ESTIMATE HERITABILITY OF SPROUTING
FROM A PARTIALLY THINNED PLANTATION

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ABSTRACT.--In a black walnut progeny test plantation, the two
smallest trees within a five-tree-plot were thinned. Number
of sprouts on each stump was recorded. This paper presents a
procedure to calculate single tree heritability of sprouting
based on the thinned trees.

INTRODUCTION

Forest tree improvement workers probably look at sprouting with
mixed feelings. Following heavy cutting, an aspen stand can repro-
duce as many as 2800 sprouts per acre (Stoeckeler and Mason, 1956).
Thus, a plantation of superior aspen clone can perpetuate itself
asexually with a minimal reforestation cost to its owner. Further-
more, sprout shoots often grow faster than shoots of nonsprout ori-
gin, because the root suckers and stump sprouts utilize larger a-
mounts of reserves while the normal shoots appear to use current
photosynthate for their expansion (Kozlowski, 1971). It was re-
ported that the rate of leaf production, leaf elongation, and inter-
node elongation, the final size of leaf and internodes were greater
in red maple sprouts of trees cut in previous winter than in long
shoots of uncut trees (Wilson, 1968).

On the other hand, stump sprouting is undesirable in the cull-
ing of seed orchards, because the inferior tree may keep coming
back and need to be cut down again periodically.

The environmental factors governing sprouting have received
major attention among silviculturists working with coppice planta-
tions (Debell and Alford, 1972; Church, 1961), while physiological
factors were under investigation by plant physiologists (Vogt and
Cox, 1970; Wenger, 1953). Yet, no forest geneticist has reported
the genetic factors in sprouting variation. According to the usual
progeny or provenance test procedures, if one wants to study the
sprouting traits similar to height growth or diameter growth, one
must cut down the whole plantation and observe sprouting on each
stump. Obviously, sacrifice of a plantation for the study of sprout-
ing is too expensive. However, it can be done at the end of the
testing cycle when the evaluation of its performances has been com-
pleted.

In this study, number of sprouts from each stump was record-
ed. Because smaller stumps usually have fewer sproutings, study
conducted on the selectively thinned trees which are the smallest
two in each plot, can not represent the expected sprouting varia-
tion of the average tree. The single tree heritability computed
from the selectively thinned trees can not be used directly as the
heritability of an average tree. How can we correct this bias due
to the selective thinning within the plot? The calculation proce-
dure is presented in this paper.

TEST PLANTATION

The black walnut wind pollinated progeny test was established
at the Union State Tree Nursery, Jonesboro, Illinois. Seed was col-
lected in the fall of 1969 from naturally growing trees in Millais,
Missouri, Tennessee, Arkansas and Kentucky, and was cleaned and
stored in a cooler (2 °C) for the winter. In early April, 1970, they
were moved to a warm greenhouse. Germinated seeds were planted in
a well-drained bottomland site about three acres in size. Five
pounds of active simazine and 15 pounds of dalapon per acre were
sprayed prior to planting.

A randomized complete block design was used. There are 85 fam-
ilies in each of the 5 blocks, and there are 5 trees in each plot.
Spacing was four feet (within plots) by 10 feet (between rows).
Filler trees were planted between plots within row to reduce neigh-
boring interaction effect and to provide more even spatial distri-
bution of remaining trees after thinning. Border trees were also
planted.

Five years after planting, the tree crowns were in touch with
each other within plots. Thinning was done in the winter of 1975
to remove all filler trees between plots and two smallest diameter
trees in each plot.

Number of sprouts was recorded in 1978. It ranges from 0 to 11
sprouts per stump for individual trees and from .5 to 6.1 for family
mean.

DATA ANALYSIS

At the time of thinning, the dbh of the thinned trees had a
mean of 1.21 inches and variance of .315 square inches.

Two years after thinning, we tallied the number of sprouts
from each stump within a plot. The mean number of sprouts was 3.40
and the variance 5.01. The correlation between diameter and number
of sprouts was 0.586; its 95% confidence interval was 0.534 to 0.632.

It was observed that the cambium of stumps in black walnut often proliferates to produce callus in which primordia originate and develop into adventitious shoots. The positive correlation supports the hypothesis that larger diameter trees have more sprouts, and smaller diameter trees have fewer sproutings. Because the thinned trees were smaller than the original population: then the mean and variance of number of sprouts in the original population should be greater than that observed in the thinning. In other words, truncation selection reduced phenotypic variance both in tree diameter and in number of sprouts, because these two traits were correlated.

However, if we compare various variance components before and after truncation selection, we will find that the component for family, block, or block and family interaction will not change but the error variance of the experiment will. Once the error variance is reconstructed, the problem of heritability estimation can be easily solved (Kung, 1977).

Let: V_y = Within plot variance for number of sprouts in a random and independent s-tree plot.

V_{ay} = Within plot variance for number of sprouts in a plot which was culled from n to s trees according to its diameter.

r_a^2 = Squared correlation between number of sprouts and diameter of the thinned trees within plot.

k = Within plot variance ratio of selected s trees to random and independent s trees.

