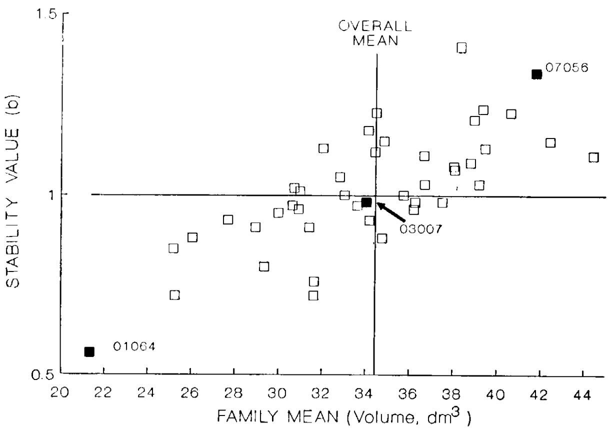


Figure 5. — The relationship of regression coefficients and mean performance for volume of loblolly pine families.

If there is genetic variation in stability and performance among families, tree breeders have the opportunity to select for different stabilities under different environmental conditions and determine the optimum genotypes and management systems for each environmental condition. For example, families in the Responsive High Yield group have greater specificity of adaptability to high quality environments and should respond well to intensive silvicultural practices. Although there were few of these families found in this study, it would be most valuable to use these families such as 07056 on high site index lands to maximize yield and to obtain the best use of genetically improved stock. If forests are being established on less favorable sites or over a large range of average sites, families in Responsive High Yield group or in the Average Stability group with above average performance would be very productive genotypes. The Average Stability group has general stability and adaptability to all environments.

Conclusion

The strong trend in this study for selected loblolly pine families to have average stability and perform in a predictable manner over a wide range of sites is very valuable information for tree breeders. Significant G × E interaction in the analyses of variance was contributed by very few families for height, DBH, volume and percent rust-free trees in the study. An important implication to the breeding program is that families usually need not be tested over environmental extremes to determine breeding values. With few exceptions, a family's performance on good sites was highly correlated with its performance on poor sites. It may be valuable to test over environmental extremes to identify the few Responsive High Yield families which should be used to increase forest productivity on intensively managed sites.

Literature Cited

Barnes, R. D., Burley, J., Gibson. G. L. and Garcia De Leon, J. P.: Genotype-environment interactions in tropical pines and their effects on the structure of breeding populations. Silv. Genet. **33** (6): 186—198 (1984). —— Eberhart, S. A. and Russell, W. A.: Stability parameters for comparing varieties. Crop Sci. **6**: 36—40 (1966). —— Finlay, K. W. and Wilkinson, G. N.: The analysis of adaptation in a plant-breeding programme. Aust. J. Agric. Res. **14**: 742—754 (1963). —— Freeman, J. H. and Perkins, J. M.: Environmental and genotype-environmental components of variability. VIII. Relations between genotypes grown in different environments and measures of these environments. Heredity **27**: 15—23 (1971). —— Fripp, Y. J.: Genotype-environmental interactions in *Schizophyllum commune*. II. Assessing the environment. Heredity **28**: 223—238 (1972).. —— Fripp, Y. J. and Caten, C. E.: Genotype-environmental interactions in *Schizophyllum commune*. I. Analysis and character. Heredity **27**: 393—407 (1971). —— Goddard, R. E.: G-E interaction in slash pine. Third world consultation on forest tree breeding. FAO/IUFRO, Canberra, Aust., March, 1977. 8 pp. (1977). —— Goebel, N. B. and Warner, J. R.: Volume tables for small diameter loblolly pine, shortleaf and virginia pine in the upper South Carolina piedmont. Forest Research Series No. 7, Clemson Univ. Clemson, SC. (1966). —— Gray, E.: Genotype × Environment interactions and stability analysis for forage yield of orchard grass clones. Crop Sci. **22**: 19—23 (1982). —— Hardwick, R. C. and Wood, J. T.: Regression methods for studying genotype-environment interactions. Heredity **28**: 209—222 (1972). —— La Farge, T. and Kraus, J. F.: Genotype × environment interactions of loblolly pine families in Georgia, U.S.A. 1981. Silv. Genet. **30**: 156—162 (1981). —— Lin, C. S., Binns, M. R. and Lefkovitch, L. P.: Stability Analysis: Where do we stand? Crop Sci. **26**: 894—900 (1986). —— Morgenstern, E. K. and Teich, A. H.: Phenotypic stability of height growth of jack pine provenances. Can. J. Genet. Cytol. **11**: 110—117 (1969). —— Namkoong, G.: Genotype by environment interaction: some theoretical considerations. In: Proc. Fifth North American Forest Biology Worshop. Univ. Fla., Gainesville (1978). —— Owino, F.: Genotype × environment interaction and genotypic stability in loblolly pine. II. Genotypic stability comparisons. Silv. Genet. **26** (1): 21—25 (1977). —— Perkins, J. M. and Jinks, J. L.: Environmental and genotype-environmental components of variability. III. Multiple lines and crosses. Heredity **23**: 339—356 (1968a). —— Perkins, J. M. and Jinks, J. L.: Environmental and genotype-environmental components of variability. IV. Non-linear interactions for multiple inbred lines. Heredity **23**: 339—356 (1968b). —— Plaisted, R. L.: A shorter method for evaluating the ability of selections to yield consistently over locations. Am. Potato. J. **37**: 166—172 (1960). —— Shukla, G. K.: Some statistical aspects of partitioning genotype-environmental components of variability. Heredity **29**: 237—245 (1972). —— Yates, F. and Cochran, W. G.: The analysis of groups of experiments. J. Agric. Sci. (Cambridge) **28**: 556—580 (1938). —— Yeiser, J. L., van Buijtenen, J. P. and Lowe, W. J.: Genotype × environment interactions and seed movement for loblolly pine in the Western Gulf Region. Silv. Genet. **36** (6): 196—200 (1981).

