loci in the companion study (MERKLE and ADAMS, 1987). Although Douglas-fir is highly variable at the single-gene level, less than 1% of the genetic diversity in 22 breeding zones could be attributed to differences among zones. Furthermore, the small amount of variation in allele frequency among zones was not related to geography. At least in this species, the common-garden approach and allozyme studies appear to give different information when used for identifying geographic patterns of adaptive differentiation.

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The Incorporation of Early Testing Procedures into an Operational Tree Improvement Program

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Abstract

Seedling shoot dry weight can be used as an early testing trait for loblolly pine. Seedlots that have both good germination and a small shoot dry weight in greenhouse tests tend to have average or below average volume growth in field tests. This relationship allows the use of shoot dry weight in the greenhouse to be used as a trait for culling some progenies prior to field testing in a tree improvement program. Two-step testing procedures combine independent culling at the end of the first test (greenhouse) with assortative mating for the second test (field) to both reduce progeny testing costs and increase genetic gain. These procedures increase the efficiency of an operational tree improvement program by reducing the funding required for field testing to obtain the same or slightly greater genetic gain. The implementation of shoot dry weight as an early testing trait in the first and second generation loblolly pine breeding program for the Western Gulf Forest Tree Improvement Program is discussed.

Key words: Loblolly Pine, genetic gain, breeding, progeny testing, assortative mating.

Introduction

Tree improvement is widely accepted as a valuable silvicultural tool in the southeastern United States. To meet regeneration demands, approximately 4,000 hectares of seed orchard have been established. About 83 percent of the planting programs in this region utilize improved planting stock produced by these seed orchards. The resulting improvements in growth, form, and disease resistance represent significant economic benefits to forest landowners. Progeny testing is the backbone of any tree improvement program and intensive testing programs

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have been developed to support current and future seed orchards. These testing programs are the most expensive component of a tree improvement program. Progeny tests may be established to satisfy numerous objectives; however, in operational tree improvement programs, the major objectives of progeny testing are parental evaluation and the production of a base population for advanced generation selection (McKinley, 1983).

Tree species have long generation intervals. The major contributing factors to the long breeding cycle are the delay between grafting and flowering, and the time required to grow progeny tests prior to parental evaluation and selection. Substantial efforts have been committed to reducing both of these factors. Fertilization, drought stress, and the application of plant hormones are now widely used to accelerate flower production. Initially, selection in progeny tests was delayed until approximately one-half of the projected rotation age. It was believed that this age was needed to obtain an adequate estimate of performance at harvest age. Recent work has indicated that adequate estimates of rotation age performance can be obtained at much earlier ages (Lambeth *et al.*, 1983); therefore, most selection is currently done between the ages of five and ten years.

Efforts have been made to further reduce the selection age. For instance, superior seedlings selected in nurserybeds often maintained their superiority in field trials; however, it has not been possible to separate the nurserybed effects from the genetic effects in these studies (Zobel *et al.*, 1957; LaFarge, 1975). Later work utilizing the results of either greenhouse and/or growth chamber studies appears to be more useful in selecting seedlings of superior genotypes. The first work with loblolly pine (*Pinus taeda* L.) showing a correlation between first-year seedling growth characteristics and field data was reported by Cannell *et al.* (1978). Seedling growth rates were significantly correlated with eight-year volume production in the field and the correlations were improved when the seedlings were grown in regimes which simulated field conditions. Other studies with loblolly pine have indicated varying degrees of success in predicting field performance from greenhouse and/or growth chamber tests (Waxler, 1980; Miller, 1982; Davision, 1984; and Strickler, 1984).

The objectives of this paper are to examine existing data from early testing studies which utilized loblolly pine seedlots from the Western Gulf Forest Tree Improvement Program (WGFTIP) and to describe how early testing procedures can be incorporated into an operational tree improvement program.

