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## Genetic Variance and “C” Effects in Balsam Poplar Rooting

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(Received 14th December 1987)

### Summary

Dormant cuttings of *Populus balsamifera* L. clones from six natural populations between latitudes 45° N and 54° N at longitude 90° W were propagated to (1) evaluate the pattern of genetic variance in number of roots and (2) assess the influence of environmental preconditioning on variance in rooting. Geographical source accounted for less than 10 percent of variance in number of roots per cutting. Clonal variance within populations ranged from 15 percent to 81 percent of total variance, depending upon collection time between November and April. Physiologically dormant cuttings propagated in September rooted poorly. Environmental preconditioning associated with primary ramets in a nursery or in a long-term field test was not a statistically significant source of variance.

**Key words:** Rooting, genetic variance, environmental preconditioning.

### Introduction

Rooting of cuttings via growth of preformed root primordia has been extensively studied in *Populus* mostly with interspecific hybrids, and variation in root development has been associated with cutting size and location on

parent plant (e. g. BLOOMBERG, 1959, 1963; SMITH and WAREING, 1972b), carbohydrate reserves (e. g. SMITH and WAREING, 1972b; FEGE and BROWN, 1984), dormancy (SMITH and WAREING, 1972a, b; CUNNINGHAM and FARMER, 1984), and rooting environment (see ZSUFFA, 1976; and FEGE, 1983 for reviews). However, since most of the studies have involved small numbers of clones, our knowledge of genetic variation in rooting is incomplete. A study in *P. deltoides* BARTR. ex MARSH (WILCOX and FARMER, 1968) revealed moderate genetic control over number of roots and demonstrated that rooting was positively correlated with resumption of shoot growth; environmental preconditioning, or “C” effects, (LERNER, 1958) accounted for about 10 percent variance in rooting. THIELGES and BECK's (1976) observations in *P. deltoides* led them to hypothesize that growth of root primordia causes bud break. They reported variable broadsense heritabilities for both dates of root initiation ( $h^2 = .33$  to  $.95$ ) 2nd bud break ( $h^2 = .51$ – $.98$ ). While broad phenotypic variation in number of roots per cutting has been observed in balsam poplar (*Populus balsamifera* L.) by CUNNINGHAM and FARMER (1984), genetic control of this variation has not been reported.

Under natural conditions, the presence of preformed root primordia on balsam poplar probably has some fitness value under circumstances where flooding may deposit soil

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around tree bases. To exploit and/or tolerate this condition, new roots must be formed. Many populations in north-western Ontario have been subjected to this periodic flooding. On the other hand, within a given geographical area, balsam poplar is found on a variety of sites. Hence it is expected that considerable variation in selection pressure for preformed root primordia exists within provenances, from high pressure along geologically old rivers and their deltas, to essentially none on uplands. Therefore, some variation in rooting characteristics would be expected within provenances.

In this study, we evaluated genetic variance in rooting within natural populations of balsam poplar in north-western Ontario and northern Wisconsin with the objective of testing the above hypotheses. We also estimated "C" effects associated with primary ramets growing in a nursery and in a long-term clonal test.

### Methods

Material for the two experiments in this study was collected in each of four locations at longitude 90° W: Bearskin Lake (53° N to 54° N), Pickle Lake (50° N to 51° N), Thunder Bay (48° N to 49° N) and northern Wisconsin (45° N to 46° N). In 1982 and 1983, shoots were collected from the upper lateral branches of 50 ortets situated at least 1 km apart in these locations. Plants (primary ramets) were propagated from these cuttings in a greenhouse, then transferred to a nursery. These primary ramets were the source of material for Test I. At time of secondary cloning (1984 to 1985), primary ramets were two and three years old and had been exposed to the same environmental conditions for at least one full growing season. Material grown in the nursery was the source of cuttings which were used to establish a long-term clonal test in 1984. Cuttings from three-year-old ramets in this clonal test were used in Test II.

