Variation in Rooting Capability of Populus deltoides1)

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Introduction

Vegetative propagation is a valuable tool which facilitates basic genetic research and practical tree improvement programs (Libby 1974 a). Since cottonwood plantations can be established by planting stem cuttings, goud rooting ability is a very important criterion in selecting clones for commercial culture (Schreiner 1970). Rooting ability is genetically controlled, responsive to selection (Wilcox and Farmer 1968), and transmitted to progeny (Heimburger 1940). Zsuffa (1976) recently reviewed the factors affecting rooting of cottonwood cuttings.

Variation in rooting ability associated with geographic origins (provenances), parent trees (family), and individual clones within families were evaluated in this experiment.

Materials and Methods

Cottonwood cuttings used in this study were part of the cooperative tree improvement project of the North Central Agricultural Experiment Stations (NC-99). Four clones each of 48 open-pollinated families from seven provenances were included in a greenhouse test, and 188 clones from 47 families were represented in a field evaluation. Experimental design was a split-split-plot with four replications of a single cutting plot with family as main plot, clone as subplot and cutting position as the sub-sub-plot.

Eight wands of similar size, 2 m. long, were harvested from each clone in the stool bed in late January. They were stored at 5^0 C. Cuttings 25 cm. long which were free from defect and disease were selected from tip, middle and base of the wands. Positions of the cutting, excep for the apical one, were relative rather than absolute, and varied somewhat from clone to clone. Diameter of each cutting was measured at mid-point. They ranged from 3–8 mm., 6–20 mm., and 9–31 mm., respectively, for apical, middle and basal cuttings.

The greenhouse test was planted soon after collection of cuttings in a conventional rooting bench with moist sand as a medium. Air temperature in the greenhouse averaged 21^0 C. Cuttings were lifted and roots counted in late February after 4 weeks in the bench. The field test was plantcd May 1 at Linculn, Nebraska in a silt loam soil. The cuttings were lifted and rooting evaluated during the first week of June. Soil was moist at planting and during the test due to ample rainfall.

Analyses of variation follow the format for split-split plot design (*Table* 1). Satterthwaite's approximate F-test was used to determine the effect of families (σ^2_f) and families within geographic origins ($\sigma^2_{f(g)}$) (Snedecor and Cochran 1967, p. 369).

Heritabilities of clonal means in both narrow sense (h^2_1) and broad sense (h^2_2) were estimated by adopting the model suggested by Burdon and Shelbourne (1974).

$$h^2_1 = \frac{\sigma^2_{f(g)} + \sigma^2_{c(f)}}{\sigma^2_{f(g)} + \sigma^2_{c(f)} + c\sigma^2_{rf}/r + \sigma^2_{rc(f)}/r + \sigma^2/_{rp}}$$

$$h^2_2 = \frac{\sigma^2_g + \sigma^2_{f(g)} + \sigma^2_{c(f)}}{\sigma^2_g + \sigma^2_{f(g)} + \sigma^2_{c(f)} + c\sigma^2_{r/fr} + \sigma^2_{rc(f)/r} + \sigma^2_{/rp}}$$

Variance components of various sources are explained in *Table* 1.

Results

Number of roots initiated varied widely amang clones. Ruot systems ranged from barely initiated to well developed. Cuttings with more roots had the best developed root systems. The correlation between number and length of roots was highly significant, r = 0.85 in the greenhouse test. The effects of geographic origin, family, clone, and position on the wand were all statistically significant (*Table* 2). Variance components of position-family and posiiton-clone interactions were relatively smaller than those of the main effects. There is appreciable genetic variation at all three levels — among clones, among family, and among regions of geographic origin (*Table* 2). Both narrow and broad-sense heritability of clonal means was high.

Table 1. — Variance anaiysis used to estimate the effect of clone, family, geographic origin and parent shoot position on the rooting of cuttings. All effects except position were considered to be random