Early Testing Studies

The efficiency of breeding programs may be evaluated by comparing the amount of gain obtained per year in the breeding cycle or the funding required to obtain a given amount of genetic gain. To reduce the length of the breeding cycle and therefore increase the amount of gain obtained per year, early testing studies have concentrated upon identifying families with outstanding field performance at an early age. Because this objective has not been consistently realized, an alternative approach for the utilization of early testing procedures would be the elimination of average or below-average performing families from field tests. This approach would not increase the amount of genetic gain obtained per breeding cycle for a constant-sized breeding population; however, it would result in a reduced cost for field testing. This would increase the efficiency of an operational program by decreasing the cost required to obtain a given amount of gain. In utilizing complementary mating designs, combined with a step-wise testing procedure, the elimination of poor performing families prior to developing the selection population could also result in increased genetic gain.

As shown in *Figure 1*, there are two types of errors in selecting or rejecting families based on early testing data. The first type of error (A) would be the rejection of families with poor greenhouse performance that would later perform very well in field tests. The second type of error (B) would be to select families with a good greenhouse performance that would not perform well in later field tests. These types of errors assume different levels of importance if early testing is viewed as the selection of a few outstanding families or the rejection of a few poor families. When selection of the best performing families is the objective, both types of errors are detrimental to the breeding and testing program. One can simultaneously select families with poor field performance and reject families with good field performance. When the early testing procedure consists of the rejection of a few poor families, the important consideration is the rejection of a family that would perform well in the field (type A error). Assuming that all of the families would originally have to be field tested, the families with good performance in a greenhouse test and poor field performance would still be eliminated on the basis of field tests.

Eleven studies have benn completed utilizing material from throughout the Western Gulf Forest Tree Improvement Program's operating area (*Table 1*). The first six studies (study numbers 1 to 6) consisted of M. S. theses and investigated the effects of different growing conditions upon the ability to predict field performance from seedling traits. These studies were completed under either greenhouse or growth chamber conditions. Studies 1 to 4 utilized the same 10 open-pollinated families from East Texas. One of the ten families was changed for study numbers 5 and 6. Shoot dry weight at 6 months was the seedling trait which was most consistently correlated with field data. The remaining studies (numbers 7 to 11) were intended as operational trials to verify the results of the previous studies and, with the exception of study 10, were conducted under greenhouse conditions. Study 10 was

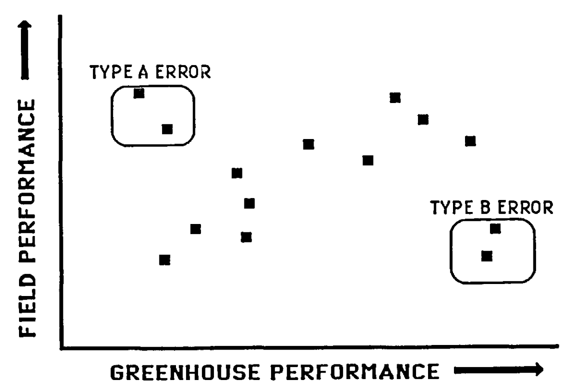

Figure 1. — An illustration of type A and B errors in early testing studies. Type A error involves the rejection of families with good field performance based on greenhouse data. A type B error occurs when a family with good performance in a greenhouse test does not perform well in field tests.

Table 1. — List of studies used to develop the early testing procedure described in the text.

Study No.	Seed Provenance	Environmental Variable	No. of[1] Families	Reference
1	East Texas	Water	10	Waxler, 1980
2	East Texas	Fertilizer	10	Miller, 1982
3	East Texas	Daylength (14 hr.)	10	Davison, 1984
4	East Texas	Daylength (18 hr.)	10	Davison, 1984
5	East Texas	CO_2	9	Strickler, 1984
6	East Texas	Temperature	9	Strickler, 1984
7	South Arkansas		9	TX For. Service Unpublished Data
8	South Louisiana		6	TX For. Service Unpublished Data
9	East Texas, South Louisiana		7	Louisiana State Univ.[2] Unpublished Data
10	South Arkansas		10	TX For. Service Unpublished Data
11	East Texas		20	TX For.Service Unpublished Data

[1]) Where data were available, families with less than 85 percent germination were deleted.
[2]) Personal communication, Dr. JOHN R. TOLIVER, Louisiana State University, Baton Rouge, LA.