Tree Improvement Strategies: Modelling and Optimization: the Model*)

By L. E. Paques

I.N.R.A., Station d'amélioration des Arbres forestiers,
Ardon, 45160 Olivet, France

(Received 3rd February 1988)

Abstract

A model of a complete cycle of tree improvement is proposed that combines in the equivalent annual rent (E.A.R.), both genetic and economic factors affecting tree

---

*) Based on a thesis presented to North Carolina State University in partial fulfillment of the requirements for the degree of Master of Science.

improvement strategies. The model is used to study the effect of the mutual interactions of various technical and management alternatives on the economic response for any pattern of genetic variability. The E.A.R. is used to determine the efficiency of tree improvement strategies and as a mesure for optimization.

The effects of level of seed yield in the seed orchard, size of the land base, length of the rotation of forest plantations, and techniques of breeding on selection alternatives are examined.

Key words: Tree breeding strategy, modelling, simulation, economics.

Zusammenfassung

Ein Modell eines kompletten Zyklus zur Verbesserung von Baumeigenschaften wird vorgeschlagen, das die für die Strategie der Baumeigenschaftsverbesserungen wichtigen genetischen und ökonomischen Faktoren in der 'Equivalent Annual Rent' (E.A.R.) kombiniert.

Dieses Modell wird benutzt, um unabhängig des Musters der genetischen Variabilität die Wirkung der gegenseitigen Beeinflussung der verschiedenen technischen und verwaltungsmäßigen Alternativen auf die Wirtschaftlichkeit zu untersuchen.

Das E.A.R. wird für die Bestimmung der Wirksamkeit der Baumverbesserungsstrategie und als Maß für die Optimierung angewendet.

Die Einflüsse der Ausbeute an Saatgut in der Samenplantage, der Größe der Waldfläche, der Länge der Wechselwirtschaft der Forstplantage und der Züchtungstechniken auf die Selektionsalternativen werden betrachtet.

I. Introduction

Recent progress in breeding and selection techniques offer tree breeders alternative genetic and investment strategies. The value of early seed production and testing depends on the magnitude of the realized genetic gain and the costs incurred from the time of investment to final harvest of the improved forests. Investments in early seed production can accelerate plantation establishment with improved seed and, if combined with early testing, can reduce the carrying cost of both seed production and testing cost. On the other hand, if genetic correlations between juvenile and mature tree performance are low, plantation harvest value will be low.

