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Estimation of Gamete Pool Compositions in Clonal Seed Orchards

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Summary

Nineteen loblolly pine clones were monitored for flowering activity during three successive years. Phenology data and flower production data were used to develop a mathematical model to predict the genetic composition of the resulting seed crops. Variation in pollen production, flower production, foreign pollen intrusion and clone size were found to impact the final gamete distribution. The mathematical model proved useful for evaluating the effects of seed orchard roguing and implementation of cultural treatments.

Key words: phenology, pollen management, seed orchard management.

Zusammenfassung

Das Blühverhalten von 19 *Pinus taeda* Klonen wurde während 3 aufeinanderfolgenden Jahren beobachtet. Phänologische und Daten über den Blütenansatz wurden für die Entwicklung eines mathematischen Modells verwendet, um Voraussagen über die genetische Zusammensetzung des resultierenden Saatgutes machen zu können. Variation in der Pollenmenge, des Blütenansatzes, Fremdpollenflug und Klonegröße hatten Einfluß auf die Gametenverteilung. Das mathematische Modell erwies sich als nützlich für die Überprüfung des Effektes einer Negativselektion und Pflegemaßnahmen in Klonsamenplantagen.

Introduction

Seed orchards are designed and managed to produce forest tree seed that are superior in value to that obtained from seed production areas or random unimproved collections. Superiority of the seed can be judged for quantity and quality which is a function of the percentage of filled seed and the genetic composition of the seed crop. Clonal seed orchards are established by careful selection and testing of many "elite" trees and ideally will provide a gamete pool whose mean genetic value is greatly superior to "unimproved" seeds.

Determining the exact composition of the genetic pool in a wind-pollinated orchard is an improbable task. Roguing, specific combining abilities, and foreign pollen intrusion can affect the accuracy of predicting the genetic composition (ASKEW, 1986), and obtaining accurate estimates of both gamete sources may be difficult. Seed parent contributions can be measured by partitioning the cone harvest into family lots, which is a common practice for forest products companies that plant trees in family blocks. However, pollen-parent contributions are not as easily measured. Electrophoretic analysis of seed samples can be used to provide some insight into the distribution of pollen from clones that have recognizable "markers" and to

measure foreign pollen contamination, (FRIEDMAN and ADAMS, 1981; SHEN, RUDIN and LINDGREN, 1981; MÜLLER-STARCK, 1982; SMITH and ADAMS, 1983; EL-KASSABY and RITLAND, 1986), but laboratory techniques may prove to be impractical and costly to use on a regular basis by forest-product organizations.

The difficulty involved in estimating the pollen contributions of individual clones and the degree of foreign pollen contamination often causes a complete exclusion of pollen values when the potential genetic gain of orchard seed is estimated. An orchard's genetic value is often based solely on seed-parent contributions with either an implicit or explicit assumption that the pollen contributions are evenly distributed among the orchard clones or that they are distributed in similar proportions to the seed-parent contributions (ZOBEL and TALBERT, 1984). Such assumptions place too little concern on fifty percent of the gamete pool.

Roguing and selection decisions are based on these seed-parent value estimates, and predictions of future yields and values of the outplanted forest are calculated from the estimates of the seed's genetic value. Poor estimates of seed-crop worth and misunderstandings of an individual tree's true relative genetic value can drastically alter the future yields of the "improved" forest.

This paper proposes a technique to account for the pollen contributions, and a method for estimating the relative gamete contributions of each clone when sophisticated techniques such as electrophoresis are not available.

Methods

Factors needed to reasonably estimate the gamete pool composition include seed-parent contributions which are reflected in the measurable seed yields at harvest, pollen parent contributions which are controlled by the relative quantity of viable pollen produced by each clone, the duration of its availability and its synchrony with flower receptivity (EL-KASSABY *et al.*, 1984), and the presence of foreign pollen and variation in germination rates on the micropyle which influence fertilization results.

A 19 clone, 20+ year-old loblolly pine (*Pinus taeda* L.) seed orchard in Georgetown, S.C. was chosen for this study. Initial spacing of 16' × 16' was increased to an average of 16' × 32' by a series of roguing prior to the initiation of this study. Two ramets per clone were selected for measurement.

