Financial Analysis of Testor Numbers Used in Establishing Second Generation Forest-Tree Seed Orchards

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Introduction

Progeny tests of clonal seed orchards derived from mass selection in natural stands are usually established to determine breeding values of clones in the first generation orchard, heritability values of economically important traits, and general and specific combining ability. One additional objective, and the one discussed in this paper, is to provide tree-breeders with plantations of full-sib families in appropriately designed replication. Such plantations are ideally suited for selection of trees for the establishment of second-generation forest-tree seed orchards. A commonly used method of testing clones in a first generation tree-seed orchard utilizes Design II of Comstock and Robertson (1952). From *3—6* testors are each crossed with every clone in the orchard. The F_1 progeny derived from these crosses may then be used for second-generation selection.

Although the testor system is adequate to meet a variety of objectives its use causes problems for the breeder who wishes to make selections among the F_1 progeny. If four testors are used, selections must be made among only four half-sib families. This procedure causes increased probabilities of half-sib and full-sib mating in the second generation clonal orchard. Sib mating results in some inbreeding depression and a consequent loss in genetic gains may be expected. There are several methods to resolve the inbreeding problem. The genetic base of the scond generation orchard may be increased by exchange of superior plant materials from other orchard progeny tests composed of genotypes from different geographic areas. This method, if done without reciprocal testing may lead to decreased gains because of genotype-environment interactions. A second alternative is to use a large number of testors from other orchards and to cross sets of two testors with only a few clones in the first generation orchard. Such a design would decrease the efficiency of determining the breeding value of clones in the first generation orchard. Without reciprocal testing of testors, genotype-environment interactions also could decrease genetic gains.

Prior to the execution of these alternatives it is advisable to determine if inbreeding in second generation orchards, derived from a relatively small number of half-sib selections, would be financially significant. If inbreeding is financially significant, how many testors should be used in the testing of first-generation orchards to maximize profits from a second generation orchard derived from selected individuals in progeny tests? The purpose of this paper is to determine the number of testors that will maximize the profitability of a second generation orchard under certain assumptions and then test the sensitivity of the results to certain variations in the assumptions.

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Methods

The following biological assumptions were used to estimate the number of testors to maximize profits when progeny tests of first generation orchards are used for selection of trees for second generation orchard establishment:

1. Selections for the second generation orchard are randomly distributed over both the male and female parents of the F_1 generation.
2. Inbreeding depression in volume growth is equal to 4% for each 0.1 increase in the coefficient of inbreeding (F) (See: Franklin, 1970; Gansel, 1971).
3. Depression in sound seed yield from inbreeding effects exceeds tree volume inbreeding depression by a factor ranging from 1.5 to 2.0.
4. Pollination in the second generation orchard is completely random with the probability of half-sib matings equal to $\left(\frac{1}{FE}+T\right)$ where FE = number of females and T = number of testors used to produce the F_1 progeny; and with the probability of full-sib matings equal to $\left(\frac{1}{FE}\times\frac{1}{T}\right)$. Selfing probability is not considered since it is a function of the number of clones in the second-generation orchard, not the number of testors used for progeny testing of first-generation orchards.
5. Loblolly pine (*Pinus taeda* L.) yields are used in the example developed in this paper, but the methodology should not be restricted to loblolly pine management.

Logically there should be some point at which returns from various testor numbers are maximized, all other factors held constant. In order to develop a model to determine this point, a hypothetical but realistic situation was created. The following set of postulates describes the seed orchard model.

1. The goal of the seed orchard operator is to establish a second-generation seed orchard in such a way that the difference between his costs and potential returns from the orchard is greatest. For this particular situation, he is only interested in how the number of testors affects his goal.
2. The time schedules assumed for the second generation seed orchard and subsequent plantation establishment are shown in *Tables* 1 *and 2,* respectively.
3. The maximum possible dollar amount will be paid for seed by the plantation owner based on his marginal returns with respect to the number of testors.

It is fully realized that the above situation and assumptions will not hold in all cases, and it is doubtful that any set would apply to more than one or two improvement programs now in existance. However, it is felt that the program and assumptions outlined above are sufficiently realistic to allow trends to be assessed under various conditions.

Table 1. — Time schedule for second generation seed orchard establishment.

Year	*Action*
1	Bagging, pollinating, etc., in first generation orchard.
2	Cone collection, seed extraction and storage from first generation orchard. Years one and two repeated for each two testors.
X	All test-crosses completed.
X + 1 to X + 2	Nursery growth and final outplanting of progeny to be tested.
X + 3 to X + 13	Measurement of progeny at specified years.
X + 14 to X + 15	Grafting and planting of clones.
X + 16 to X + 24	Growth of orchard to reach commercial seed production (no seed production).
X + 25 to X + 55	Years of second-generation seed orchard commercial seed production (constant seed production is assumed).