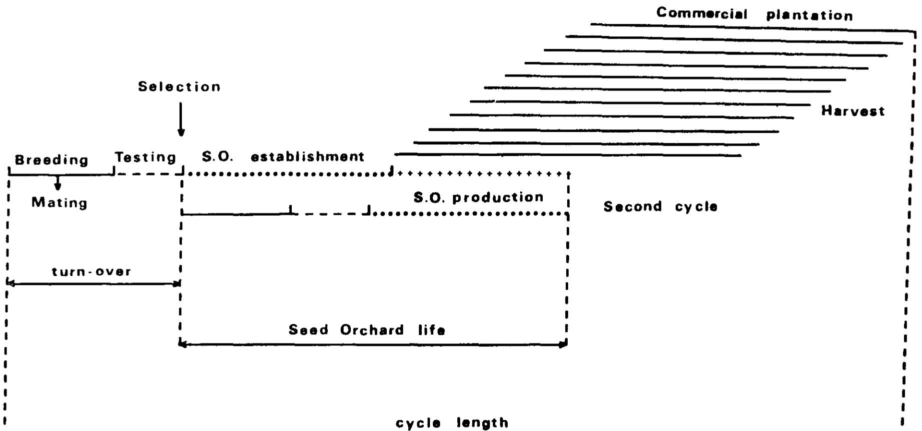
An analytical method is needed to evaluate the investment in breeding alternatives which include the time and intensity of selection as functions of genetic parameters and of the effects of accelerated breeding techniques. Studies on the economics of genetic improvement strategies are rare and have used in either oversimplified economic value functions in genetic problems (Namkoong, 1970) or in simple genetic options in economic analyses (Porterfield, 1973). In this paper we attempt to introduce moderate complexity into the economic analysis of a complete tree improvement cycle which includes alternative selection and breeding schedules. We first describe the model and then examine specific alternatives for selection age and intensity. In particular, we examine the effect that economic variables such as interest rate, land base, seed production rates, rotation length, and breeding techniques have on choices of selection intensity and on the value of juvenile selection.

II. The model

We consider only tree improvement programs in which seed orchards are established from clones selected after progeny tests are conducted using parents selected from the previous generation. The progeny tests serve two functions. In addition to providing data on family performance, the individual seedlings which are selected are the ortets which are used to produce seed orchard ramets and are the parents for the next generation. We assume that it may take a few years for the seed orchard to produce commercial quantities of seed, but that mating among selected ortets can be started immediately and a new cycle of testing started with these seedlings. The seed orchard of the initial cycle is assumed to be used until the next cycle's seed orchard begins producing commercial quantities of seed.

Investments in various phases of the operation carry different costs and expected gains from either improving gain or shortening the breeding cycle or both. The return on investment occurs from the harvest time of plantations from the first seed orchard production year, to the harvest of the last plantation from that cycle's orchard seed. The general plan of improvement tested in this study follows the North Carolina State University-Industry Cooperative Pine Breeding program which also supplied the data used in our analysis on costs, seed production, and the times required for the various operational phases. A complete cycle is diagrammed in *Figure 1.*

In *Figure 2,* we diagram some options which exist for shortening the breeding cycle. In option A, breeding (B) is



S.O. = Seed Orchard

Figure 1. — Schematic representation of a complete cycle of Tree Improvement.

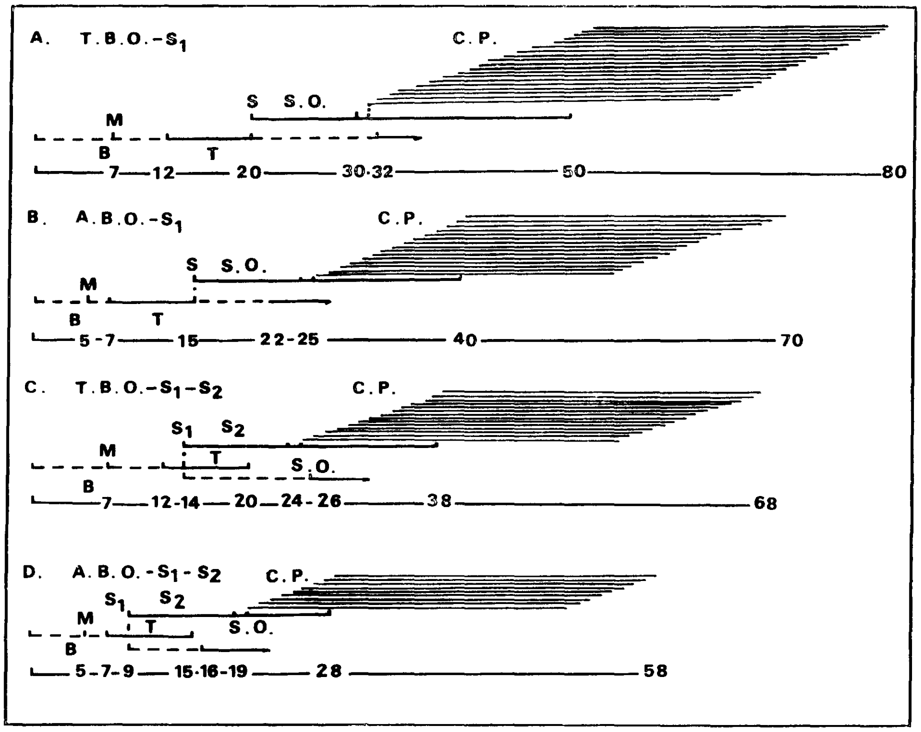


Figure 2. — Examples of four tree improvement strategies combining various options of breeding methods and selection processes (T.B.O. = traditional breeding orchard, ABO = accelerated breeding orchard, M = mating, B = breeding, T = Testing, S = selection, S.O. = seed orchard and C. P. = forest plantations).