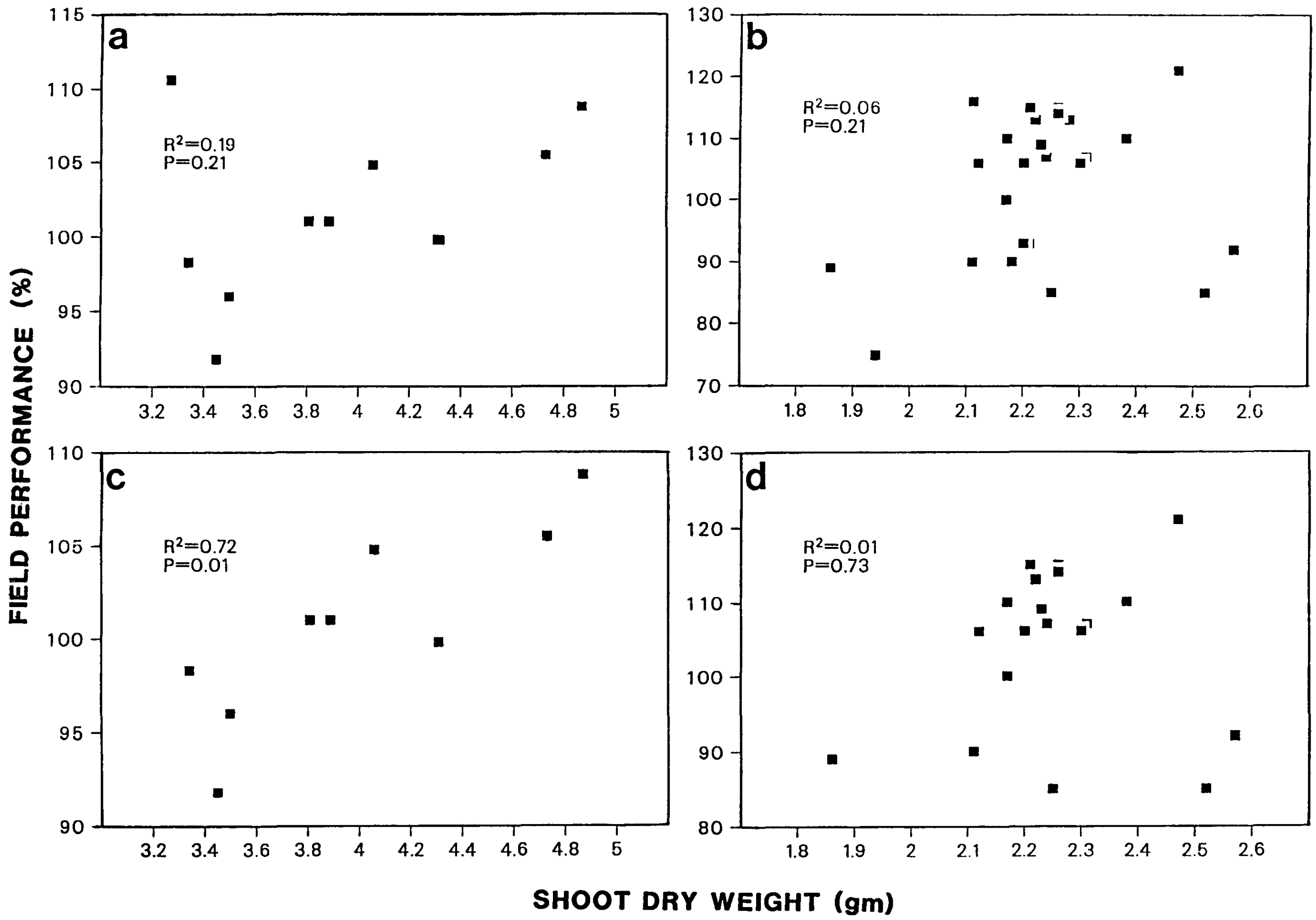

Figure 2. — Scatter diagrams, coefficients of determination (R^2) and the occurrence of type A error in study no. 6(a); type A and type B errors in study no. 11(b). Type A errors are eliminated after culling at 85% germinative capacity (study no. 6 c and study no. 11 d).