Ramets were selected at random with regard to productivity records but were somewhat biased by attempts to select an array of trees that could be examined without excessive movement of the bucket truck which was used for access into the crowns of the 25-meter-tall trees. Maturity of both the conelets and the pollen strobili was monitored every other day on five randomly selected branches/tree and the presence or absence of receptivity and pollen flight were recorded. Conelet receptivity was assumed when the conelet reached Stage 4L of BRAMLETT and O'GWYNN's (1980) scoring system and continued until the conelet reached Stage 5L. Pollen flight initiation was determined by visual inspection of the strobili for pollen release. Relative levels of both conelet production and pollen production were estimated by empirically surveying the selected ramets of all clones in the orchard, determining which clone was the most prolific and then rating all other clones as a proportion of that most prolific clone. Pollen viability of each clone was assessed by germinating fresh pollen on agar plates and calculating the proportion of

germinating grains. Seed-parent contributions were measured by partitioning each clone's cones at the time of the following year's harvest.

The composition of the harvested gamete pool was estimated by developing a mathematical model that incorporated both the phenology data and the productivity data.

Model Development

Pollen production and seed production data were standardized to provide estimates of the relative productivity of each clone. If we let PP_j = relative pollen production proportion of clone j (with a range of 0 to 100) and let PV_j = % pollen viability of clone J , then:

$$PF_j = \frac{PP_j \cdot PV_j}{\sum_j (PP_j \cdot PV_j)} ; \quad (1)$$

where PF_j is the standardized relative pollen production proportion of clone j .

$$PS_i = \frac{S_i}{\sum_i S_i} ; \quad (2)$$

where PS_i = the standardized relative seed production proportion of clone i .

Also, if we let S_i = the seed production value for clone i then:

After standardization, a clone's pollen production value and seed production value represented the proportion of the total resource produced by that clone. Summation of pollen values across all clones resulted in a value of 100. Likewise, the sum of all seed production values was 100.

The potential pollen contribution of each clone to every other clone's seed crop was calculated by setting RD_{ij} = # receptive days of clone i that overlap with the pollen shedding period of clone j ; so that:

$$\frac{RD_{ij}}{RD_{i.}} = \text{proportion of clone } i\text{'s total pollen capture days that are accounted for clone } j, \text{ and;} \quad (3)$$

$$VP_{ij} = \frac{\frac{RD_{ij}}{RD_{i.}} \cdot PF_j}{\sum_j \left[\frac{RD_{ij}}{RD_{i.}} \right] \cdot PF_j} \quad (4)$$

where VP_{ij} was the proportion of viable pollen on flowers of clone i that originated from clone j . This procedure was repeated for each seed parent. Self-pollination was assumed to be negligible.

The proportion of total gametes in the pool that was expected to arise from the mating of clone i and clone j was:

$$GC_{ij} = VP_{ij} \cdot PS_i, \quad (5)$$

and the total proportion of gametes contributed to the pool by clone i was:

$$G_i = \frac{1}{2} (GC_{i.} + GC_{.i}). \quad (6)$$

The genetic value of the orchard crop is then:

$$GVO = \sum (G_i \cdot gv_i); \quad (7)$$

where gv_i is the genetic value of clone i . Finally, the percentage improvement estimate was:

$$PI = \frac{GVO - GVC}{GVC}; \quad (8)$$

where GVC was the genetic value of the checklot.

Foreign pollen impacts were estimated by assuming that a constant percentage of the orchard pollen cloud was attributable to foreign pollen throughout the breeding season. Foreign pollen can enter the gamete pool of the final seed crop as the sole pollinator during periods of conelet receptivity that do not coincide with pollen shedding from any orchard clone, and during orchard pollen shedding, as a proportion of the total pollen cloud in the orchard. Inclusion of foreign pollen in this model was accomplished by treating it as another clone with a specified pollen contribution level and assigning it a genetic value for inclusion in the genetic value calculations.

This mathematical model was used in a computer simulation model that allowed for the direct computation of seed orchard genetic worth after entering the production and phenology data for a given pollination season. The simulation procedure also allowed for manipulation of the data to simulate several orchard conditions:

- 1) uniformity in # of ramets per clone;
- 2) uniformity in pollen production;
- 3) uniformity in pollen viability;
- 4) uniformity in seed production;
- 5) total synchrony in phenology;
- 6) any combination of these factors.

These simulation options allowed for estimation of the change in genetic value of the seed crop as a result of manipulations of the orchard structure and function.

Flowering phenology results from three pollination seasons and genetic estimates for a single example year were studied in detail.