done in field orchard (T.B.O.: 'Traditional Breeding Orchard') and is completed after 12 years. Testing (T) of the progeny is then conducted and is followed by a single stage early selection (S) at 8 years. The selected material is grafted in the commercial seed orchard (S.O.) and in the breeding orchard of the next generation After an establishment period (10 years), the seed orchard starts producing seed and forest plantations (C.P.) can be established. Option B is similar to option A for the testing and selection phases but differs in the technique of breeding: Accelerated Breeding (A.B.O.) is used. The orchard is established in a greenhouse facility and trees are submitted to various flower and seed production stimulation techniques. Breeding can be completed after only 7 years. Options C and D are similar to A and B options respectively but depart from them in that a two-step selection is performed. The material selected in S1 is grafted in both the seed orchard and the breeding orchard and is rogued (S2) some years later. Between options A and D for example, a time advantage of some 22 years in the reduction of the cycle length and of 11 years in the fastening of the turn-over of the generation is clearly depicted in *Figure 2.*

The analytical approach consists of the decomposition of complete tree improvement strategies into their various phases of breeding, testing, selection, seed orchard establishment and production, and commercial forest plantations, and the evaluation of the economic input and output at each level. We reduce these costs and gains to their present values at the time of the beginning of the cycle.

Since the options diagrammed in *Figure 2* change the length of the breeding cycle and of the turn-over of the generations, economic values are better compared on the basis of a unit time. We therefore multiplied the present value by a depreciation factor K equal to:

$$K = \frac{r\,(1 + r)^n}{(1 + r)^{n-1}} \quad \text{with} \quad \begin{array}{l} r = \text{discount rate} \\ n = \text{cycle length} \end{array} \qquad (1)$$

The equivalent annual values of gains and costs were obtained and the equivalent annual rent:

$$\text{E.A.R.} = \text{K x P.N.W} \quad \text{with} \quad \text{P.N.W} = \text{present net worth} \qquad (2)$$

was used as a single base of comparison. As the input and output refer to different management units (breeding orchard, tests, seed orchard, forest plantation, etc.), it was necessary to reduce the previous values to a common spatial base of comparison, arbitrarily chosen as an acre of commercial forest plantation.

To estimate genetic gains we used the COTTERILL and JAMES (1981) approximation, derived from TALLIS (1961):

$$\delta G_{M/1,2} = \beta_1 \,.\, \delta G_1 + \beta_2 \,.\, \delta G_2 \qquad (3)$$

where $\delta G_{M/1,2}$ = correlated genetic gain at mature age after selection at juvenile stages 1 or 2;

β_i = partial regression coefficient between breeding values at stages i and M;

δG_i = partial gain due to selection at stage i

and

$$\delta G_{M/1,2} = i_1 \,.\, r_{XZ} + i_2 \,.\, [(r_{YZ} - r_{XY} \,.\, r_{XZ.H})/(1 - r^2_{XY.H})^{1/2}] \qquad (4)$$

where i_1, i_2 = selection differential at stages 1 and 2;
r_{XZ}, r_{XY}, r_{YZ} = phenotypic correlations between traits at ages X, Y, Z;
$H = i_1 . (i_1 - x_1)$

Equation 4 can be rewritten for stepwise selections gain analysis when the second stage selects only from the materials remaining from the first stage as:

$$\delta G_{M/1,2} = [i_1 . h_1 . h_M . r_{1-M} + i_2 . K] . \sigma_p \qquad (5)$$

$$\text{with} \quad K = \frac{h_2 . h_M . r_{2-M} - h^2{}_1 . h_2 . h_M . r_{1-M} . r_{1-2} . H}{(1 - h^2{}_1 . h^2{}_2 . r^2{}_{1-2} . H)^{1/2}}$$

where h_1, h_2, h_M = square root of heritability at stages 1, 2, and M;
$r_{1-2}, r_{1-M}, r_{2-M}$ = genetic regression coefficients;
i_1, i_2 = selection differentials;
σ_p = phenotypic standard deviation at mature age (M);
1, 2, and M = refer to juvenile (1 and 2) and mature (M) stages of selection.

