. A promising line deriving from this program succumbed to anthracnose only during large-scale, pre-release seed multiplication and the projected release had to be aborted.

Selection in naturalized *S. humilis* populations in Australia led to the release of three named cultivars, differing in flowering time (Barnard, 1972). However, the unforeseen introduction to Australia of *Colletotrichum gloeosporioides*, the causal agent of *Stylosanthes* anthracnose, as well as better *Stylosanthes* germplasm (e.g. *S. hamata*: Clements, 1989) resulted to only minor adoption of the new Townsville stylo cultivars. Similarly, a 20-yr breeding effort in *M. atropurpureum*, aimed at developing an improved Siratro (Hutton & Beal, 1977), failed to produce a released cultivar owing, among other factors, to an unforeseen rust disease, first observed in Australia in 1978, to which selected lines were susceptible.

Sometimes a breeding project has been rendered irrelevant owing to unforeseeable developments in a completely different research field. Many years were dedicated to developing low-mimosine lines of *Leucaena leucocephala* (Gonzalez et al., 1967; Hutton, 1985b) before the mimosine-toxicity problem was simply and effectively overcome, at least for ruminants, by introduction of a rumen bacterium capable of degrading the toxic metabolic product 3-hydroxy-4(1H)-pyridone (Jones & Bray, 1983; Jones, 1985).

Conclusions

Many publicly funded, tropical forage plant breeding programs have been carried out in Australia and Latin America. The successes and the failures of these programs are amply documented. As a whole, tropical forage plant breeding has arguably not been a very productive endeavor to date, if success is measured by release *and adoption* of bred cultivars. However, as pointed out by Clements (1989), there is apparently a learning period in the process of plant breeding before programs become productive. Past breeding experiences have produced a large published literature, so that future generations of tropical forage plant breeders will at least start out from a more informed base.

The common failure to produce commercially successful forage cultivars from plant breeding has many causes. An important one has been inappropriate choice of species. Premature launching of hybridization programs in species still only a few generations removed from the wild, and without a proven record in agriculture or adequate knowledge of biology, genetics, or often even the extent of environmental and production adaptations has been common. Inadequate germplasm resources and knowledge of these resources has frustrated many well-intentioned programs. Successful plant breeding is difficult (bordering on impossible) in situations where the target species is not widely used in commercial production systems, or where an extensive base of germplasm resources are not available.

Successful forage plant breeding is a long-term, complex, and expensive process. It demands a wide range of disciplinary expertise and a stable institutional base, conditions rarely found in the tropical world. It seems that in today's economic environment, pasture plant development research programs are contracting rather than expanding worldwide, certainly at least, in the public sector.

On the positive side, a strong commercial forage seed industry, with international scope, exists in several tropical countries. This commercial enterprise will ensure that any really useful new cultivar can quickly achieve wide diffusion, adoption and use. Increasing adoption of plant variety protection legislation provides the incentive for cultivar development and promotion by the private sector. As long as tropical pasture plant breeding remains predominantly a public sector activity, probably the single factor that would most improve chances of success (or at least avoid many of the failures) is intimate contact and constant communication between the public sector plant breeder and the seed industry that will be the vehicle for diffusion of his new bred cultivars.

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Table 1 - Present status of bred cultivars of tropical grasses and legumes in Australia[a]

Species	Cultivar	Year of release	Market share[b]	Status[c]
Grasses:				
Sorghum sp.	Silk	1984	15% (for the cv.)	"Major"
Digitaria eriantha	Apollo	1984	Species unlisted (included in 5% "Other")	"Did not become commercially available"
Setaria sphacelata	Solander	1984	6% (for the species)	"Minor"
Setaria sphacelata	Splenda	1989	6% (for the species)	"Minor"
Chloris gayana	Finecut	1993	15% (for the species)	"Recent release"
Chloris gayana	Topcut	1993	15% (for the species)	"Recent release"
Legumes:				
Centrosema pascuarum	Cavalcade	1984	Species unlisted (included in 5% "Other")	"Medium"
Stylosanthes scabra	Siran	1990	15% (for the genus)	"Recent release"
Macroptilium atropurpureum	Aztec	1993	Species unlisted (included in 5% "Other")	"Recent release"

[a] From Cameron, 1997.
[b] Share of Australian commercial grass or legume seed sales for the species or genus. From Loch & Ferguson, 1999, Table 1.3.
[c] Importance, extent of commercial use at historical maximum. From Loch & Ferguson, 1999, Tables 1.1 and 1.2.