Results

Variation in Phenology and Productivity

Both male and female flowering phenologies varied among clones in all three years 1983 to 1985 (*Figure 1*). Yearly variation in flowering duration was also apparent but relative clone performance was fairly consistent from year to year. In each of the three years, several clones were releasing pollen prior to the beginning of flower receptivity and, in several cases, at least one clone (e.g. # 14) had finished shedding pollen before the beginning of the receptivity period of a major portion of the orchard clones. Several clones also continued to produce receptive flowers after all but a few clones had finished shedding pollen. The duration of the flowering season in 1984 was less than in the other two years. This may have been due to colder weather than usual during the pollination period. Overall the orchard was fairly stable in its phenology pattern; *i. e.*, some clones consistently produced receptive

Table 1. — 1983 phenology values for 19 loblolly pine seed orchard clones, based on examination of two ramets per clone.

| Clone # | # days of pollen shedding | # days of flower receptivity |
|---------|---------------------------|------------------------------|
| 1 | 13 | 8 |
| 2 | 18 | 11 |
| 3 | 17 | 9 |
| 4 | 16 | 7 |
| 5 | 13 | 7 |
| 6 | 12 | 9 |
| 7 | 16 | 10 |
| 8 | 17 | 9 |
| 9 | 18 | 10 |
| 10 | 18 | 10 |
| 11 | 11 | 8 |
| 12 | 15 | 8 |
| 13 | 14 | 10 |
| 14 | 13 | 12 |
| 15 | 13 | 11 |
| 16 | 13 | 10 |
| 17 | 12 | 7 |
| 18 | 15 | 8 |
| 19 | 18 | 12 |

flowers or shed pollen early in all three study years. The 1983 pollination season and the subsequent cone harvest of 1984 will be used as an example throughout the remainder of this paper.

In 1983, pollen shedding duration for a single clone varied from 7 days (# 17) to 16 days (# 3 and # 8) and flower receptivity varied from 5 days (# 4 and # 5) to 11 days (# 19) (*Table 1*). The product moment correlation between pollen shedding duration and flower receptivity duration was $r = 0.45$. Synchronization of pollen shedding and flower receptivity was such that many clones had virtually no opportunity to cross-pollinate with other specific clones. For example, clone # 1 had finished shedding pollen before clones 4, 5, 7, 9, 10, 11, 12, 13, and 18 had become receptive. Moreover, some clones were completely finished shedding pollen before the vast majority of the other clones developed receptive flowers and many clones continued to produce receptive flowers during periods of little orchard pollen shedding (*Fig. 1*). Pollen shedding by loblolly pine trees in the vicinity of the orchard continued throughout the pollination season.

Variation in production of flowers and in pollen viability was also apparent. Flower productivity measured by seed parent contribution proportions varied from 0 to 14 percent of the total seed crop. Pollen viabilities ranged from 32 percent to 100 percent. Relative empirical estimates of productivity ranged from 70 percent to 100 percent of the maximum producing clone for pollen and 25 percent to 100 percent of the maximum producing clone for female flowers.