Then: $V_y = V_{ay} (k + r_a^2 - k\, r_a^2) / k$ (Kung and Funk, 1979).

In order to solve for V_y, we need to have the value for r_a, k, and V_{ay}. By using data from Table 1, we first complete the squared correlation between the number of sprouts and the diameter of the thinned trees within a plot as follows:

$$r_a^2 = 2.94^2 / (10.91 \times 3.13) = 0.253$$

Because sproutings were counted on the two smallest trees in a five-tree-plot, the within plot variance ratio for the two selected trees as contrasted to two random trees can be obtained from Table 2 as:

$$k = 0.378$$

The third variable, V_{ay}, or the within plot variance for number of sprouts is obtained from Table 1 as 3.13.

Therefore, the within plot variance for two random trees should be:

$$V_y = 3.13 (0.378 + 0.253 - 0.378 \times 0.253) / 0.378 = 4.43$$

TABLE 1.--Component of variance and covariance

Source	Component of		
	Variance		Covariance
	Diameter	Sprout	Dia. x Sprout
Block	2.59	.05	.33
Family	5.07	.49	1.13
B x F	12.08	.95	2.58
Error	10.91	3.13	2.94
Total	30.65	4.62	6.98

TABLE 2.--K ratio of within plot variance for s selected trees to within plot varance for s random trees

Number Selected		Original Plot Size							
	n =	3	4	5	6	7	8	9	10
s = 2	k =	.585	.450	.378	.335	.305	.283	.270	.252
3			.632	.496	.422	.375	.342	.317	.298
4				.667	.533	.457	.408	.372	.346
5					.694	.961	.487	.436	.399
6						.715	.588	.511	.460
7							.733	.610	.534
8								.749	.629
9									.762

Because the within plot variance contains three quarters of the genetic variance and the total environment variance, we have:

$$V_y = 4.43 = (3/4) V_g + V_e$$

Assuming that the other one quarter of genetic variance is distributed among half-sib family means, we have $V_f = .49$ (Table 1.) and hence:

$$V_g = 4(.49) = 1.96$$
$$V_e = 4.43 - (3/4) 1.96 = 2.96$$

Finally, we have heritability for mass selection as:

$$h^2 = V_g / (V_g + V_e)$$
$$= 1.96/(1.96 + 2.96)$$
$$= 0.40$$

DISCUSSION

The estimated heritability of number of sprouts ($h^2 = .40$) is similar to some growth traits in black walnut. For example, the heritability values were between .4 to .45 for diameter, height, number of lateral buds on current year's terminal, and index of crook in a Southern Illinois study (Bay, Hawker, and Roth, 1971). The heritability of number of sprouts is low in comparison to germination ($h^2 = .84$ to .94; Beineke and Masters, 1973), but is high in comparison to branch angle ($h^2 = .20$; Beineke, 1974). If one is interested in selection for, or against, number of sprouts, a moderate genetic gain is obtainable.

The method of using data from truncated population to estimate heritability as I have illustrated here, open the door for genetic study of traits which involves destructive observation. For example, the assessment of heartwood color, the sapwood/heartwood ratio, or the total tree weight is usually destructive to living trees, but now we can conduct such study on culled trees and adjust the result for the original unthinned plantation.

The method can be useful, also, in the study of traits on remaining trees after selective thinning. Suppose that twenty years after thinning we have recorded nut yield on each tree, then the heritability of nut yield for a normal unthinned population can be calculated as follows:

(i) obtain within plot variance for nut yield as V_{ay} from an analysis of variance table.

(ii) compute the product moment correlation between the current nut yield data and the previous diameter measurements, square the correlation efficient as r_a^2.

(iii) find the value of the k-ratio from Table 2. Because
       in this example, 3 trees were left from the original
       5-tree plot, the value for the k-ratio is 0.495.

(iv)   use the value of Vay from (i), r_a^2 from (ii), and k
       from (iii), compute the within plot variance for nut
       yield as if the plot is consisted of 3 randomly sampled
       trees by the following formula:

       $$Vy = Vay \ (k + r_a^2 - k \ r_a^2) \ / \ k$$

(v)   compute family variance component, V_f, by equating the
       expected mean squares to the sample mean squares in an
       analysis of variance table for the current nut yield data.

(vi)   solve the following simultaneous equations for Vg and Ve:
       $$V_f = Vg/4$$
       $$Vy = (3/4) \ Vg + Ve$$

(vii) compute: $h^2 = Vg \ / \ (Vg + Ve)$

Thus, the method presented here can be used to estimate herita-
bility of any trait existing in a progeny test plantation after se-
lective thinning within plots. However, for plot size greater than
ten, the value for k is not available from Table 2, and must be
calculated by the following formula:

$$k = [(r-1) \sum_{i=1}^{r} VXi + r\sum_{i=1}^{r} Xi^2 - (\sum_{i=1}^{r}Xi)^2 - 2\sum_{i \neq j}^{r} COV \ Xi \ Xj]/r(r-1)$$

where Vxi and COV Xi Xj are variances and covariance of order statis-
tics Xi, Xj (Sarhan and Greenberg 1962).

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