Table 2. — Time schedule for loblolly pine plantation establishment and harvest.

Year	*Action*
0	Obtain seed from second generation orchard.
1	Plant and grow at nursery.
2-Rotation	Outplant and grow.
*Rotation	Harvest (no thinnings).

* Rotation varied so as to maximize present net worth.

The model used in determining the appropriate number of testors to maximize profit is derived from economic precepts. In general, the variable costs and revenues with respect to the number of testors are discounted to one point in time (the time the seed orchard starts to produce), and then the marginal values of the costs and revenues are determined. The number of testors for which the total marginal cost equals the total marginal revenue is the point at which the goal is achieved. It should be stressed that only the costs and revenues that vary with number of testors are considered. Other costs and revenues involved in a seed orchard program are irrelevant for this situation.

Marginal cost calculation[2])

The total variable cost, from which the marginal cost is calculated, is the sum of the variable costs of pollination and seed harvest, progeny test establishment, and progeny measurement. All other seed production costs are fixed with respect to the number of male testors. The total pollination cost per year is equal to the product of the number of testors crossed per year, the number of bags per cross, the number of females (clones), and the average cost per bag of the total operation. In this model, it is assumed that only two testors are crossed with all female clones per year and that collection, extraction, and storage which occur in the following year are equal in cost to those incurred in pollination.

The progeny test establishment cost is considered to be a function of establishment costs per acre and land used. Area used for outplanting seedlings of each cross was assumed to be 0.4 acres. The establishment cost was apportioned: 40% the first year for sowing and growing and 60% the second year for transplanting. In addition the land cost of the test area is included.

The final variable cost to be considered in the orchard establishment is the progeny measurement costs. These measurements are assumed to be made at various annual intervals with the measurement cost for any particular year being the product of the progeny measurement cost per acre, the number of crosses, and the number of acres used per cross.

The total variable cost of orchard establishment compounded to the point in time when the orchard starts producing is the sum of the individual variable costs appropriately compounded. The marginal cost is derived by taking the first derivative of total variable cost function with respect to the number of testors.

Marginal revenue calculation

The determination of marginal revenue depends primarily on the proposition that the firm producing the seed will obtain the maximum additional amount payable for its product. That is, the assumption is made that the difference between the price paid for improved seed above the regular seed price is equal to the present value of the expected increased returns from the use of the genetically improved seed. These increased returns can then be considered variable with respect to testor numbers according to the effects of inbreeding depression on seed and plantation yields.

The variable revenue with respect to the number of testors is calculated by determining the number of plantation acres that can be produced from a given year's seed orchard production and discounting the returns minus the costs associated with these acres of plantation to the time of seed purchase. From this value is substracted the comparable returns minus costs associated with an umimproved plantation discounted to the same point in time. This determines the additional annual income from the use of genetically improved seed. The additional income is assumed to be paid to the orchard owner. Then the annual additional income from seed sales for each year is discounted to the time the seed orchard starts producing.

The revenue derived from harvesting a plantation is a function of the price per unit and the number of units harvested. The price per unit net of marketing costs is assumed to be constant over time. The yield of the plantation on the other hand is considered to vary according to the increased yield due to the use of genetically superior seed minus the decreased yield due to inbreeding depression.

From the revenue must be substracted the cost of establishing the plantation and its annual management and land costs. The cost of establishing and planting per acre is assumed to be a function of the nursery costs and the number of trees planted per acre. The management cost is assumed to be annual over the life of the plantation at a value of $ .75. Combining the above costs and revenues and discounting to the appropriate time period gives the present net worth per acre of the plantation at time of seed purchase. Since only the added value is relevant the present net worth of a non-genetically improved stand is substracted from the present net worth of the stand developed from the second generation seed orchard. To change this added

[2]) Detailed economic analysis is available on request to the authors.

Table 3. — List of variables considered for the financial analysis of testor numbers in loblolly pine.

Pollination of First Generation Orchard

1. Number of pollination bags/testor × female cross = 50
2. Cost per testor × female cross = $ 0.75, $ 1.00
3. Number of testors crossed/year = 2
4. Number of clones in first generation orchard = 20, 35, 50

Progeny Testing

1. Acres per testor × female combination = 0.40
2. Measurement cost per measurement per acre = $ 150.00
3. Progeny test cost per acre = $ 100.00

Second Generation Seed Orchard

1. Seed production per acre per year = 25, 50, 75 lbs.
2. Viable seedlings per pound of seed = 7,500*
3. Inbreeding depression of viable seed yield = 2 and 1.5 times self-inbreeding depression for growth.