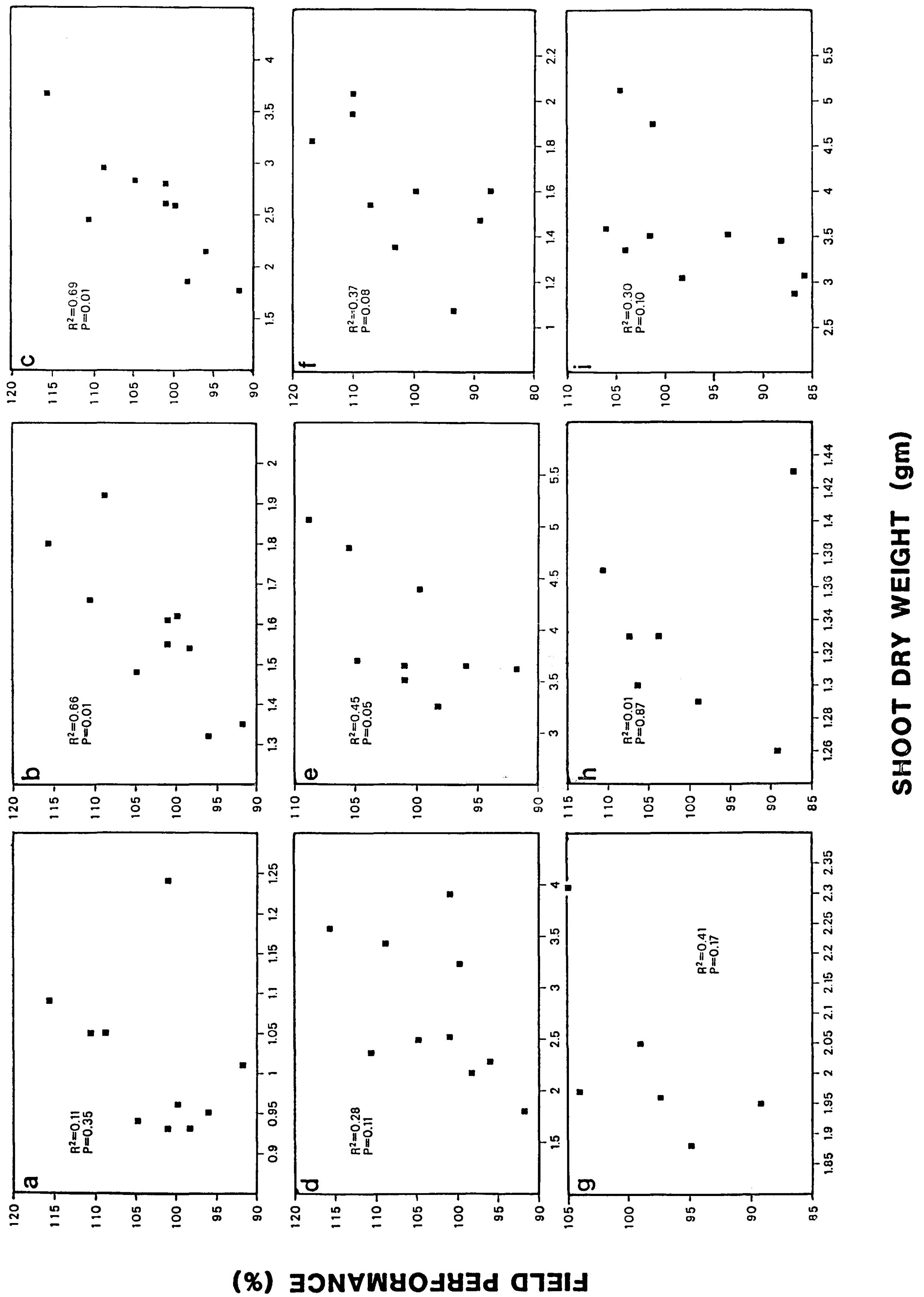

Figure 3. — Scatter diagrams and the coefficients of determination (R^2) for: a) study no. 1; b) study no. 2; c) study no. 3 d) study no. 4; e) study no. 5; f) study no. 7; g) study no. 8; h) study no. 9; and i) study no. 10 from *Table 1*.

conducted in growth chambers. Study numbers 7, 8 and 11 used different sets of open-pollinated families from South Arkansas, South Louisiana and East Texas. Control-pollinated families of a different set of parents from South Arkansas were used in study 10. A portion of the open-pollinated families used in study 9 were used in some of the other studies. Approximately 60 different families were used in these studies.