#### Test I

Six randomly selected clones from each provenance were used in Test I, which evaluated rooting of cuttings collected from September to April. A single upper lateral branch was taken from each of two primary ramets in each clone on each of five dates: September 26, November 6, December 3, 1984 and January 4, April 17, 1985. At the time of collection, each branch from primary ramets was sectioned into four 10-cm-long cuttings which ranged in diameter from 4 mm to 8 mm. A collection on each of the dates thus included a total of 192 secondary ramets (4 provenances × 6 clones/provenance × 2 primary ramets/clone × 4 cuttings/primary ramet). Secondary ramets (i.e. cuttings) were assigned to one of four blocks on the basis of position on branch, i.e., all apical cuttings were grouped in the same block, while basal cuttings were assigned to another. Immediately after collection cuttings were planted in Spencer-LeMaire (Tinus) containers filled with rooting

medium (60% peat, 40% vermiculite) and arranged in a randomized complete block design on a greenhouse bench.

A 28-day propagation period was used for all collections. Photoperiods were 16 hours and temperatures were about 16° C at night and 24° C during the day. During this period cuttings were watered daily and date of bud break was recorded for each cutting beginning shoot growth. Upon completion of the propagation period shoot length and number of primary roots per cutting were recorded. Roots were predominantly from preformed primordia on the basal 3 cm of the stem and very few emerged from basal callus. Data were subjected to the analysis of variance outlined in Table 1.

#### Test II

In order to evaluate a larger sample of clones, cuttings were taken in mid-March 1987, from two ramets of 25 clones per provenance in the long-term clonal test. These two ramets were located in different replications of the test. The sampling and propagation procedure was identical to that used in Test I. Analysis of variance took the form outlined in Table 1.

### Results

#### Test I

Cuttings collected in September did not break bud during the propagation period. Only 52 percent of these cuttings developed roots, and rooting percent of clones ranged from 0 to 100. Geographical source of material was not a significant source of variation in any rooting characteristic in this collection (Table 2).

Percent rooting and bud break averaged over 94 for all other collections with the following exception: Percent bud break for the November collection averaged 73, and ranged significantly (.05 level of probability) from 50 for northern Wisconsin material to 92 for cuttings from Bearskin Lake, the most northern source. Clones within sources were also a significant source of variation in this characteristic.

Days to bud break decreased from over 26 for the November collection to 6 in April (Table 2), and analyses indicated that in December and January collections about one-half of the variance in this characteristic was associated with clones. Variation among primary ramets within the nursery accounted for 4 percent of variance in December and January, and provenance was not a statistically significant source of variation. Bud break in the April collection was rapid and uniform, as suggested by the fact that essentially no variance was associated with clones or primary ramets within clones.

Average number of roots per cutting was similar in November, December and January collections (Table 2). Twenty to thirty percent of variance in rooting was associated with clones and essentially none with primary ramets. There was a trend of increased number of roots from Wisconsin (5 per cutting) to northern provenances

Table 1. — Outline of analysis of variance used in Tests I and II.

Source of Variation	Degrees of Freedom		Expected Mean Squares
	Test I	Test II	
Blocks (B)	3	3	$\sigma^2_S + \text{src}\sigma^2_B$
Provenance (P)	3	3	$\sigma^2_S + s\sigma^2_R + \text{sr}\sigma^2_C + \text{src}\sigma^2_P$
Clones/Provenance (C)	20	96	$\sigma^2_S + s\sigma^2_R + \text{sr}\sigma^2_C$
Primary ramets/clones (R)	24	100	$\sigma^2_S + s\sigma^2_R$
Secondary Ramets (S)	141	597	$\sigma^2_S$
Total	191	799	

Table 2. — Bud break, root and shoot characteristics of balsam poplar.

