Adjustment and Interpretation of Progeny Tests when only the Best Tree in Each Plot is measured

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Randomized block design with multiple-tree plots has been commonly practiced in tree improvement programs. It offers efficiency of land use and convenience in record keeping. The experimental unit is the plot rather than individual tree. In other words plot means are used in information processing and variance among plot means is considered as error term.

Plot mean can be obtained either by measurement of all trees in the plot or by sampling. In the study of traits such as color grades, tree form, survival, the whole plot is judged at the same time. On the other hand in the'study of traits such as needle length, wood density, gum composition, samples are taken for measurement. Between these two extremes are growth traits such as height, diameter and volume. Measurement of all trees is precise but expensive as compared to partial measurement.

Partial measurements may be done by deliberate sampling or random sampling. In deliberate sampling trees within plots are ranked and certain individuals are chosen for measurement. In random sampling each tree within plot has an equal and independent chance of being taken for measurement.

Deliberate sampling seems to be more efficient than random sampling. In a nursery study of ponderosa pine, LEE (1974) measured all 12 trees within plots as well as the tallest 1, 2, 3, 4, 5, 6, 8 trees. The correlation between family means of 12 trees and those of selected trees ranged from 0.978 to 1.000. When he used random sampling the correlation dropped to 0.917 for 1 tree and .994 for 10 trees.

Random sampling is better known and is easier to infer.

Given b = total number of blocks.
m = total number of trees within plot.
n = the number of trees sampled per plot.
Vf = variance component for family.
Ve = error variance for individual tree.

We can see that when n trees are sampled
Standard error of plot mean = SE = $(Ve/n)^{1/2}$
Standard error of family mean = $(Ve/nb)^{1/2}$
Phenotypic variance of family mean = Vf + Ve/nb
Heritability of family mean = Vf/(Vf + Ve/nb)
Correlation of family mean of m trees and family means of n trees

$$\frac{Vf + Ve/\sqrt{mbnb}}{\sqrt{(Vf + Ve/mb)\,(Vf + Ve/nb)}}$$

Therefore, it is possible to convert results of partial random measurement to a general case. For example, in a half sib progeny test which involves sampling 4 trees (n = 4) from a plot of 100 trees (m = 100) in 9 blocks (b = 9), the standard error from the analysis of variance table is 5 (SE = 5) and the mother tree variance component is 6 (Vf = 6). We can compute the error variance of the original individual as Ve = 5 X 5 X 4 = 100. The heritability of mass selection in the wild stand is 4 Vf/(Vf + Ve) = 4 X 6/(6 + 100) = 0.23. The correlation between family means if measuring all 100 trees and those of 4 trees is

$$\frac{6 + 100/\sqrt{100 \times 9 \times 4 \times 9}}{\sqrt{(6 + 100/100 \times 9)\,(6 + 100/4 \times 9)}} = .90$$

The statistical behavior of the deliberate sampling is not well known. In this paper computer simulation was used to study the mean and variance of the tallest tree from each plot. Adjustment of family mean, selection differential, heritability and genetic gain based on empirical results were suggested.

Variance of the Tallest Trees Population

It is easier to choose the tallest tree in the plot than to use a randomizing device to locate a tree for height measurement. What is the variance among the tallest trees in each plot? To answer the question, 950 pseudo-random numbers were generated as input to simulation. These 950 numbers were separated into groups of 2, the top ranked number in each group was taken out for variance computation. The same procedures were repeated for the top one in groups of 4 and groups of 10. Results of 20 runs are shown in *figure* 1. The inputs to the random number generator were normal distributed with mean equal to zero and variance equal to 100. The variance of the top ranked individuals can be viewed as percentages of the original variance. For example, if the tallest seedling in a two-tree plot was measured, the variance of the tallest tree is 68.70, or 68.7% of the variance among all original trees.

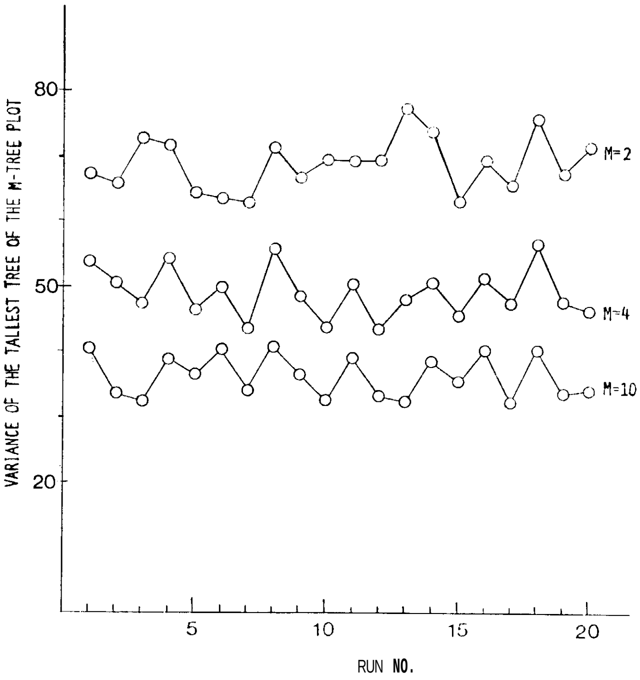

Figure 1. — variance of the tallest tree of each plot. The original variance of individual trees is 100. Smaller size of plot (m) has greater mean variance (V) as well as greater variance of variance.