Source of variation	Field	Greenhouse	Expected Menn Squares
Replications (R)	3	3	
Families (F)	46	47	$n^7 + p\sigma^2_{rc(f)} + pc\sigma^2_{rf} + rp\sigma^2_{c(f)} + rpc\sigma^2_f$
Geographic origins (G)	6	6	$\sigma^2 + p\sigma^2_{pc(f)} + pc\sigma^2_{rf} + rp\sigma^2_{c(f)} + rp\sigma^2_{f(g)} + k\sigma^2_g$
Families (F)/G	40	41	$\sigma^2 + p\sigma^2_{rc(f)} + pc\sigma^2_{rf} + rp\sigma^2_{c(f)} + rpc\sigma^2_{f(g)}$
R x F (error a)	138	141	$\sigma^2 + p\sigma^2_{rc(f)} + pc\sigma^2_{rf}$
Clones (C)/F	141	144	$\sigma^2 + p\sigma^2_{rc(f)} + rp\sigma^2_{c(f)}$
R x (C)/F (error b)	423	432	$\sigma^2 + p\sigma^2 rc(f)$
Positioris (P)	2	2	$\sigma^2 + r\sigma^2_{pc(f)} + rc\sigma^2_{pf} + rfc\theta^2$
P x F	92	94	$\sigma^2 + r\sigma^2_{pc(f)} + rc\sigma^2_{Pf}$
P x (C)/F	282	288	$\sigma^2 + ro^7_{pc(f)}$
Residual	1128	1152	σ^2

* r. p, f and c the number of replications, positions, families and clones within families. k = 274.3 and 267.6 for greenhouse and field tests respectively because of unequal number of families within different geographic origins.

Clones of Nebraska and Minnesota-Wisconsin origins produced significantly higher number of roots than other origins (*Table 3*) (*Figure* 1). Results of greenhouse and field

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Table 2. — Estimates of variance components* and heritabilities for rooting ability (number of roots) of cottonwood clones under both greenhouse and field conditions

Variance component and heritability	Field	Greenhouse
σ_g^2	3.73 ± 2.44	4.02 ± 2.33
$\sigma_{f(g)}^2$	4.48 ± 1.43	2.46 ± 0.82
σ_{rf}^2	0.61 ± 0.31	0.24 ± 0.13
$\sigma_{c(f)}^2$	5.51 ± 0.87	4.05 ± 0.57
$\sigma_{rc(f)}^2$	0.33 ± 0.57	0.37 ± 0.24
σ_{pf}^2	2.33 ± 0.36	2.04 ± 0.49
$\sigma_{pc(f)}^2$	1.45 ± 0.59	2.95 ± 0.42
σ^2	20.70 ± 0.87	8.20 ± 0.34
h_1^2	0.80	0.86
h_1^2	0.85	0.91

* All components are statistically significant at 0.01 percent level.

Standard error of variance component = $\sqrt{\frac{2}{\nu^2}\left(\Sigma\frac{V_i^2}{f_i+2}\right)}$

k = coefficient of the component of variance.

V_i^2 = mean square involved in the computation of the component of variance.

f_i = the degree of freedom for each mean square.

Table 3. — Comparison of average number of roots per cutting among cottonwood clones of different geographic origin

Geographic sources	Field mean	Field Range of clone means	Greenhouse mean	Greenhouse Range of clone means
Nebraska	7.4	0.2 - 20.0	8.0	1.8 - 17.8
Minnesota-Wisconsin	7.0	1.7 - 22.5	7.7	2.8 - 17.8
N. Illinois	3.8	0.6 - 10.8	4.3	1.5 - 8.7
Missouri	3.4	0.3 - 6.7	4.6	1.7 - 9.2
Indiana	3.4	1.0 - 6.7	3.5	1.4 - 7.1
Ohio-Pennsylvania	2.8	1.0 - 6.6	4.5	1.6 - 9.1
S. Ohio	1.3	0 - 6.7	2.2	0.4 - 7.8
mean	**4,7**		**5,4**	

Lines connect means that are not significantly different at the 5 percent level, on the basis of Duncan's Multiple Range Test.