When single-step selection is performed, formula 4 reduces to the general expression of the correlated genetic gain (Falconer, 1981; Nanson, 1968):

$$\delta G_{M/J} = i_J . h_J . h_M . r_{J-M} . \sigma_p \qquad (6)$$

The parameters have the same meaning as above but refer to J, the unique juvenile stage of selection and M, the mature stage.

Several matrices of genetic parameters (heritabilities, genetic correlations between ages of selection, and phenotypic variances at mature age) were constructed. Those of interest for this study are given in *Table 1*. The results were expressed for $i = 4$ when single-step selection was tested and for selection intensities (i_1) ranging from 0.8 to 3.6 when two-step selection was performed. The final proportion selected, p, was chosen equal to 1:10,000.

Gains were determined for a single trait, height, and with the assumption that improvement in height can be viewed as an apparent increase in site index (Lundgren and King, 1965), conversion of height gains in terms of volume gains was done using Hafley *et al.* (1982) yield models and stock tables. This information together with the market stumpage prices is used for the computation of the total economic gain over time and space and its equivalent annual value.

Stumpage prices and costs used in this study represent average conditions for pine improvement programs in the southeastern United States of America. They are described in detail by Paques (1984).

III. Results

Tree improvement activities and parameters can be seen as acting in three main ways:

a. alteration of the cycle length; e.g. rotation length, techniques of breeding, length of the testing period, age of selection;
b. modification of the level of input (costs); e.g. the size of the land base, the level of seed production in the seed orchard, management activities;
c. modification of the level of genetic gains; e.g. number of steps of selection, age of selection.

Each parameter was analyzed separately by varying its level while other factors were held constant, to study the nature and magnitude of its response on the equivalent annual rent (E.A.R.).

1. Interest rates

Computation of the present net worth and equivalent annual rent requires the choice of an interest rate, which affects the time value of money.

The general scheme of the strategy considered is represented in *Figure 1*. A fixed land base of 600,000 acres, a seed orchard yield of 70 lbs/acre/year and a rotation length of 30 years were used as constant factors. Discount rates of 6%, 8% and 10% were tested. A stumpage rate of increase of 2% and a rate of increase of forestry practices of 2% (Moak, 1982, cites figures ranging from 0.70% to 5.14%) were included in the study.

For the conditions of this study, it appears (*Table 2*) that tree improvement strategies tested remain beneficial for real discount rates as high as 8%;' which is about the double of the rate usually cited for governmental projects in the United States (Row *et al.*, 1981). Secondly, the nature of the response is not modified with variation of the discount rates, but its magnitude is (*Table 3*). Therefore, the other parameters may be studied independently.

The time value of money is also clearly illustrated in *Table 2* where selection at later ages 4 and 6, compared tc 2 years postpones the realization of gains; they are therefore discounted over a longer period of time which seriously reduces their profit.

Table 1. — Matrix of the genetic parameters patterns tested.

Age of selection (years)	model r_{Gi-8}	A r_{Gi-M}	B r_{Gi-M}	H
2	0.30	0.20	0.20	0.71
4	0.50	0.35	0.21	0.55
6	0.60	0.48	0.23	0.45
8	1.00	0.57	0.27	0.35
M		1.00	1.00	0.22

r_G: genetic correlation between age i and j
H: square root of heritability

Table 2. — Equivalent annual rent (after tax) for different levels of interest rates (i) and selection intensity (model B).

i	Selection age	Selection intensity 0.8	1.2	1.6	2.0	2.4	2.8	3.2	3.6
6%	2-8	0.49	1.40	1.99	2.33	2.51	2.59	2.62	2.62
	4-8	0.56	1.29	1.76	2.03	2.17	2.22	2.24	2.24
	6-8	0.59	1.19	1.57	1.79	1.90	1.34	1.95	1.95
8%	2-8	-1.50	-0.61	-0.03	0.30	0.46	0.53	0.54	0.56
10%	2-8	-2.09	-1.24	-0.70	-0.39	-0.23	-0.17	-0.15	-0.15

Table 3. — Decrease in equivalent annual rent ($) for an interest rate of 8% compared to 6% (a) and 10% compared to 8% (b).