Character and Collection Date	Test Mean	Range of Clone Means	Percent Variance		If Due to:	
			Geographical Source	Clones Within Sources	Primary Ramets	Secondary Ramets
<b>Test I</b>						
Days to Bud Break						
November	2.6 *	2.1 - 4.0 *	2/		-	
December	2.1	1.4 - 3.0	15 *	46 **	4	34
January	1.6	1.1 - 2.4	9	62 **	4	25
April	6	3 - 9	<1 *	0	0	99
Roots per Cutting						
September	1	0 - 4	0	<1 **	0	100
November	7	2 - 11	6 *	19	0	75
December	7	3 - 12	9 *	15 **	0	76
January	7	2 - 12	11	28 **	6	55
April	13	4 - 22	0	81 **	1	18
Shoot Length, cm						
November	0.9	0 - 2.2	33 **	15 **	9 *	43
December	1	0.3 - 1.5	13 **	0	28 **	59
January	2.8	1.2 - 5.0	2	30 **	0	68
April	14.5	6.9 - 20.2	0	27 **	7	66
<b>Test II</b>						
Days to Bud Break	6	2 - 11	0	34 **	11 **	55
Roots per Cutting	8	3 - 20	5 **	21 **	5	69
Shoot Length, cm	10.6	3 - 19	2	15 **	9 **	75

\* Source of variance significant at .05 level of probability  
 \*\* Source of variance significant at 0.1 level of probability  
 /J Variance components expressed as percent of total variance.  
 2/ Analysis of variance not completed due to high number of cuttings which did not root.

(7 per cutting) which accounted for 6 percent to 11 percent of variance, but was not statistically significant for all samples. In the April collection, clonal differences in number of roots per cutting accounted for 81 percent of variance in this character.

In the November and December collections, where shoot growth averaged < 1 cm, variance in shoot length associated with provenance, clone, and primary ramets was significant (Table 2). In later collections only variance due to clones was significant.

Correlation analysis of clone means for number of roots per cutting in the several collections gave the following correlation coefficients:

	December	January	April
November	.78**	.57**	.25
December		.52**	.29
January			.25

Coefficients followed by asterisks are statistically significant at the .01 level of probability. Thus while ranking of clones was roughly similar in November, December and January trials, these rankings were not similar to those in April.

Using additional correlation analyses of clones means, it was found that time from planting to bud break was negatively correlated with number of roots in November ( $r = -.44$ ). Shoot length, which ranged from an average of 0.9 cm in the November trial to 14.5 cm in April (Table 2) was positively correlated with root number ( $r = .55$  to  $.82$ ) in all collections except December, when the average shoot growth was only 1.0 cm.

#### Test II

The larger sample of material was rooted from March to April 1987, after physiological dormancy was broken by chilling. Bud break took place within an average of 6 days after planting. Clone means varied from 2 to 11 days, a range 3 days broader than that observed in the smaller sample taken in April in Test I (Table 2). Provenance did not influence bud break time, but there was a small amount of variance associated with primary ramets.

The mean rooting percent for the test was 90, and provenance means ranged from 88 percent to 94 percent. Fifty-three of the 100 clones exhibited 100 percent rooting, and only 2 clones had less than 50 percent rooting. Number of

roots per cutting averaged 8 for the test (Table 2). The mean for Thunder Bay clones was 11 roots per cutting, which was significantly higher than that of the other three provenances (Mean = 7—8). However, clonal differences within provenances accounted for 21 percent of variance in roots per cutting, and primary ramet effects were not statistically significant. Most of the variation was among individual cuttings from single plants, i.e. error variance.

Significant variance in shoot growth was related to both clonal differences and primary ramet effects. Number of roots was positively correlated with shoot growth ( $r = .59$ ).

#### Discussion

As expected from results of previous studies (e.g. WILCOX and FARMER, 1968; SMITH and WAREING, 1972b; THIELGES and BECK, 1976; CUNNINGHAM and FARMER, 1984), root development in this study increased as physiological dormancy was released by chilling and it was positively related to shoot growth. A small amount of variance in rooting characteristics was associated with geographical source, but there were wide clonal differences within provenances. Thus our observations in both tests tend to support the hypothesis that little genetic differentiation in number of preformed root primordia has taken place among provenances, but that there is considerable genetic variation within provenances. It must be noted, however, that we did not directly observe root primordia, but rather that portion of them which developed into roots. The assumption that there is a good correlation between number of primordia and number of roots is reasonable, but not yet supported by experimental evidence.