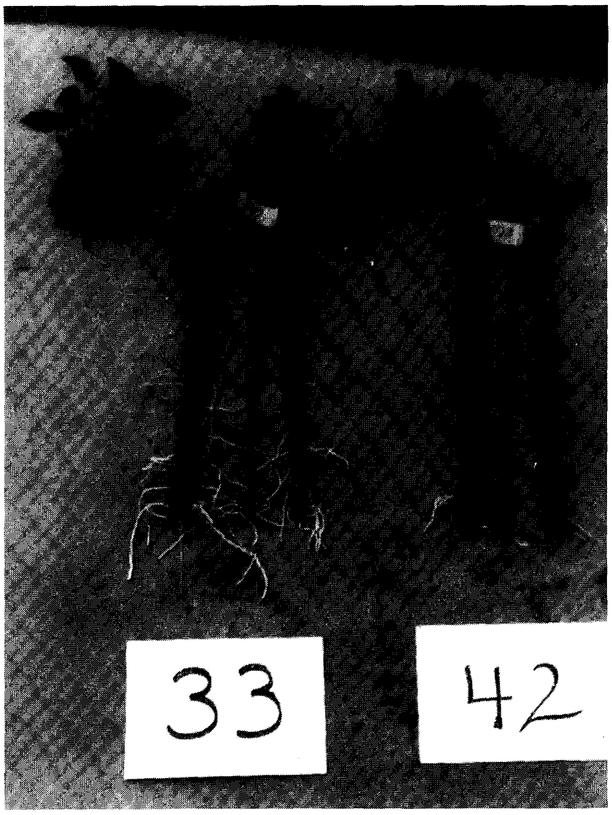

Figure 1. — Cuttings from a Nebraska origin (33) rooted more vigorously than those from Indiana (42).

tests were highly correlated (r = 0.76 based on clone means and 0.89 on family means).

Cuttings from the base of the wands produced significantly more roots than those from upper portion *(Table 4)*. No correlation between cutting diameter and number of roots within each position was found. Correlation coefficients were around 0.1 and negative in most cases. Root distribution within cuttings also differed. The cuttings from the tip of the wand developed roots almost exclusively in their lower portion while roots developed along the entire buried portion of the basal cuttings *(Figure 2)*.

Discussion and Conclusions

Variation in rooting capability of cottonwood clones has been reported previously, but it has not been associated with race or geographic origins (Wilcox and Farmer 1968; Cunningham 1953). Association with geographic oirigin suggests the adaptative value of the character (Libby 1974 b). Geographic variation seems to follow the north and west to south and east pattern which is prevalent in most characteristics investigated in cottonwood (Ying and Bagley 1976). Marcet (1961) concluded that ability to form a new root system vegetatively was more crucial to the survival of cottonwood trees growing along the lower Mississippi River than to those on the upper part of the river because of the repeated flooding which deposits sedimentary materials around the existing trees. The tree's ability to form new roots close to the surface is essential to its survival. We found that clones from Nebraska and Minnesota-Wisconsin

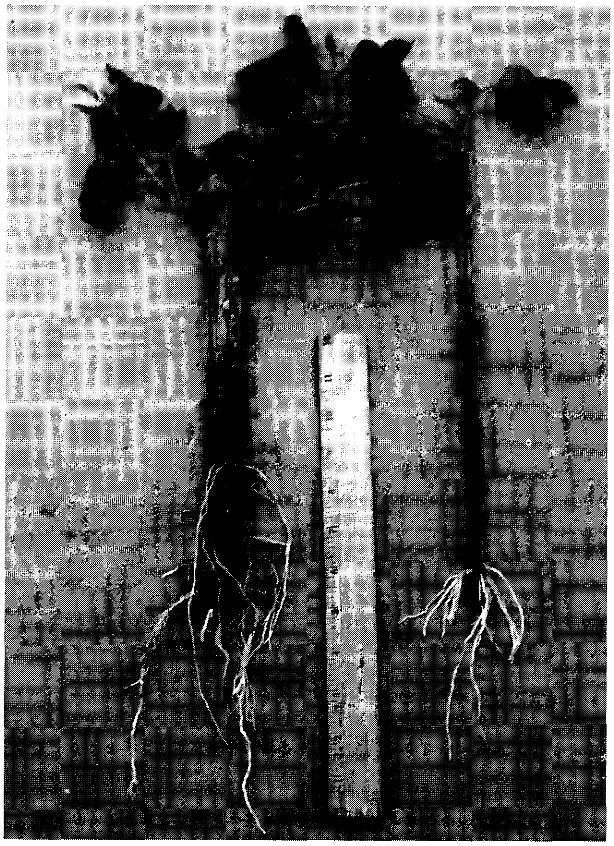

Figure 2. — A cutting from the tip of a branch (right) rooted at the base with less vigor than a cutting from the base (left) with roots initiated over most of the buried part of the cutting.

Table 4. — Comparison of average number of roos among cottonwood cuttings from the tip, middle and base of the wands without regard to geographic source

Position	Field test number	Greenhouse test number
Tip	3.1	4.3
Middle	3.5	3.6
Base	7.4	8.2

Lines connect means that are not statistically different at the 5 percent level, on the basis of Duncan's Multiple Range Test.