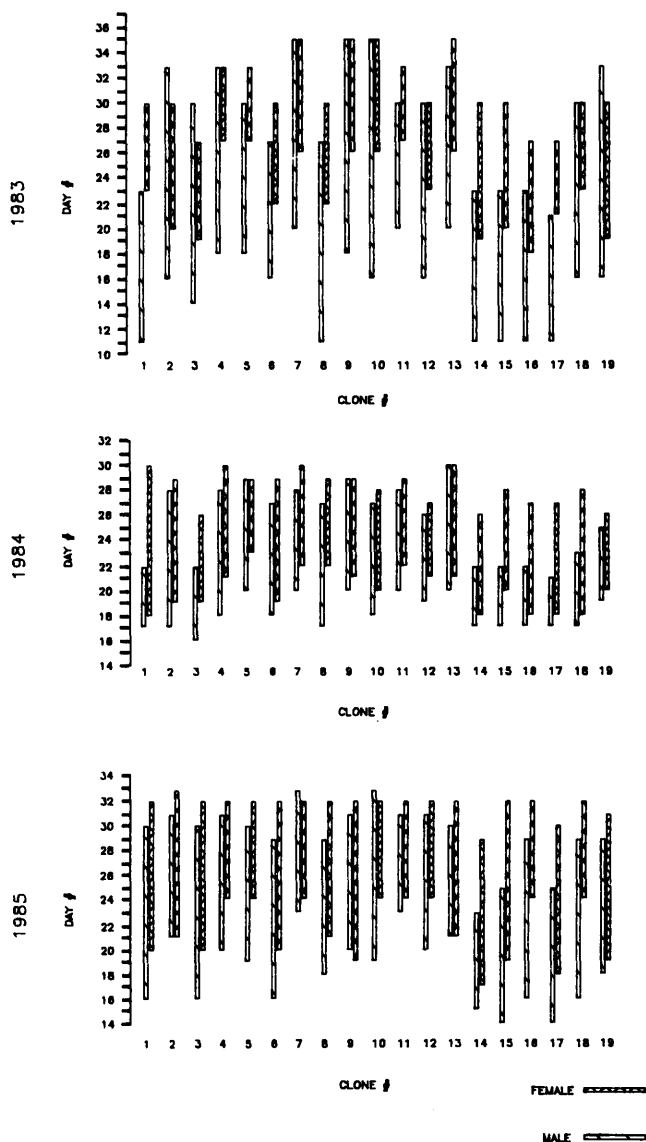


Figure 1. — Duration of female flower receptivity and pollen flight for 19 loblolly pine clones in three consecutive years measured in days from observation Day # 1.

Variation in Genetic Value Estimates

Genetic worth of the final seed crop was calculated as a straightforward mean of individual clone genetic values which will be used as a benchmark for comparing other techniques. Progeny test averages for height (ft) and volume (cu. ft.) at age 8 years were used as the genetic volumes in this study. A series of mathematical weightings was then applied to the orchard values and a new genetic mean was calculated and expressed as a % increase over the checklot value level:

| | vol. | ht. |
|--|------|-----|
| 1) Straight mean | +42 | +63 |
| 2) Weighted by # of ramets per clone | +48 | +55 |
| 3) Weighted by seed production per clone | +46 | +72 |
| 4) Weighted by total gamete production | +45 | +46 |

In this example, the impact of not weighting the mean by the total gamete contribution when calculating the genetic mean is small. Even so, a 3% difference in estimated genetic value for volume may be translated into large volume differences when applied to large planted areas and

capitalized over several rotations. On a smaller orchard with fewer clones or in an orchard with a more scattered phenology, the results could be more dramatic.

If individual clones are examined for their genetic values, several different adjustments can be used. The true genetic value of a clone in a given orchard is not its general combining ability as calculated from progeny test scores but is a weighted average of its gca and the gca its pollen contributors which will probably change from year to year, particularly during the early years of the orchard. If equal pollination from all orchard clones is assumed for all seed parents, the individual clone values would be equal to $\frac{1}{2}$ gca of the clone plus $\frac{1}{2}$ of the average gca of the orchard. Clones with gca's below the orchard average will have their genetic scores improved and those above the average will have their scores reduced; thus, use of an average pollen parent value is an over-simplification. A weighted pollen parent average should be calculated for each clone based on its phenology relative to the potential pollen parents' phenologies.

Both of these techniques were used on the example orchard. The ranking of the individual clones was not changed by either technique but using a unique weighted average for each clone caused a positive increase in the average genetic value for 13 of the 17 seed producing clones. Two clones were not used in this exercise because their seed contributions were negligible. Any decisions about roguing based on individual clone genetic values may be affected by this shift in scores even though the rankings remain the same. Orchards with more severe synchrony problems or orchards with greater variance scores may have changes in rankings as well as changes in relative values.

Variation in Genetic Mean Due to Orchard Manipulation

Impacts of roguing or other cultural treatments were tested by selecting an appropriate option in the computer simulation prior to execution. Values were computed both with and without a 20% foreign pollen (FP) influence and expressed as a % increase over the checklot value:

| | vol. | | ht. | |
|--|-------|--------|-------|--------|
| | 0% FP | 20% FP | 0% FP | 20% FP |
| 1) Without manipulation | +45 | +41 | +66 | +60 |
| 2) Equal ramet # | +39 | +35 | +58 | +52 |
| 3) Equal flower production | +44 | +40 | +66 | +60 |
| 4) Equal pollination | +45 | +40 | +69 | +62 |
| 5) Synchronized phenology | +46 | +42 | +70 | +63 |
| 6) Completely uniform orchard (integrating 2, 3, 4, and 5 above) | +42 | +38 | +63 | +57 |
| 7) Roguing a) 1 clone | +46 | +46 | +69 | +63 |
| b) 2 clones | +48 | +50 | +70 | +63 |
| c) 3 clones | +50 | +45 | +70 | +64 |

Most orchard manipulations resulted in little or no change in the expected genetic mean of the seed crop for this particular orchard configuration. However, equalizing the number of ramets reduced the volume gain by 6%. This should be expected in a rogued orchard because varying the number of ramets will increase the relative contributions of the larger, better clones. Synchronization of the phenologies produced a 1% gain and equalizing the pollen production resulted in no changes. Equalizing the flower production caused a 1% loss of expected gain which indi-

cates that trees with few flowers are the recipients of the poor orchard pollen and the foreign pollen. Roguing increased the expected gain in all cases. Loss of gain in the uniform orchard is the result of increasing the relative contributions of the smaller, poorer clones, mainly by increasing their number of ramets.