Selection		Selection intensity 0.8	1.2	1.6	2.0	2.4	2.8	3.2	3.6
model A									
2-8	a	2.18	2.18	2.18	2.19	2.18	2.18	2.16	2.13
	b	0.66	0.71	0.74	0.74	0.76	0.75	0.74	0.73
4-8	a	1.89	1.93	1.95	1.98	1.99	1.99	1.99	1.97
	b	0.51	0.57	0.62	0.63	0.64	0.65	0.64	0.64
6-8	a	1.66	1.72	1.76	1.78	1.80	1.81	1.81	1.80
	b	0.39	0.45	0.50	0.53	0.54	0.55	0.55	0.54
model B									
2-8	a	2.00	2.01	2.02	2.03	2.05	2.06	2.06	2.06
	b	0.58	0.63	0.66	0.69	0.69	0.70	0.71	0.71
4-8	a	1.71	1.75	1.77	1.79	1.80	1.80	1.81	1.80
	b	0.44	0.49	0.53	0.55	0.56	0.57	0.57	0.57
6-8	a	1.49	1.53	1.57	1.58	1.60	1.60	1.60	1.60
	b	0.32	0.39	0.42	0.46	0.46	0.47	0.47	0.47

2. *Land base size*

With the same hypothesis as above and a discount rate of 6%, four land base sizes were tested corresponding to holdings of 300,000, 600,000, 900,000, and 1,200,000 acres. The land base size (LB) was considered as the limiting factor. Along with the rotation (T), the seed yield in the seed orchard (P), the density of plantation in the commercial forest plantations (D), and the number of plantable seedlings per pound of seed (N) it determines the size (S) of the seed orchard required to satisfy regeneration needs:

$$S = \frac{LB \,.\, C}{P.T.D.N} \qquad \text{with C, a safety-margin coefficient} \qquad (7)$$

A decrease of costs of about 5% can be expected when working with the largest land base compared to the smallest. This low value may seem paradoxical as the largest base is more than three times the size of the smallest. However, regardless of the size of the land base, the breeding-testing and selection costs remain the same and can be considered as fixed costs. They are therefore proportionately much larger for small holdings than for large ones. But, it is also clear that larger land bases require larger seed orchards and involve as a consequence, higher costs for installation and management of the orchard. The larger size of the orchard somewhat offsets the advantage of the economy of scale permitted by larger land bases.

The uniformity of the response for the various values tested (at least for high selection intensities) allows us to study other factors independently of the size of the land base, at all but the lowest selection intensities, which involve a very different pattern of distribution of the costs over time (*Table 4*).

3. *Level of seed production*

The level of seed production in seed orchard was also analyzed as rentability of tree improvement programs was recognized to be significantly dependent on its volume (Talbert *et al.*, 1983). Five levels: 40, 50, 60, 70, and 80 lbs/acre/year were input in the model with the same assumptions as above. It was furthermore assumed for simplicity that higher levels of yield occur by a better choice of establishment site without any supplementary costs such as for extra irrigation or fertilization.

Seed yield levels do not change expected genetic gain nor economic gain/acre, but directly modify the amount of cone collection and seed extraction costs, and indirectly affects the size of the seed orchard required (see formula 7).

As indicated in *Figure 3*, an economy of scale makes larger crops more profitable as they are associated with proportionately smaller costs per acre. However, the profit is not as large as one might expect: the decrease in size of the seed orchards made possible by heavy crops is somewhat offset by added cost of cone collection and seed extraction.

It has also been observed that the optimum allocation of selection intensities between the two stages may depend on the level of the seed yield. Nevertheless, the difference in response (E.A.R.) was usually so small that the seed production effect can be neglected.

Table 4. — Percentage increase of the equivalent annual rent for increasing land base size compared to the previous level (model B).

Selection age	Land base (acres)	Selection intensity 0.8	1.2	1.6	2.0	2.4	2.8	3.2	3.6
2-8	600,000[a]	29.9	6.0	2.9	1.9	1.5	1.4	1.4	1.4
	900,000	9.9	1.9	0.9	0.7	0.5	0.4	0.4	0.4
	1,200,000	3.6	0.9	0.5	0.3	0.3	0.2	0.2	0.2
4-8	600,000[a]	20.0	5.4	2.8	1.9	1.5	1.4	1.4	1.4
	900,000	6.6	1.7	0.9	0.6	0.6	0.5	0.5	0.4
	1,200,000	2.6	0.8	0.5	0.3	0.3	0.2	0.2	0.2
6-8	600,000[a]	15.3	5.0	2.8	1.9	1.5	1.4	1.4	1.4
	900,000	5.1	1.5	0.8	0.6	0.6	0.5	0.4	0.5
	1,200,000	2.1	0.8	0.4	0.3	0.2	0.2	0.2	0.2

(a) EAR (600,000)/EAR (300,000).

4. *Rotation length*

The effect of the rotation length on the economic response was tested through two rotation options: 25 years and 30 years; which are common for loblolly pine in the Southern part of the U.S.A. It is assumed that the genetic parameters of the material tested (h^2, r, p) are not modified between age 25 and 30. This is unlikely: young material is presumably better correlated to 25 years old material compared to 30 years. However, this simplification allows us to study the time effect of the rotation length independent of the genetic problems.