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When the value of the tallest tree is used as a substitute for the mean of the plot, then the variance of the tallest trees is the variance of plot means under deliberate sampling. However, the variance of plot means when all m trees are measured should be reduced to 1/m of the original variance. The results of simulated tallest tree measurement and the expected all tree measurement are shown in *table 1*.

Table 1. — Relationship among variance of the tallest tree in each plot, variance of the original individual trees and variance of plot mean.

Plot Size (m)	Variance			Variance Ratio	
	Tallest Trees (VTT)	All Trees (VAT)	Plot Means (VPM)	$k_1 = \frac{VPM}{VTT}$	$k_2 = \frac{VAT}{VTT}$
2	68.70	100.0	50.00	.7278	1.456
3	56.51	100.0	33.33	.5898	1.770
4	49.10	100.0	25.00	.5092	2.037
5	45.05	100.0	20.00	.4440	2.220
6	42.02	100.0	16.67	.3967	2.380
7	38.84	100.0	14.29	.3679	2.575
8	37.54	100.0	12.50	.3330	2.664
9	36.85	100.0	11.11	.3015	2.714
10	36.42	100.0	10.00	.2746	2.746

Conversion from Variance of the Tallest Trees to Other Variance

Unless the plot is thinned to the tallest tree, the variance of the tallest tree has limited utility. On the other hand variance of individual trees and variance of the plot means are useful in a selection program. Selection differential and consequently genetic gain are related to the variance of the original population. The variance ratios in the last two columns of *table 1* provide an empirical conversion ratio. It is interesting to note that when plot size is equal to 4 (the most common plot size used by tree breeders) the conversion is easy. The variance of plot means is about one half of the variance of tallest trees and the variance of individual trees is about twice of the variance of tallest trees. For example, if the variance of the tallest ones of a 4 tree plot is 4 feet the estimated variance of plot mean would be 2 feet and the estimated variance of individual trees would be 8 feet.

Mean of the Tallest Tree Population

Because only the top individual is measured, the average of the top ones should be higher than the average of plot means. The difference is predictable as selection differential. The result from this simulation agreed with Nanson's (1967) calculation. The small discrepancies between the simulated and the predicted values are shown in *table 2*.

Table 2. — Reduction factors to correct overestimate of plot mean by measuring the tallest tree of a m-tree plot.

Tallest tree of a m-tree plot m	Simulated mean of the tallest trees	Theoretical selection differential
	standard deviation	
2	.562	.56
3	.843	.85
4	1.029	1.03
5	1.165	1.16
6	1.268	1.27
7	1.353	1.35
8	1.422	1.42
9	1.477	1.49
10	1.529	1.54

Once the selection proportion is known we can find out the selection differential in standard units. For plot size larger than 10, the reader should consult Nanson's table. For example, if the tallest one of the 16-tree plot is used for plot means, the table gives 1.76 standard units. Therefore, the plot mean is overestimated by 1.76 standard deviations.

The standard units given in the table are in reference to the original population, not the tallest trees. Therefore, we need to convert the standard deviation of the tallest tree to that of the original population before the correction is made. The conversion ratios for standard deviation is the square root of the variance ratio. Suppose that the tallest tree of a 4 tree plot is used for plot mean, and the standard deviation for the tallest tree is 2 feet. Then the correction becomes $1.03 \times 2 \times \sqrt{2.0} = 2.9$. Therefore, all plot means should be reduced by 2.9 feet. Family means, ecotype means, population means should likewise be reduced by the same amount.

Selection Differential

Because both the mean of the selected group and the population mean are reduced by the same amount when they are restored to the original value, there should be no adjustment for selection differential. For example suppose the mean of the selected group is 15 feet and the population mean is 12 feet when only the tallest tree in a plot is measured. The selection differential, therefore, is $15 - 12 = 3$ feet. Suppose that the correction is 2.9 feet as shown in the above section, the original mean of the selected group should be corrected to $15 - 2.9 = 12.1$ feet and the population mean should be $12 - 2.9 = 9.1$ feet. The selection differential here again is 3 feet.