Progeny test data were available for all of the families. Field performance was evaluated as estimated percent genetic gain in volume production at age 20 compared to the plantation average using standard WGFTIP data summary procedures. Each of the families used in all of the studies except number 11 was evaluated in several field tests, the families in study 11 were established in only one field trial. Ages of field trials varied from five to 20 years.

Figure 2a shows an example of a type A error in study 6 while Figure 2b shows examples of both types of errors (study 11). Since experience has indicated that families with poor germinative capacity usually produce small seedlings, the germination data were reviewed for as many of the studies as possible. The germination data for the studies shown in *Figures 2a* and *2b* revealed that families producing type A errors had below average germination. *Figures 2c* and *2d* show the same studies with the deletion of any family that averaged less than 85 percent germination. The incorporation of a culling level on seed germination eliminated type A errors, faster growing families in the field were not eliminated on shoot dry weight in greenhouse tests.

Figure 3 shows scatter diagrams for the remaining nine studies in *table 1*. When germination data were available, a family with less than 85 percent germination was deleted except for study 10. In that study, some control-pollinated families with less than 85 percent germination had to be included in the analysis to maintain belance in estimating general combining ability for shoot dry weight. The correlation between shoot dry weight and field performance was significant at the ten percent level in six of the 11 studies (2, 3, 5, 6, 7 and 10) and at the 11 percent level in study 4. In three studies (1, 8 and 11), the lack of a significant correlation with field performance was caused by the occurrence of one to three families that resulted in a type B error. The general trend of the data was evident even in these studies. There was no occurrence of type A error where a good performing family in the field would be eliminated because of low shoot dry weight.

The trend of families with small shoot dry weights to have average or below-average field performance was similar for studies with a wide variety of environmental factors and seed sources. These studies support the conclusion that early testing can be an effective procedure for eliminating some of the average or below-average performing families from a progeny testing program. This would result in reduced expenditures for progeny testing, and increased efficiency by reducing the amount of money spent per percent gain.

Incorporation into the WGFTIP

In any progeny testing program, it is important to maintain properly balanced field tests to estimate the general combining ability of the parents. Because different mating and progeny test systems have been and will continue to be used in the first and second generation breeding program of the WGFTIP (Lowe and van Buijtenen, 1986), different procedures have been developed to incorporate early testing into the breeding programs for the different generations.

First Generation

The WGFTIP program utilizes a partial-diallel mating scheme for its first generation loblolly pine breeding program (*Figure 4*). Most of the partial-diallels contain either eight or nine first generation parents. This results in 16 or 18 full-sib families being established for each partial-diallel. Two partial-diallels are commonly planted with standard checklots in one progeny test. Each progeny test is planted three times; at least one planting is required to be in a year different from the other two plantings. Assuming the progeny test meets standard quality guidelines, the best 15 percent of the families, based on mid-parent values, within each test are screened for second generation selections.

Because an imperfect correlation between greenhouse and field data exists, the poorest performing parent in the field may not be identified on the basis of greenhouse data. The elimination of an average performing parent in the field, based on greenhouse data, may affect the genetic gain obtained in the second generation breeding population.

To evaluate the potential effect of deleting first generation parents upon the second generation breeding population, the clones contained in each study in *table 1* were randomly mated, utilizing the standard Western Gulf partial-diallel mating design, for 50 computer iterations. Since the number of control-pollinated families generated in each partial-diallel is twice the number of parents, the computer iterations simulated a total of 11,000 control-pollinated families. The best 15 percent of the families were selected on field data midparent value from each

FEMALE \ MALE	A	B	C	D	E	F	G	H	I
A		X	X						
B			X	X					
C				X	X				
D					X	X			
E						X	X		
F							X	X	
G								X	X
H	X								X
I	X	X							

Figure 4. — WGFTIP first generation partial-diallel mating scheme for loblolly pine.

Table 2. — The effect of incorporating an early testing procedure based on the correlation of shoot dry weight with field data upon the midparent value of the control-pollinated families considered for second generation selections from field tests.