The percentage of clonal variance for number of roots per cutting (which is equivalent to broad-sense heritability for this character) varied from 15 to 28 during winter and early spring to over 80 in the April collection where shoot growth was advanced after the four-week propagation period. These estimates of genetic variance for the November to March collections are lower than those of WILCOX and FARMER (1968) for *P. deltoides*, but higher than theirs for the April collection. An increase in heritability from fall to spring collections was also observed by THIELGES and BECK (1976) in *P. deltoides*. Additionally, in Test I there was little correlation between patterns of clonal variation in winter months and in spring, as evidenced by low correlations of clone means. Thus it appears that different factors may be influencing the degree of rooting in winter and spring. By evaluation time in May, shoots were 10 cm to 20 cm long and may have had a dominating influence on root initiation. These changes in ranking and the changing percent of clonal variance in rooting with collection time suggest that general estimates of heritability for number of roots per cutting are of limited utility. However, the wide clonal range in number of roots per cutting (e.g. 3—20 in Test II) does indicate that selection for high root number may be useful in field establishment, though we observed generally high rooting percent and survival under greenhouse conditions.

In contrast to other reports (WILCOX and FARMER, 1968; FOSTER *et al.*, 1984), environmental preconditioning of primary ramets under nursery or field conditions in this study did not significantly influence rooting. Our data thus suggest that if one is selecting for rooting potential after propagating stock plants in a uniform nursery there will probably be little error in selection due to "C" effects. The major selection problem will be the change in clone rank

with propagation time and the variance among cuttings from a single stock plant. In our tests, we observed wide variation among cuttings taken from a single 40 cm-long shoot. On the other hand, it is well documented (HARTMANN and KESTER, 1975; FEGE, 1983) that variation in the physiological quality of stock plants induced by major environmental differences will influence propagation success. It has also been noted (FARMER *et al.*, 1986) that primary ramet effects can account for variance in first year growth (including number of primary roots) of balsam poplar cuttings. However, in the study of FARMER *et al.* (1986) primary ramets (the source of cuttings) were grown in separate pots rather than a nursery, and there were other experimental conditions which differed from this test. Thus work to date on balsam poplar indicates that "C" effects may be highly variable from test to test, depending upon the nature of preconditioning, the characteristics observed and the environmental conditions under which they are observed. While this does not reduce their importance, it does make evaluation of "C" effects complex and generalization inappropriate.

#### Acknowledgement

This study was supported by an Operating Grant from the Natural Sciences and Engineering Research Council of Canada.

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## Genetic Consequences of Combining Selective Cone Harvesting and Genetic Thinning in Clonal Seed Orchards

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(Received 23rd December 1987)

#### Summary

For a clonal seed orchard with progeny-tested clones, there are two options to increase the genetic gain, selective cone harvest and genetic thinning. This paper evaluates the effect of combining these two options. Formulae are given to calculate consequences on genetic gain, effective population size (these two effects are tabulated), selfing, and flexibility. Selective harvesting and genetic thinning regimes that maximize genetic gain at a preset effective population size were calculated. An example was given to demonstrate how to choose a thinning regime, given a certain fraction of clones which must be harvested. In a situation where seed orchards produce surplus seeds, a combination of selective harvesting and genetic thinning may often be more beneficial than a more intensive ge-

netic thinning. Also, optimal clone number when all clones are harvested is calculated.

*Key words:* Genetic gain, genetic diversity, selfing, roguing, cone harvest, clonal number.

#### Zusammenfassung

Die Konsequenzen selektiver Klonbeerntung und genetischer Durchforstung in Klonsamenplantagen

In nachkommenschaftsgeprüften Samenplantagen gibt es zwei Möglichkeiten der Verbesserung: Klonweise Beerntung der besten Klone oder Entfernung der schlechtesten Klone. In diesem Beitrag wird die Möglichkeit untersucht, beide Verfahren zu kombinieren.

Formeln für Genetic Gain, effektive Populationsgröße (Tabellen), Selbstung und Flexibilität werden erläutert. Genetische Verbesserung durch verschiedene Alternativen von Klonbeerntung und Durchforstung, ausgehend von der gegebenen effektiven Klonzahl, werden berechnet. An einem Beispiel wird die Durchforstungsintensität demonstriert für den Fall, daß eine gewisse kleinste Anzahl von Klonsamen beerntet werden soll.

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