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INITIATION OF A PLANT BREEDING PROGRAM IN ANDROPOGON GAYANUS KUNTH.

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SUMMARY :

Andropogon gayanus is a productive, palatable, pest and drought resistant grass of moderate nutritional quality. Work at CIAT has shown it to be a promising species for sown grass-legume pastures using low-input technology on the acid, infertile soils of the Tropical American savannas. The species is presumed to be naturally cross-pollinated and materials in the CIAT collection exhibit a wide range of phenotypic variability.

Initial plant breeding work will be directed at evaluating CIAT accessions, selecting superior clones for recombination, and obtaining quantitative data on the genetic structure of this species.

Tentative breeding objectives in Andropogon gayanus include improved nutritional quality through increased leaf:stem ratio, improved seed production and seedling vigor, and decreased plant height.

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Andropogon gayanus is a large, perennial, bunch grass native to the tropical savannas of Africa. The species is distributed throughout sub-saharan Africa in areas receiving between 400 and 1500 mm of rainfall annually (3).

Andropogon gayanus has been recognized in Africa as being a productive, highly palatable, and drought resistant forage grass of moderate nutritional quality (2). A. gayanus was introduced at least as early as 1961 into South America (9) but its true potential there was apparently not recognized until CIAT began to evaluate accession number 621 in the acid infertile savannas of Eastern Colombia in 1974.

The original CIAT introduction N^o 621 was obtained in 1973 from the Shika Agricultural Research Station in Nigeria. Until late 1978 no systematic introduction and evaluation of additional germplasm was made. Even now only a limited sampling of the range of species distribution is available at CIAT.

The original introduction has undergone five years of evaluation and shows promise for sown grass-legume pastures with low input technology in the acid, infertile soils of the Eastern Colombian savannas (5).

One of the outstanding attributes of Andropogon gayanus noted in Africa is its ability to remain green well into the dry season and then resume growth rapidly at the onset of the rainy season (2). It is tolerant of burning, a common management practice in the savannas, due to underground rhizomes (3). Forage is readily consumed by cattle (2).

No serious disease or insect pest has been identified after five years of trials in Colombia and even in Africa no economically important pest problems are reported (5).

Probably the major limitation of A. gayanus as a forage grass is its relatively low nutritional quality, especially after flowering has occurred.

The effect of flowering on crude protein content has been studied in Nigeria (cited in 2) (Table 1). The reduction in crude protein content with advancement of flowering is a result of decreasing leaf:stem ratio and the lower crude protein content of stems. Another study from Nigeria (cited in 9) shows the clear difference in protein content between leaves and stems (table 2), where green leaves were found to have nearly double the crude protein content of stems. The in vitro dry matter digestibility of leaves and stems was not shown to differ in this study. Work on other tropical grass species has shown a relationship between leaf:stem ratio and animal intake due to the shorter retention time in the rumen of leaf tissue relative to that of stems (11).

If grazing pressure is sufficiently low to allow selective grazing of green leaf an adequate diet can be obtained for most of the year.

In Colombia, the range of flowering date of plants within CIAT 621 is very broad. Some genotypes will apparently flower at any time during the year, while others exhibit only weak flowering response even under the shortest natural photoperiod in December. Early flowering genotypes have greater stem production and hence, presumably lower nutritional quality during a greater part of the year than late flowering genotypes.

Seed production of A. gayanus is considered acceptable in Colombia, but is certainly reduced by uneven flowering. The earliest and latest flowering plants in the population do not contribute to seed yields with a single harvest at the peak seeding period.

Seed production is also reduced by shattering of ripe seed of this undomesticated species.

Excessive plant height is considered a problem in A. gayanus under grazing since dense, tall growth of undergrazed pastures makes animal management difficult (I. Kleinheisterkamp, unpublished).

Some concern has been expressed about low seedling vigor as compared with other tropical grasses (I. Kleinheisterkamp, unpublished), and improvement in this trait would lead to more reliable establishment under often less than ideal conditions.

Published information on the reproductive biology and genetic variability in A. gayanus is limited.