Impacts of Foreign Pollen

Foreign pollen serves to dilute the pollen gamete resource. It is reasonable to assume that any background pollen that enters the breeding program will be of lesser genetic value than that of the individual orchard clones. Due to the diversity of genotypes of trees of like species that surround most seed orchards it is also reasonable to assume that the foreign pollen influence will be present throughout the entire pollination period of the orchard.

Foreign pollen poses two threats. First, when an orchard clone is producing receptive female strobili and orchard pollen is not being shed, the background pollen serves as the only source of male gametes. If the receptivity period of those clones is finished before the orchard pollen is available, there will be no competition for fertilization within the affected ovules. Second, when orchard pollen is being shed, the foreign pollen is part of the pollen cloud and in some cases will play a larger role than any one orchard clone. In this model, the foreign pollen was incorporated as an additional clone with its genetic value set to be equal that of the commercial check and a variable degree of impact determined on a daily basis by the availability of orchard pollen. For this demonstration, the foreign pollen's genetic value was set to be the same as the checklot genetic value. The impact of this setting was slight for all orchard manipulations. About four percent of the gain was lost due to a 20% foreign-pollen contribution to the pollen cloud.

Discussion

The purpose of conducting a monitoring program on pollen dispersal and strobili receptivity is to attempt to account for all of the gametes contributed to the seed crop. Many factors can alter the supposed gamete composition and some cultural treatments imposed on the orchard can have unanticipated impacts. Any accounting procedure will quickly focus on the pollen contributions as the most difficult factor to quantify. Efforts should be concentrated on the pollen factors that can be measured with some degree of accuracy or those that can be reliably estimated.

Synchronization of pollen shedding and flower receptivity are of major importance in gamete pairings and in the impact of foreign pollen. EL-KASSABY *et al.* (1984) found variation in phenology to be a problem with Douglas-fir (*Pseudotsuga menziesii* (MIRB.) FRANCO), but GRIFFIN (1984) found it to be negligible in radiata pine (*Pinus radiata* D. DON). Major variations in pollen production levels and viability are also of importance, but minor variations have no appreciable effect on the outcome. If variation in production and viability are slight they should be considered as equal for overall genetic value estimation.

This model does not account for specific combining abilities, which, if sizable, may greatly affect the production value of the seed crop. Disproportionate mating combinations may result due to flowering synchronization or physical location of individual clones within the orchard. The specific combining abilities of these clones need to be investigated if the mating proportion is significantly large,

in which case the roguing pattern may be adjusted to alleviate potential problems. The value of utilizing a model such as the one proposed is that the individual mating types can be estimated and the clones screened to eliminate potential problems.

Orchard size as determined by the number of clones and the number of ramets per clone may also play an important role in the genetic value estimate. As the number of clones is decreased, the importance of non-synchrony becomes greater. Orchards with large numbers of clones will more than likely have sufficient pollen mixtures throughout the pollination period to dilute the effect of foreign pollen and to minimize any disproportionate mating possibilities. Smaller orchards may have periods where little or no orchard pollen is available, and the opportunity for a severe impact of foreign pollen is created. Increasing the number of ramets per clone in small orchards will help to minimize this lack of pollen by providing more source trees from the few clones that are producing at any given time.

The orchard used for this study is of first-generation origin. As the generations advance, the degree of relatedness among orchard members is also likely to increase and may result in greater threats of inbreeding depression and perhaps exacerbate synchrony problems. Advanced generation orchards need to be carefully evaluated to assess both the gamete contributions of individual trees and the physiological limitations that may affect the viability of the seeds and the genetic value of the resulting seedlings.

Roguing of the orchard in any generation will have an effect on the genetic value of the seed crop. One of the factors to consider in any roguing plan is the role that pollen from inferior trees play in seed yields, and the role a potential roguing victim would play as a receptor of pollen from the good combiner trees. Most roguings for genetic purposes are based on the genetic value of the individual clone as measured from a progeny test not from a seed sample collected from the orchard trees after natural orchard pollination. Rankings based on progeny tests may be very different from those based on orchard collected seed if variation in pollen production and pollen viability and synchrony problems are present. Hence removing a tree that tested poor in a progeny test may, in fact, be removing a tree that is a prime receptor of the major portion of the pollen contribution of the better clones in the orchard. If this is the case, the orchard value may be lowered rather than raised after the roguing.