Plantation Derived From Second Generation Seed Orchard

1. Volume inbreeding depression of trees derived from second generation orchard = 0.04 per 0.1 increase in the inbreeding coefficient.
2. Establishment cost = $ 80.00/acre
3. Number of trees/acre planted = 680
4. Site Index = 50, 70, 90
5. Volume gain for trees derived from second generation seed orchard seed over unimproved seed: 10.2%; 21.0%; 32.3% (Equivalent to 5%, 10%, 15% improvement per orchard generation).
6. Stumpage value = $ 3.00, $ 5.00, $ 7.00 a cord.

* Base figure for noninbred trees (Bergman, 1968).

present net worth per acre to pounds of seed per year, it is multiplied by acres planted per pound of seed which is equal to the number of viable seed per pound divided by the number of trees planted per acre. The resulting present net worth is expressed in terms of dollars per pound of seed. This figure is then multiplied by the number of pounds of seed the orchard produces per year to yield the additional present net worth or income from a year's seed production where the seed orchard production is considered to be a function of ordinary seed orchard production and inbreeding depression.

Finally, since the resulting income is assumed to occur annually over the period of seed orchard production, each annual revenue is discounted back to the year the seed orchard starts producing to yield variable revenue or the present value of the expected increased returns affected by changes in the number of testors. The marginal revenue of course is obtained by differentiating variable revenue with respect to the number of testors.

The last step in developing the model consists of setting the marginal revenue equal to the marginal cost and solving for the number of testors. This gives the number of testors which will be most profitable for the firm.

Sensitivity and Results

Various ranges of values suggested by Davis (1967) and McElwee[3]) were used in assessing the sensitivity of the model and for deriving some conclusions about the important variables and their effect with respect to the number of testors. The values used in the sensitivity analysis are shown in *Table 3*, and the results are discussed in the succeeding paragraphs.

[3]) Personal communication with Dr. Robert McElwee, Virginia Polytechnic Institute and State University, Blacksburg, Virginia, 1971.

Results of the financial analysis when no inbreeding occurred indicated that under all conditions (combinations of variables) the number of testors to be used to maximize net returns from second generation orchard seed production equalled one *(Fig. 1A)*. This is to be expected.

When inbreeding depression occurs, however, the appropriate number of testors to be used increases. The increases were not highly dependent upon any one variable but the four variables to which the model was most sensitive included interest rate, number of clones in the first generation orchard, seed yield of the second generation orchard, and the site index (and thus yield) of the location where trees from second generation orchard seed were to be planted. The profitable testor numbers were inversely correlated with interest rate and number of clones, but were directly correlated with seed yield, site index, and stumpage value. Other variables such as genetic gain from a second generation orchard, cost of pollination and seed collection of testor crosses, and inbreeding depression of seed yield over and above volume inbreeding depression were relatively unimportant considerations over the ranges tested. In general, increases by one testor were observed under conditions of a site index of 70, low interest rates and high genetic gains (10—15%):

1. When seed set inbreeding depression decreased from 2.00 to 1.5 times volume inbreeding depression.
2. When volume gain increased from 10% to 15% per orchard generation.
3. When pollination and seed collection costs decreased from $ 1.00 per testor-clone combination to $ .75.
4. When stumpage values increased from $ 3 to $ 7/cord.

Figure 1 demonstrates the trends observed in testor numbers under varying conditions of interest rate, site index, number of clones in the first generation orchard and seed yields. Under conditions delineated in *Figure 1B*, it can be seen that profits will be maximized if 3 testors are used under conditions of a 2% interest rate, 20 clonal first generation orchard, 75 lbs. of seed yield/acre/year in the second generation orchard, and a site index 50 for the planting site of seedlings derived from the second generation orchard. Testors numbers are decreased:

1. as interest rate increases
2. as clonal numbers in the first generation orchard increase
3. as seed yields decrease.

Similar trends were observed for other site index values. For a site index of 70 *(Fig. 1C)* testor numbers vary from one to five while for a site index of 90 *(Fig. 1D)* testor numbers vary from one to eight.