Apparently the species comprises both diploids ($2n = 20$) and tetraploids ($2n = 40$). The tetraploids are thought to be allotetraploids resulting from the hybridization between diploid A. gayanus and A. tectorum (8).

Flowering is induced by short daylengths. The range of critical photoperiod for induction is reported to be 12 to 14 hours for plants collected at different latitudes in Nigeria (8). The full short-day response of a plant is reported to be achieved by induction of a single leaf (12).

Although no critical studies have been found, the general opinion is that A. gayanus is a naturally cross-pollinated species and that individual clones are highly heterozygous. This is indicated by the strong inbreeding depression observed in first generation, selfed (S_1) lines and by the phenotypic variability observed within S_1 lines (8).

Observations of plant-to-plant variability within and among accessions suggests that considerable genetic variability exists within the species for growth habit, plant height, basal diameter, vigor, leafiness, flowering date, leaf width and length, degree of pubescence, stem thickness, stigma color, and foliage color. A quantification of observed variability, in terms of the proportions due to genetic and to environmental factors and genetic and environmental correlations between different traits, has not been reported. Nor have reports been found on the response to selection for any trait.

With this background of existing information, priorities were established and the initial steps of a research and breeding program formulated.

The quantification of natural cross-pollination under field conditions is critical to the design of an efficient breeding program and to establish isolation distances for seed production.

Establishment of clear breeding objectives is, of course, indispensable to effective plant breeding.

With clear breeding objectives, measurable selection criteria may be specified and the variability of these criteria and the associations among them studied. Once selection criteria are established, selections among and within accessions can begin.

Based on CIAT's previous experience with A. gayanus, six tentative breeding objectives have been identified:

1. Improved nutritional quality.
2. Improved seed production.
3. Improved seedling vigor.
4. Decreased plant height.
5. Maintained drought resistance.
6. Maintained dry matter yield.

These objectives may be refined or modified as experience with this grass under Latin American conditions accumulates.

Selection criteria must be chosen which will allow efficient progress to meet these objectives. A successful selection criteria must be:

1. A character for which genetic variability exists,
2. Measurable on large populations, and
3. Correlated with breeding objectives.

Nutritional quality of a pasture species must ultimately be measured by animal live weight gains. Animal intake and analyses of content and digestibility of dry matter and protein have been suggested as useful criteria of the nutritional quality of forages. With respect to nutritional quality, it appears that the simplest criterion is leaf:stem ratio or leafiness, since leaves have higher nutritional quality than stems and intake of leaves has been found to be greater than that of stems (14). Leaf:stem ratio might be measured by actual cutting, separation, and weighing or by simple subjective estimation on plants in the field. Nutritional quality during the critical dry period probably is reflected by production of green leaves during the dry season and this again could be measured by cutting and weighing or by subjective rating. The supposition that leafiness truly reflects nutritional quality should be confirmed by analyses of nutrient content and digestibility and ultimately by live weight gain studies with animals.

Improved total production of pure seed can be broken down into several specific components. Number of flowering culms per plant, number of panicles per culm, number of spikelets per panicle, percent fertility (caryopses per spikelet), and caryopsis weight are the traits which determine final seed yield per plant. Harvestable yield will be strongly influenced by seed retention. Seed retention can be measured as percent of spikelets retained on a panicle over time after initial anthesis (1). Since seed is harvested on a single date, uniformity of flowering and seed maturation both within and among plants in a population will increase harvestable seed yield.

Seedling vigor can be measured by dry matter production of seedlings at some fixed time after planting. If results with other forage grasses (10) are valid for Andropogon gayanus, the correlation between caryopsis weight (or size) and seedling vigor may be strong enough to allow effective indirect selection of seedling vigor by selection on seed weight or size. Preliminary observations of caryopses of single plants suggest that differences in seed characteristics exist.

Plant height could be actually measured or rapidly estimated on a rating scale.

Drought resistance is reflected by dry matter production during the dry season which could be measured directly or estimated.