Conclusion

Estimation of projected genetic gains from a seed orchard need to include information on the production levels of both male and female gametes as well as flowering phenologies. Clonal variation in production of pollen and female strobili may be diluted in orchards with large numbers of clones, but smaller orchards may vary greatly in productivity from unadjusted estimates. Roguing decisions need to encompass the trees' value as both a seed contributor and as a pollen contributor and pollen receptor. Foreign pollen must be accounted for if the average genetic value estimates are to reflect the orchard's potential. Genetic value estimates are only as good as the information on which they are based. Ignoring or deletion of pertinent information because it is difficult to obtain or is incomplete serves only to confuse the breeding program goals and achievements.

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Genetic Variation in Growth and Form Characteristics of *Pinus caribaea*

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Abstract

Significant difference in total height and highly significant difference in stem form were found among 16 provenances of a 10 year old provenance trial of *Pinus caribaea* in one location within the savanna region of Nigeria. No significant differences were found for dbh, branch thickness and branch angle. The average height of the 15 provenances of *P. caribaea* var. *hondurensis* was significantly better than the one provenance of *P. caribaea* var. *caribaea* represented in the study. However, the variety *caribaea* provenance had straighter stems than the variety *hondurensis* provenances.

Except in total height in which the Los Briones provenance had the lowest performance, no significant differences existed in the five characteristics examined among the provenances of *Pinus caribaea* var. *hondurensis*. As a result of this and because very low genetic parameters were recorded for all the characteristics, the conclusion is that limited genetic improvement can be obtained by selecting any one of these provenances for use in the savanna region of Nigeria. However, genetic improvement through the selection of individual trees with outstanding phenotypes across the provenances is feasible because of consistently large tree-to-tree variation. Moreover, moderately high heritability estimates were recorded for total height (0.46) and stem form (0.56).

Stem form had the highest heritability estimate (0.56) and the greatest potential for genetic advance (expressed as a percentage of the mean, 7.5%), among the characteristics examined. It is a possible characteristic to be selected for among the *Pinus caribaea* provenances tested.

Key words: *Pinus caribaea*, height diameter, stem form, branch thickness, branch angle, phenotypic coefficient of variation, genotypic coefficient of variation, heritability, genetic advance.

Introduction

Pinus caribaea MORELET, grown as an exotic tree species in Nigeria, has adapted itself well to many ecological zones of the country. For this reason and its well known economic values, considerable interest has developed for use of

this species in afforestation and reforestation programmes in different parts of the country.

To identify the most suitable seed source of *Pinus caribaea* for use in afforestation programmes in the savanna region of Nigeria, provenance trials were started in 1968. They were established at three locations, and contained nine provenances covering the three described varieties — *hondurensis*, *caribaea* and *bahamensis*. Subsequent reports on this trial by OJO and SHADO (1973), OTEGBEYE (1980), and OTEGBEYE and SHADO (1984) showed that variety *hondurensis* was superior to the other two varieties in growth rate. It was closely followed by variety *caribaea* while variety *bahamensis* had the least growth rate.

Since *Pinus caribaea* var. *hondurensis* has the best growth rate among the tree varieties tested in Nigeria, subsequent provenance trials were composed almost solely of that variety. One such trial, established at Afaka in 1973, contains 16 provenances of the species, 15 of which were of variety *hondurensis* and one of variety *caribaea*.

The objectives of the study were to: determine the variation pattern in some growth and morphological characteristics among 16 provenances of *Pinus caribaea* and estimate some genetic parameters for each of the characteristics under consideration.

Materials and Methods

Fifteen provenances of *Pinus caribaea* var. *hondurensis* and one of var. *caribaea* were assessed for total height, diameter at breast height (dbh), stem form, branch thickness and branch angle in 1983 at 10 years of age. A description of the seed sources is given in Table 1. The trees were planted at Afaka in June, 1973 using potted seedlings raised in Savanna Forestry Research Nursery at Samaru. Afaka is about 30 km south of Kaduna at altitude 10°37'N, longitude 7°17'E, altitude of about 600 m; it has a mean annual rainfall of about 1290 mm.

The experimental design was a randomized block with five replications. The trees were planted at an espacement