	Standard Testing Program	Early Testing Program
No. of Families	1700	1700
No. of Families Rejected	0	45
Avg. Mid-parent Value	108.87	108.85

computer iteration. In practice, these families would be screened for second generation selections. A total of 1,700 families were selected with an average midparent value of 108.87 percent (*Table 2*). Shoot dry weight, based on greenhouse tests, was used as an independent culling trait to delete the four control-pollinated families that had the parent with the smallest shoot dry weight from each partial-diallel. Each partial-diallel was reviewed for the effect of the deleted parent upon the selected families from the random mating option.

Forty-five of the 1,700 families originally selected (2.6 percent) would not have been field planted if shoot dry weight had been used as an early testing procedure. However, 1,700 selections would still be needed to maintain a constant-sized breeding population. Families that passed the early test procedure with the next highest midparent value based on field data were selected to replace the families that would not have been field planted. The average midparent value for the 1,700 families selected after incorporating the early testing procedure for shoot dry weight was 108.85 percent (*Table 2*). Under the conditions of these studies, there would have been a net loss of 0.02 percent in the average midparent value of the selected families for second generation selection. However, because four control-pollinated families would not have been field tested in each partial-diallel, there would have been approximately a 22 percent reduction in the number of test seedlings required for progeny testing. This would have significant economic benefits in that less area would have to be located and site prepared for progeny testing and less labor and supplies would be required for progeny test maintenance and measurement activities.

The following guidelines will be imposed to implement this early testing procedure in the first generation breeding program for the WGFTIP:

1) The progeny test must have satisfactory genetic balance to allow valid estimates of general combining ability for each of the parents.
2) The progeny test will be grown in a replicated design in a greenhouse. Particular attention should be given to maintaining uniform growing conditions.
3) Only families with at least 85 percent germination will be used to estimate each parent's general combining ability for shoot dry weight.
4) Shoot dry weight will be obtained from 30 seedlings per family in the progeny test. An equal number of seedlings will be sampled per family from each replication.
5) Significant differences at the 10 percent level for shoot dry weight must be detected among families.
6) Satisfactory genetic balance to obtain acceptable general combining ability estimates from subsequent field data must be maintained after families have been eliminated on the basis of early testing results.

If these requirements are not satisfied, the entire progeny test must be field planted.

Seedlings will be harvested at approximately five months of age, just prior to outplanting the field test. Parental general combining ability estimates for shoot dry weight will be determined and the crosses containing the parent with the smallest shoot dry weight will be deleted from the test. A composite checklot, containing an equal number of seedlings from each deleted cross, will be planted with the progeny test to evaluate the efficiency of the early selection procedure. This will result in approximately a 17 percent reduction in the number of progeny test seedlings planted in the test. If the early testing procedure is successful in the first year of test establishment, the crosses containing the parent with the smallest shoot dry weight will not be planted in the second year. This will result in a 22 percent reduction in test seedlings for the second year's progeny test. All other activities associated with progeny test establishment and maintenance will remain constant.

Second Generation

A complementary mating and testing scheme has been selected for second generation breeding by the WGFTIP. General combining ability estimates for second generation selections will be obtained by using a polymix mating system. Standard pollen mixtures utilizing first generation selection have been developed for the different breeding zones within the WGFTIP (Lowe and van Buijtenen, 1981). The partial-diallel mating scheme shown in *figure 4* will be used to develop a population for third generation selection activities.

The concept of a step-wise testing procedure allows shoot dry weight, determined in greenhouse tests, to be incorporated into advanced generation breeding strategies. Female flowers typically occur one or two years before pollen production in young loblolly pine. By utilizing a pollen source from the previous generation, polymix crosses should be completed prior to the initiation of partial-diallel matings to form the selection population. Based on results of shoot dry weight determined from greenhouse measurements prior to establishing the polymix field tests, an independent culling level can be used to eliminate the poorest performing families., This translates into reduced expenditures for establishing the polymix progeny tests.

Additional reductions in progeny test costs can also be obtained by deleting those selections from the partial-diallel mating scheme. Pollen does not ned to be collected, pollinations made, seedlings produced or field planted from selections deleted on their offspring's shoot dry weight. Because of early female flowering and using pollen from the previous generation for the polymix, the length of the breeding cycle should not be increased by using the two-step testing procedure.