Conclusions

The use of four or five testors in tree-improvement programs has been justified in the past by consideration of three primary factors: (1) the logistics of hybridizing forest trees, (2) the diminishing gains in precision of estimates of general and specific combining ability and heritability values beyond four or five testors, and (3) the maintenance of a sufficiently large genetic base for future genetic selection. The financial analysis presented herein demonstrates that in some cases four to five testors are also justifiable

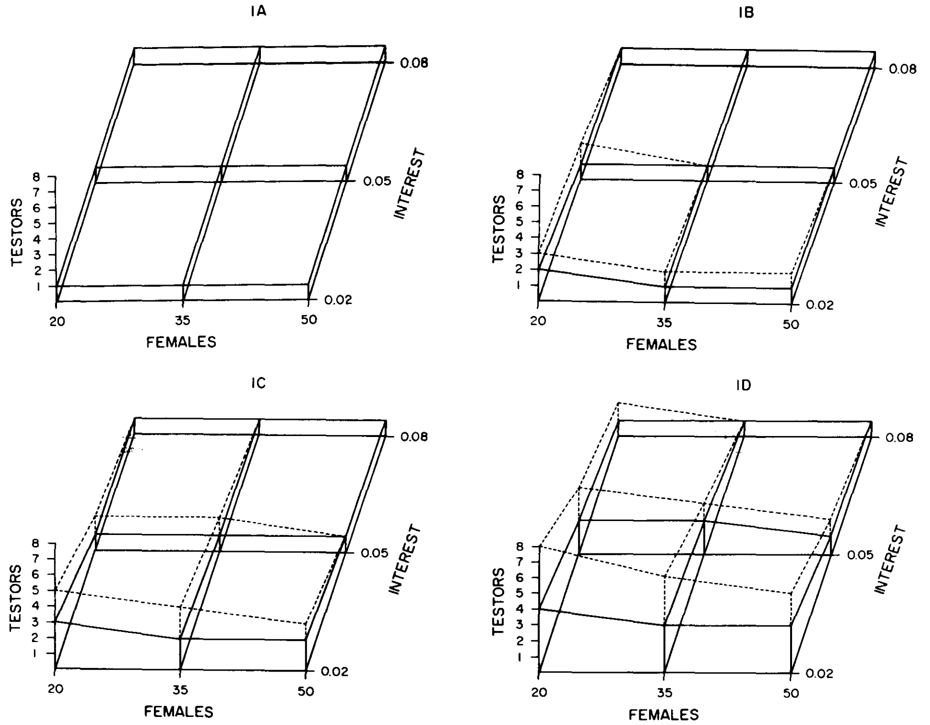

Fig. 1. — Results of financial analysis for testor numbers. Testors = number of testors used for testing first generation orchard. Females = number of clones crossed with the testors in the first generation orchard and is also equivalent to the number of clones used for establishment of the second generation orchard. Volume inbreeding depression, assumed to be 4%/0.1 increase in F for second generation orchard progeny; Seed yield decreases in second generation orchards caused by inbreeding depression assumed to be 8%/0.1 in F increase. Cost per testor × female cross = $ 1.00 and volume increase assumed to be 10%/orchard generation. Solid line (———) designates seed yields in second generation orchards of 25 lbs//acre/year and dotted line (- - - - -) 75 lbs/acre/year. — *Fig. 1A:* Testor numbers for all combinations of variables with no inbreeding depression. — *Fig. 1B—1D:* Testor numbers with planting of second generation progeny on site index = 50 *(Fig. 1B)* site index = 70 *(Fig. 1C)* and site index = 90 *(Fig. 1D).*

on a financial basis where the goal is to maximize profits from a tree improvement program. However, even under the most ideal financial condition, eight testors should not be exceeded.

From this analysis, it is apparent that if four or five testors are to be justified solely on the basis of maximizing profits under considerations of sib-mating accompanied by inbreeding depression, moderate to low interest rates must be generally assumed. This may be a valid assumption if genetic improvement is believed to be essential to the continued growth of forest industries.

If low interest rates (i. e. less than 7%) can not be assumed by an organization planning first generation seed orchard tests using four or five testor trees then the number of testors must be justified on other than economic grounds, such as research. However, if research objectives of an organization can not justify the expense of four or five testors the only alternative using high interest rates is to accept a polycross method or a half-sib test of the seed orchard. If polycross or half-sib tests are used it is of course accompanied by the assumption that inbreeding depression is not a significant (financially) part of second generation seed orchard establishment.

It must be realized however that use of a half-sib or polycross testing procedure will probably decrease the potential gains to be realized from the second generation orchard. This decrease will be caused by decreases in the variability of the trees in the test and must necessarily cause a decrease in the selection differential achieved when selecting trees for the second generation orchard. In addition, selection of the polycross or half-sib test method removes much of the potential of the test for research purposes. This could be very detrimental if the organization's research objectives change.