Likewise, total dry matter production may be measured or estimated.

With a set of specific measurable traits, the breeder would like to have some idea of the magnitude of genetic and phenotypic variability existing for each trait, the magnitude of the genotype-environment interactions, and the magnitude of genetic correlation between traits (6). This information is particularly important in the initial stages of work with a genetically unknown species.

The ratio of genetic to phenotypic variances, heritability, will indicate the rate of genetic gain expected from a selection program and will dictate the extent of replication necessary to achieve the desired rate of genetic improvement. The magnitude of genotype-environment interaction will indicate the extent of testing over years and locations necessary to obtain reliable data on a given genotype and may indicate the necessity of subdividing the overall breeding program into separate regional programs. The magnitude of the genetic correlation between two traits will indicate the genetic change expected in one trait when selection is for another. This information is useful in choosing indirect selection criteria. For instance, a high correlation between rating of dry matter yield and actual weighing would justify the use of the much simpler rating scale as the selection criterion. Genetic correlation may also indicate undesirable genetic associations between traits which, if found, will imply the necessity of attention to both traits in order to avoid adverse response in one trait when selection is for another.

In addition to obtaining the above mentioned information basic to the rational planning of the future breeding program, the prompt initiation of selection to develop improved cultivars is a high priority for the program.

Specific steps are proposed to meet the priorities of the breeding program.

Quantification of the level of cross-pollination requires the existence of a simply inherited trait, preferable expressed in the seedling, which will permit the easy classification of crossed and selfed progeny of two contrasting types. A close examination of several thousand Andropogon gayanus seedlings has revealed two variegated plants. A study of the inheritance of this trait will be initiated to determine its usefulness as a genetic marker. Less desirable, mature plant traits such as stigma color will also be investigated as clear differences in this trait have been observed. When one or more appropriate genetic markers have been identified, critical studies of level of crossing can be done.

Two field trials will be planted this year. A small-plot replicated trial of the new CIAT accessions will be planted to compare these accessions, primarily in terms of production, leafiness, and flowering date, with CIAT 621. These accessions are also being observed in Brasilia. A comparison of the variation within the different accessions will be made from single plant data. Superior material will be subjected to further study.

The major initial effort of the Andropogon gayanus breeding program will be devoted to a detailed quantitative study of the CIAT 621 population in order simultaneously to identify superior clones and to answer the following specific questions, thus providing a basis for rational planning of future breeding work.

1. What proportion of the observed variability in any given trait is genetic?
2. What is the utility of the Quilichao substation for selection for any given trait?
3. How well do rating scales measure such traits as leaf:stem ratio and plant height?
4. How well does leaf:stem ratio reflect nutrient quality as measured by in vitro analyses?

5. What components of seed yield are most efficient for selection for this trait?
6. How well do caryopsis size and seedling vigor correlate?
7. What possible negative genetic relations (and their magnitudes) exist between two desirable traits (e.g. seed yield and leafiness, or decreased plant height and increased dry matter yield)?

A replicated trial of clonal families (4) is being established which should provide answers to these questions. One thousand random plants of the accession 621 have been established from seed in the field at CIAT Palmira (Figure 1). The 1,000 plants were assigned at random to 50 groups of 20 plants each. A replicates-within-blocks experiment will be established by clonally propagating these mother plants to single-plant plots with two replications in Quilichao and two replications in Carimagua. Thus, each genotype will be replicated four times in total. Each of the 50 groups of 20 plants constitutes a block and the same genotypes occur in the same block of 20 in each of the two locations. The 20 genotypes within a replication, within a block are allocated at random to 20 1 x 1 m plots. The two replications of a group of 20 genotypes are contiguous in the field.