The use of early test data will allow assortative mating to increase the expected genetic gain for the third generation breeding population by pairing clones of similar general combining ability estimates in the mating design. The value of assortative mating is dependent upon the correlation between field data and early testing data, the number of clones included in the mating design, the mating design, and the selection intensity. The poor correlation between field and greenhouse data (type B errors), decreases the value of assortative mating. The complexity of the mating scheme, and number of clones also affect the efficiency of assortative mating. The probability of obtaining families with high midparent values from random matings increases as the number of crosses per parent increases. This can be used to partially offset the effects of a poor correlation between shoot dry weight and field data; however, the cost of progeny testing is increased.

Independent culling of below average parents and assortative mating should both increase expected genetic gain. Six studies (1, 2, 3, 4, 10 and 11) in *table 1*, which included 10 or more parents, were used to evaluate the ef-

Table 3. — Incremental genetic gains compared to random mating without culling for random and assortative mating at different culling levels.

Culling Level (%)	Incremental Genetic Gain (%) Random Mating	Assortative Mating
0	0.0	0.5
10	0.2	0.5
20	0.4	0.9
30	0.9	1.2
40	0.2	0.6
50	0.5	0.4

fect of independent culling levels and assortative mating using shoot dry weight. All of the parents in each study were randomly mated in a partial-diallel (*Figure 4*) for 50 iterations. Using data from field tests, the best 15 percent of the control-pollinated families from each iteration were selected on midparent values. Shoot dry weight data were used to cull between 10 and 50 percent of the parents in each study. After each level of independent culling, the remaining parents were randomly mated for 50 iterations. Shoot dry weight, at each level of culling, was also used to arrange the clones in the partial-diallel to simulate assortative mating. *Table 3* shows the expected incremental genetic gains comparing random mating and assortative mating for different culling levels based upon shoot dry weight as compared to random mating without culling. The additional gain for the selected families was maximum at the 30 percent rejection level with assortative mating (1.2%). Assortative mating based on shoot dry weight resulted in greater average gains at all rejection levels, except 50 percent, than random mating.

The occurrence of type B errors is detrimental to assortative mating. Because of the occurrence of type B errors in Study 11 (*Figure 2c*), the midparent values for selected families after culling 30 percent and using assortative mating was 0.5 percent less than the average of the random mating selections. Culling at the 30 percent level combined with assortative mating in the other studies resulted in increasing excepted genetic gains from 0.4 to 1.9 percent.

The second generation breeding program for the WGFTIP will use shoot dry weight of the polymix families to cull 30 percent of the second generation selections. Requirements for implementation will be similar to those for the first generation: 1) the polymix tests must be grown in a replicated design, under uniform conditions, in a greenhouse, 2) only polymix families with at least 85 percent germination will be used to determine shoot dry weight, and 3) significant differences at the 10 percent level for shoot dry weight must be detected among families. A composite checklot of an equal number of seedlings from each rejected family will be established in the field test. This checklot will be used to evaluate the efficiency of the early selection procedure. This culling level results in a 24 percent reduction in the number of test seedlings established for the polymix progeny tests.

The rejected second generation selections will not be included in the partial-diallel mating as shown in *figure 4* to create the selection population for the third generation. Because fewer crosses will need to be completed and field tested, costs associated with this portion of the breeding and testing program will be reduced. The value of assortative mating can be increased by using parental information from first generation progeny tests. Shoot dry weight data and expected midparent values based on parental data will be used to positively arrange the remaining second genration selections in the partial-diallel mating design. This assortative mating should increase the average breeding value of the third generation selections.

Conclusions

Results of the eleven greenhouse and growth chamber studies described in this report indicate that shoot dry weight can be used as an early testing trait for loblolly pine.

Seedlots with both small shoot dry weight and good germination (at least 85 percent) have average or below average performance in field tests. The use of shoot dry weight to cull families prior to field testing will reduce the costs associated with a progeny testing program. When a two-stage testing program is used, assortative mating combined with independent culling based on shoot dry weight can result in increased gains. Both of these factors should increase the efficiency of an operational tree improvement program by reducing the required financial expenditure for each percent increase in genetic gain.