Although the model used for the analysis presented here makes several basic assumptions, both financial and biological, two factors which have not been considered include: 1) theoretical increases in genetic gain which can be realized by including more testors, and 2) elimination of some inbreeding effects by seedling grading. The first factor tends to underestimate testor numbers when inbreeding is present. The second factor causes the model to overestimate testor numbers since inbreeding effects may be partially removed by nursery techniques. However, because the model is only slightly sensitive to percent yield increases (relative to site index, interest rates, number of clones and seed yields) these compensatory factors are judged to be of only minor importance and would not alter trends observed.

In conclusion, only a few factors have been considered herein, and there are other factors which enter a practical analysis of testor numbers in addition to those mentioned above. One of the most important of these factors is the maintenance of a broad genetic base for tree seed orchards. In consideration of the long rotation periods of a forest tree crop, probabilistic consideration of disease infestation in plantations of small genic base should be made. Since probabilities of acute disease or insect infestation in plantations of limited genetic base are difficult to assess, it still seems advisable from the biological viewpoint to include as many testors as logistically possible when testing first generation seed orchards. A design using four or five testors will aid in maintaining a broad biological base for future improvement work but in many cases will not meet financial criteria.

Abstract

The financial impact of inbreeding depression on the number of testors that maximizes the profitability of second generation forest-tree seed orchard production has been determined under various assumptions. Sensitivity analysis of these assumptions indicates that optimal testor numbers vary mainly with changes in clone number in the first generation orchard, the interest rate used, the seed yield from the second generation orchard, and the site index for the resulting plantations. The range of optimal testor numbers was from one to eight.

Key words: Economics, Testor Numbers, Second Generation Seed Orchards.

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Gas Exchange in Six Populus Clones[1])

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Introduction

Short-time measurements of photosynthetic performance have often been used as an index of growth potential of trees (BOURDEAU, 1958; FERRELL, 1970; KOZLOWSKI, 1971 a, 1971 b; KOZLOWSKI and KELLER, 1966). Such measurements sometimes have limitations because both high and low (and even negative) correlations have been reported for *Populus* (HUBER and POLSTER, 1955; GATHERUM *et al.*, 1967), *Pseudotsuga menziesii* (CAMPBELL and REDISKE, 1966), *Pinus elliottii* (WYATT and BEERS, 1964), and *Pinus taeda* (MCGREGOR *et al.*, 1961). By comparison, poor correlation between photosynthesis and growth has been reported for *Larix* (NEUWIRTH, 1967), *Pseudotsuga menziesii* (SORENSEN 1964; BRIX, 1967), *Pinus contorta* (SWEET and WAREING, 1968), and *Pinus banksiana* (LOGAN, 1971). Because dry weight increment varies greatly with experimental conditions, there are difficulties in comparing photosynthetic efficiency of different species based on production data of various investigators (HELLMERS, 1964).

In addition to photosynthetic rates alone, at least three important physiological considerations determine growth potential (dry weight increment). These include the relation of photosynthesis to respiration, the distribution of photosynthate within the tree, and duration of growth or the seasonal pattern of assimilation (LEDIG, 1969). The relationship between photosynthesis and respiration is of particular interest in tree improvement because heterotic plants have more effective photosynthetic systems than do phenotypically normal plants. DECKER (1970) suggested that there may be phenotypically normal individuals within a species that have unusually high photosynthetic capacity but this is combined with high photorespiration with the net result of normal growth rate. There may also be phenotypically normal individuals with low photosynthetic rates and low photorespiration. If such individuals could be identified and if the two processes are genetically separable, genetic recombination of high-low might be possible.

As emphasized by DECKER (1957, 1970), the CO_2 compensation point, at which a plant is gaining and losing CO_2 at the same rates, is determined in strong light largely by photo-

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Table 1. — The identification numbers and origins of the experimental clones.

Identification No.	Species	Section	Origin
D 40	*P. deltoides*	*Aigeiros*	Sandy shore of L. Ontario, Canada.
M 12	*P. maximowiczii*	*Tacamahaca*	Hokkaido, Japan; collected from natural stands by Kórnik Arboretum, Poland, in cooperation with the Oji Institute, Kuriyame, Japan.
M 13	*P. maximowiczii*	*Tacamahaca*	(as M 12)
MN 1	*P. maximowiczii* × *P. nigra*	*Tacamahaca* × *Aigeiros*	Arnold Arboretum (hybrid by E. Chalmere Smith).
N 2	*P. nigra*	*Aigeiros*	Kunovice, Moravia, Czechoslovakia.
T 6	*P. trichocarpa*	*Tacamahaca*	Poplar Institute, Geraardsberger, Gramont, Belgium.