This particular experimental design was chosen with two basic objectives in mind: 1) obtaining estimates of quantitative genetic parameters, and 2) selecting superior clones. These two basic objectives are not in any way incompatible. For a given number of individual plants observed, minimum replication of the maximum number of genotypes will give the best (most precise) estimates of genetic parameters (13). Furthermore, selection efficiency will be high since for selection among clonal families, unless h^2 is very low, minimum replication of a maximum number of genotypes gives greatest efficiency (7). The 1,000 genotypes were blocked in order to control environmental variability across the field. An additional advantage of blocking is that any subset of the 50 blocks can be used to obtain data on a specific trait or set of traits without any complication of data analysis. While more reliable data obviously will be obtained with a greater number of observations, traits difficult or costly to measure, such as yield and in vitro analyses, may be measured on some fraction of the total experiment as resources allow.

The analysis of variance over locations will allow estimation of genotypic (σ_G^2), genotype-environment ($\sigma_{G \times L}^2$), and error (σ_E^2) components of variance (Table 3). Heritability is obtained from the ratio:

$$\sigma_G^2 / \left(\sigma_G^2 + \frac{\sigma_{G \times L}^2}{\ell} + \frac{\sigma_E^2}{r\ell} \right),$$

where ℓ and r are the number of locations and replications, respectively. An analogous analysis of covariance will be performed to estimate the genetic component of covariance between traits. The ratio of genetic covariance to the square root of the product of the genetic variances is then taken as the estimate of genetic correlation between two traits. Since the entries are clonal families, total genetic variance and covariance estimates will be obtained and derived heritability estimates will be "broad sense" estimates. These estimates will be larger than the more useful narrow sense estimates (the ratio of additive genetic variance to phenotypic variance) but will at least give some idea of the magnitude of genetic variability in this population.

As data are obtained from this trial, one or two superior clones in each block will be selected and clonally propagated to an isolated crossing block to form a first cycle population for further cycles of selection. The intercrossing of 50 to 100 parents to form the new population should be quite adequate to maintain a high degree of genetic diversity within the population while selection is sufficiently intense to allow significant genetic gain for the traits under selection.

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Table 1. Whole Plant Crude Protein Content of *Andropogon gayanus* at Five Ages.*

Age (Weeks)	Growth Stage	C.P. (%)
4.0	Preflowering	10.1
7.0	"	8.5
13.0	"	7.5
17.5	Early flowering	6.1
24.5	Full Flowering	4.8

* From: Oyenuga, V.A. 1957. Emp. J. Expt. Agric. 25:237.
Cited in: Bowden, B.N. 1963. Emp. J. Expt. Agric. 31:
267-273.

Table 2. Crude Protein Content and Dry Matter Digestibility
of *Andropogon gayanus*. *

Tissue	C.P. (%)	IVDMD (%)
Green Leaf	7.5	56.3
Stem	3.9	55.2

* Calculated from data presented by: Haggar, R.J. and
M.B. Ahmed. 1975. J. Agr. Sci., Camb. 77:47-52.
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Table 3. Form of the Analysis of Variance of Reps-in-Blocks Experiment of Clonal Families

Source of Variation	Degrees of Freedom *	Expected Mean Square (or Cross Product) †
Total	$lbrn - 1$	
Locations	$l - 1$	
Blocks	$b - 1$	
Locations X Blocks	$(b - 1)(l - 1)$	
Replications/Blocks/Locations	$b\ell(r - 1)$	
Genotypes/Blocks	$b(n - 1)$	$\sigma_E^2 + r\sigma_{G \times L}^2 + r\ell\sigma_G^2$
(Genotypes X Locations)/ Blocks	$b(n - 1)(l - 1)$	$\sigma_E^2 + r\sigma_{G \times L}^2$
(Genotypes X Replications)/ Blocks/Locations	$b\ell(n - 1)(r - 1)$	σ_E^2

* l = number of locations

b = number of blocks

r = number of replications

n = number of genotypes per block

$$\begin{aligned} \dagger h^2 \text{ (broad sense)} &= \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_{G \times L}^2}{l} + \frac{\sigma_E^2}{r\ell}} \\ r_G &= \frac{\text{Cov}_G(X, Y)}{\sqrt{\sigma_{Gx}^2 \sigma_{Gy}^2}} \end{aligned}$$

FIGURE 1. Establishment of Replicated Trials