The use of shoot dry weight as an early selection trait can be incorporated into existing first and second-generation breeding systems. In the first generation Western Gulf Forest Tree Improvement Program's breeding scheme, this will involve deleting the crosses that contain the parent with the smallest shoot dry weight in each partial-diallel prior to field testing. A composite checklot of the deleted crosses will be planted in the test to evaluate the efficiency of the early testing procedure. This will result in approximately a 17 percent reduction in costs associated with progeny test activities.

Two-step testing will be utilized within the Western Gulf Program for second generation breeding and testing. Thirty percent of the second generation selections with the smallest shoot dry weight based upon the polymix crosses will be deleted from the progeny testing program. This will result in a 24 percent cost reduction in establishing the polymix progeny test. Additional cost savings will result because of the reduction in the partial-diallel breeding and testing activities for the third generation selection population. Assortative mating will be used in determining the clonal arrangement for partial-diallel matings to increase the expected genetic gain from third generation selection activities.

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Pressemitteilung

INFURO Meeting on Population Genetics of Forest Trees

A joint international meeting of IUFRO Working Parties on Biochemical Genetics (S2. 04. 05) and Population and Ecological Genetics (S2. 04. 01), will be held at Oregon State University, July 31 to August 2, 1990. The theme of this meeting is: "Contribution of biochemical markers to the understanding of population genetics of forest trees — retrospect and prospect."

Twenty invited speakers will summarize current knowledge related to the theme and offer perspectives on challenges for the future. The meeting will also include voluntary poster sessions and small group discussions. For information contact: Conference Assistant, College of Forestry, Peavy Hall 202, Oregon State University, Corvallis, Oregon 97331-5707.

XIXth World Congress, a Landmark in Canadian Forestry

"Science in Forestry — IUFRO's Second Century"

August 5 to 11, 1990 will be a landmark week for forestry research in Canada. The XIX World Congress of the International Union of Forestry Research Organizations (IUFRO) will take place at the Palais des Congrès in Montréal. It will be the first time in the 100-year history of the Union that the Congress has been held in Canada and only the second time it has been held in North America. More than 2000 researchers from around the world, representing over 100 countries, are expected to attend this major event.

Organization of the Congress has been in progress for almost two years. The Canadian Steering Committee, chaired by Lorne Riley on temporary assignment from Forestry Canada, is supported by 13 Subcommittees and a large number of government, industry, and university staff across Canada. It maintains regular contact with the IUFRO Executive Board headquartered in Vienna and with IUFRO President R. E. Buckman who is located at Oregon State University in Corvallis, Oregon. The holding of the Congress is fully supported by Canadian IUFRO member agencies through the Canadian IUFRO Advisory Council chaired by J. C. Mercier, Deputy Minister, Forestry Canada.

The technical program for the Congress is being developed by IUFRO's Divisional Co-ordinators with the assistance of their many Subject Group Leaders and Working Party Chairmen. The program will treat extensively the range of interests of IUFRO members through numerous expert papers and through the presentation of over 600 posters. Each day's program will be opened by a keynote address from a knowledgeable, internationally known speaker. Special sub-plenary sessions will be held each day on topics of current importance and concern. Tropical forestry and air pollution will be featured.

A full program of events for accompanying persons has been developed. A variety of options will be available each day. The program will not only showcase the attractions of Montréal but will also include trips to Ottawa and Québec City and will highlight natural and cultural opportunities in the Montréal area.

The Congress will conclude with a program of 17 excursions ranging in length from 4 days to 8 days. The excursions will cover all regions of Canada from the east coast to the west coast and the Yukon. Several of the excursions will include important forestry sites in northern parts of the continental United States and in Alaska. Although the excursions will feature scientific and technical forestry interests, they will include also scenic and touristic attractions of the regions through which they travel.

For more information, contact:

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François Mergen

> That man is a success who has lived well, laughed often, and loved much; who has gained the respect of intelligent men and the love of children; who has filled his niche and accomplished his task; who leaves the world better than he found it, whether by an improved poppy, a perfect poem, or a rescued soul.
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> Robert Louis Stevenson

François Mergen died June 26, 1989 in Homosassa, Florida at the age of 64. He was a pioneer in forest genetics and a remarkable human being. During his career, he was a research scientist with the U.S. Forest Service in Lake City, Florida, then Professor of Forest Genetics at Yale University, and later Dean of Yale's forestry school, the oldest in the United States. For his contributions to re-

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