Heritability

After variance components are obtained from analysis of variance for the tallest trees, the error variance shoud be corrected to reflect the original error variance of individual trees, and the heritability can be constructed. For example, if VG = Genetic variance component

VET = error variance for tallest trees then

VE = error variance for individual tree = k_2VET

$$h^2 \text{ for family selection} = \frac{Vf}{Vf + VE/mb} = \frac{Vf}{Vf + k_2VET/mb}$$

Suppose that an analysis of variance table for the tallest tree in a 4-tree plot is as follows:

Source	df	SSQ	MSQ	EMS
Block	5	1378.41	275.68	VET + 25 VB
Family	24	1797.97	74.92	VET + 6VF
Error	*120*	*4468.96*	37.24	VET
Total	149	7645.34		

We have

VET = 37.24

VF = 6.28

VB = 9.54

According to *table 1*, the coefficient k_2 is approximately equal to 2 for an experiment with 4-tree plots. Therefore

$$VE = k_2 \text{ VET} = 2 \times 37.24 = 74.48$$

So we have heritability for mass selection in wild stands

$$h^2 \text{ mass selection} = \frac{VG}{VG + VE} = \frac{4\,VF}{VF + VE} = \frac{25.12}{6.28 + 74.48} = .31$$

and heritability for family selection in the test plantation as

$$h^2 \text{ family selection} = \frac{VF}{VF + VE/mb} = \frac{6.28}{6.28 + 74.48/24} = .67$$

Genetic Gain

Genetic gain is the product of selection differential and heritability. Selection differential does not need adjustment but the heritability does. By using the corrected heritability one can make a better prediction on genetic gain. For example, if the selected families exceed the population mean by 3 feet and the corrected family heritability is .67, the predicted genetic gain from the selection would be 2 feet.

Summary

In order to study the consequences of measuring only the tallest tree of a m-tree plot a computer simulation with 950 generated data points was used. Data points were drawn from a normal distribution with mean equal to zero and variance equal to 100. The average of mean and variance of the tallest trees of plot size from 2 to 10 were obtained through 20 computer runs. The mean of the tallest trees agreed with the predicted selection differential for chosen one best tree out of a m-tree plot. The empirical ratios between the variance of all original individual trees and the variance of the tallest trees were presented in this paper. The ratio is useful in adjustment of heritability estimates, expected mean of the selected group and predicted genetic gain when only the best tree in a plot is measured.

Key words: Progeny test, sampling, computer simulation, adjustment of genetic parameter.

Zusammenfassung

An Hand der Meßergebnisse aus einem randomisierten Blockversuch wird untersucht, welche Auswirkungen es hat, wenn zur Beurteilung der Wüchsigkeit jeweils nur der wüchsigste Baum jeder Parzelle gemessen wird. Hierzu wird das empirische Verhältnis der Varianz aller Bäume zur Varianz der höchsten Bäume dargestellt, welches zur Korrektur der Schätzung von Heritabilitäten von Bedeutung ist.

Literature Cited

Lee, C. H.: Effect of partial measurement on statistical precision and efficiency in a nursery study of *pinus ponderosa*. Silvae Genetica 23: 124—126 (1974). — Nanson, A.: Tables de la différentielle de sélection dans la distribution normale (0, 1). Biometrie-Praximetrie, t. VIII, n 1 (1967).

Short Note: Growth Correlations of Cottonwood Clones Developed from Mature Wood Cuttings

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Introduction

To develop improved cottonwood (*Populus deltoides* Bartr.) clones geneticists test either seedlings, clones derived from seedlings, or clones propagated from cuttings of mature trees. The growth, development, and characteristics of trees from these three classes of material may not be the same. Most reports deal with trees developed from seedlings or from cloned seedlings. This paper gives results of a study in which clones were developed from cuttings taken from the crowns of mature trees.

Methods

Twenty-four phenotypically superior cottonwoods that were about 25 years old were selected in natural stands in west central Mississippi along a 200 km section adjacent to the Mississippi River. Cuttings from branch tips of the midcrowns were collected in late February 1963. The cuttings were rooted in a greenhouse in peat pots filled with a sand-peat medium, then transplanted to a nursery. The plants grew in the nursery for one year, were cut back to rootstocks, and then allowed a second year's growth in the nursery.

A field test was planted in February 1965 with cuttings from the rejuvenated nursery plants (24 clones) and cuttings from one cloned seedling. The test design was a randomized complete block with four replications, 25 clones, and two-ramet plots. Unrooted cuttings, 46 cm long by 12 to 18 mm in diameter, from each clone were treated with Thimet^{R}[2]) and planted three per spot at 3- by 6-m spacing. In May of the first growing season, each spot was thinned to a single plant. The planting was clean cultivated the first year and mowed annually thereafter. After the fifth growing season, every other row was removed leaving one ramet per plot at 6- by 6-m spacing. Cloned seedlings in an adjacent study were used to compare with the mature wood cuttings.

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[2]) Mention of trade names is solely to identify material used and does not imply endorsement by the U. S. Department of Agriculture.