Shorter rotations obviously reduce the cycle length of the program as the final wood product is harvested earlier. Shorter rotations do not however accelerate the turn-over of the cycle: it does not allow the next cycle of breeding-testing and selection to be started sooner.

Also, it is significant that apart from the time effect, modification of the rotation also alters the level of input. Shorter rotations require larger seed orchard areas to satisfy regeneration needs, and hence, costs per acre of commercial plantation are significantly increased. In the conditions of this study, profit for the 25 years rotation option is only 65% of the profit obtained for the 30 years option. This is a surprisingly strong effect.

Shortening of a tree improvement program cycle by about 5 years is a priori a good operation: the gains are realized sooner, and are discounted over a shorter period, so that the profit over time is increased. On the other hand, this advantage is offset by the reduction of the cost due to the reduction of the size of the seed orchard, permitted by longer rotations, but also by the increased value of the product at the end of the longer rotation: not only is the total volume larger, but also the volume of more valuable product.

Under these conditions, it is apparent that the saving of 5 years on the cycle length by shortening of the rotation is not sufficient to offset the advantages of a longer rotation. Moreover, the rotation option modifies only the magnitude of the response and not its nature.

5. *Accelerated versus traditional breeding orchards*

Recent developments in the techniques of stimulating reproduction in pine (Greenwood, 1983) have given rise to great interest among tree breeders. These treatments combining physical stresses and growth substances application on plants in a greenhouse environment (accelerated breeding method) should allow a reduction by at least 5 or 6 years of the breeding phase, and therefore of the turnover of the generations, compared to field breeding orchards (traditional breeding methods). The cycle length can thereby be shortened by 5 to 6 years. This important time saving effect was partially discussed by McKeand and Weir (1983); but no cost information was included in their study.

In addition to the time saving effect, many other parameters should be modified: the number of clones, of parent-trees, of ramets/parent; the supplementary costs of

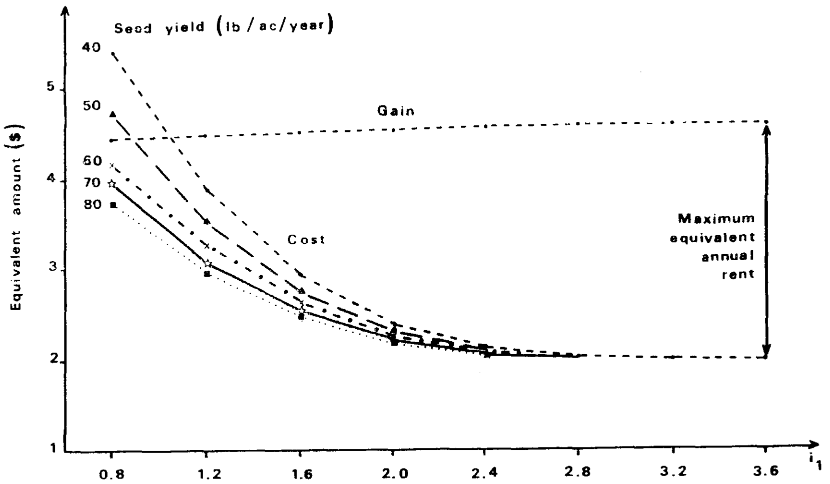


Figure 3. — Equivalent amounts of cost and gain (in $, after tax) for various levels of seed yield.

Table 5. — Increase in profit (in %) due to greenhouse accelerated breeding compared to field breeding orchard (two-step selection at 2 and 8 years).

model	Selection intensity 0.8	1.2	1.6	2.0	2.4	2.8	3.2	3.6
A	23.7	23.0	22.9	22.8	22.8	22.8	22.8	22.8
B	24.5	23.1	23.0	22.9	22.9	22.8	22.8	22.8

the greenhouse installation and management, differential costs for pollination, cone collection, etc. It was therefore necessary to examine whether or not the time saving permitted by these new methods was not offset by these new costs or costs which are at least differently distributed over time. Detailed description of these techniques can be found in Greenwood (1982, 1983) and costs figures are evaluated in Paques (1984).

The major result we observe is that an increase of profit of at least 20% can be obtained by these new techniques, compared to field breeding (*Table 5*), Moreover, only the magnitude and not the nature of the response (E.A.R.) over selection intensities is changed.

These results are given for a simplified situation in which the genetic gain remains unchanged between both alternatives. It was assumed that the number of parent trees was fixed over generations, so that the selection process does not interfere with the breeding phase. Possibility of increasing the number of clones and parent-trees in the breeding orchard opened by accelerated methods should be tested. Its interest is obviously in the larger population leading to a higher number of crosses: selection could be more severe and somewhat correct the reduced gain due to an excessively early selection or by a poorer, early juvenile selection.

IV. Conclusions

Tree improvement programs present an increasing number of technical and management alternatives which require analysis in an integrated study combining both genetic and economic parameters. Efficiency coefficients, as currently described in the literature are particularly well suited for the study and comparison of single options (such as selection processes but are not well adapted to deal with the existing level of complexity of complete cycles of improvement programs.

The complexity of the economic effects of different tree breeding options revealed in this research indicates a need to more closely examine the effects of even small variations in breeding techniques. The results obtained were based on certain assumptions of genetic parameters and operational efficiencies and the effects of variations in these should also be further examined.

Acknowledgement

We are grateful to Dr. G. Namkoong, U.S.D.A. Southeastern Forest Experiment Station, Genetics Department N.C.S.U. (Raleigh, NC.) for his helpful suggestions and his revising of this manuscript. Grateful acknowledgement is made too to the North Carolina State University-Industry Cooperative and in particular the Weyerhaeuser Co for their support to this study.

Literature Cited

Cotterill, P. P. and James, J. W.: Optimising two-stage independent culling selection in tree and animal breeding. Theor. Appl. Genet. 59: 67—72 (1981). —— Falconer, D. S.: Introduction to Quantitative Genetics. Second Edition. Longman, London and New York (1981). —— Greenwood, M. S.: Rate, timing, and mode of gibberellin application for female strobilus production by grafted loblolly pine. Canad. J. For. Res. 12: 998—1002 (1982). —— Greenwood, M. S.: Maximizing genetic gain in loblolly pine by application of accelerated breeding methods and new concepts in orchard design. pp. 290—296. Proc. 17th South. Tree Impr. Conf., Athens, GA. (1983). —— Hafley, W. L., Smith, W. D. and Buford, M. A.: A new yield prediction model for unthinned loblolly pine plantations. Tech. Rep. No. 1, School of Forest Resources, N.C. State Univ., Raleigh. 65 p. (1982). —— Lundgren, A. L. and King, J. P.: Estimating financial returns from forest tree improvement programs. Proc. Soc. Am. For., 45—50 (1965). —— McKeand, S. E. and Weir, R. J.: Economic benefits of an aggressive breeding program. pp 99—105. Proc. 17th South. For. Tree Impr. Conf.-Athens, GA. (1983). —— Moak, J. E.: Forest practices cost trends in the South. South. Jour. Appl. For. 6 (3): 130—132 (1982) —— Namkoong, G.: Optimum allocation of selection intensity in two stages of truncation selection. Biometrics 26: 465—476 (1970). —— Nanson, A.: La valeur des tests précoces dans la sélection des arbres forestiers en particulier au point de vue de la croissance. Dissert. Doct. Gembloux. Sta. Rech. Eaux et For., Groenendaal, H.S. No. 38, 242 pp. (1968). —— Paques, L. E.: Tree Improvement Strategies Modelization and Optimization. Unpubl. M. S. thesis, N.C. State Univ., Raleigh. 99 pp. (1984) —— Porterfield, R. L.: Predicted and potential gains from tree improvement programs. A goal programming analysis of program efficency. Unpubl. Ph.D. Thesis, Yale University. 240 pp. (1973). —— Row, C., Kaiser, H. F. and Sessions, J.: Discount rate for long-term forest service investments. J. For. 79: 367—376 (1981). —— Talbert, J. T., Weir, R. J. and Arnold, R. D.: Loblolly pine tree improvement, an attractive forestry investment. SOFEW Workshop, Mobile, AL. 16 pp. (1983) —— Tallis, G. M.: The moment generating function of the truncated multi-normal distribution. Roy. Stat. Soc. J. Ser. B 23: 224—279 (1961).

Breeding Systems and Genetic Structure in some Central American Pine Populations

By A. C. Matheson[1], J. C. Bell[1]) and R. D. Barnes[2])

(Received 4th February 1988)

Abstract

The breeding systems, genetic structure and identity of populations of *Pinus caribaea* var. *bahamensis*, *P. caribaea* var. *hondurensis*, *P. oocarpa* and *P. maximinoi* were in-

---

[1]) CSIRO, Division of Forestry and Forest Products, P.O. Box 4008, Queen Victoria Terrace, Canberra, A.C.T. 2600, Australia

[2]) Oxford Forestry Institute, Department of Plant Sciences, South Parks Rd, Oxford OX1 3RB, England