(upper course of the Mississippi River) had better rooting ability than those from other regions, but this does not refute the theory that ease of rooting would be an aid to survival. Zsuffa (1976) suggested that the rooting differences among clones of different geographic origins may be caused by genotype-environment interactions. This can best be verified by testing the same set of clonal materials under different environmental conditions. However, consistency in results in our experiments under greenhouse and field conditions which differed in temperature, moisture and medium indicates that rooting differences were largely genetic. Our observations agreed with Bloomberg (1959) and de Phillippis (1966) in that basal cuttings always produced more roots than apical cuttings of poplar clones.

Additive genetic variance (σ^2_A) can be estimated by either of the following formulae assuming half-sibs of open-pollinated progenies and absence of epistasis:

$$\sigma^2_A = 4\sigma^2_{f(g)}$$
$$\sigma^2_A = \sigma^2_{f(g)} + \sigma^2_{c(f)}$$

Both formulae should give equal estimates of σ^2_A if assumptions associated with the interpretation of the component of variances are valid. But average genetic correlation among open-pollinated offsprings is very likely higher than 0.25 (Namkoong 1966; Squillace 1974). In this case the second formula is preferred because of the balancing effect of the two terms. Increasing genetic correlation among family members would decrease the within-family genetic variation and increase the between-family variance proportionally and vice versa.

In view of the high estimated heritabilities, improvement of clonal rooting ability can be realized through selection either by means of sexual or asexual propagation. Broad-sense heritability (h^2_3) on an individual cutting basis was 0.54 and 0.39 for the greenhouse and field tests respectively, which is very close to those reported by Wilcox and Farmer (1968). Removal of 'position effect' ('c' effect or 'topophysis') (Burdon and Shelbourne 1974) reduced considerably the phenotypic variance and thus increased the heritability ratio of clonal means.

Genetic potential of a cottonwood clone is usually evaluated by replicated clonal tests. Differences among clones in early root development could affect establishment and mask the genetic difference of early growth if the planting was established by unrooted cuttings (Ying and Bagley 1976). This problem could be alleviated by adjusting growth rate to rooting difference or by rooting cuttings before planting in the field plots.

Summary

Cuttings from clones of Nebraska and Minnesota-Wisconsin origins produced significantly higher number of roots than those of other geographic sources in greenhouse and field tests. Heritability of clonal means was very high, over 0.8. Substantial gain can be achieved through selection. Cuttings from basal part of the parent shoot produced more roots than those from the upper part of the shoot.

Key words: Cottonwood, *Populus deltoides*, provenance test, vegetative propagation.

Zusammenfassung

In Versuchen zur Stecklingsbewurzelung von *Populus deltoides* zeigten Stecklingsklone aus Nebraska und Minnesota-Wisconsin eine stärkere Wurzelbildung als solche anderer Herkünfte. Die Unterschiede waren signifikant. Stecklinge aus der unteren Triebregion hatten mehr Wurzeln als Stecklinge aus der oberen Region der Triebe.

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Untersuchungen über die natürliche Selbstbefruchtung in Beständen der Fichte (Picea abies (L.) Karst.) und Kiefer (Pinus sylvestris L.)

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Ziel der hier beschriebenen Experimente ist die Einschätzung der in Waldbeständen nach freier Abblüte zu erwartenden Selbstbefruchtungsraten einzelner Individuen. Als Selbstbefruchtungsrate wird im folgenden derjenige relative Anteil der Nachkommen eines Individuums bezeichnet, der aus der Verschmelzung männlicher und weiblicher Gameten ein und desselben Individuums hervorgegangen ist. Als Nachkommen gelten in diesem Zusammenhang alle mit keimfähigen Embryonen ausgestatteten Samen. Die Selbstbefruchtungsrate wird stets auf die Verhältnisse während einer Blühperiode bezogen.

1. **Bedeutung**

Die Bedeutung des Phänomens Selbstbefruchtung für die theoretische und angewandte Genetik beruht auf seiner Wirkung auf die genotypische Struktur einer Population, d. h. die Häufigkeitsverteilung der Genotypen dieser Population bezüglich einzelner oder aller polymorpher Genloci. Sind alle Paarungen zu einem gegebenen Zeitpunkt uneingeschränkt möglich (Zufallspaarung), so stimmt die Wahrscheinlichkeit, mit der ein Individuum sich selbst befruchtet überein mit der Wahrscheinlichkeit, sich mit jedem der anderen Individuen der Population zu paaren und ist gleich dem Reziprokwert der Populationsgröße (vgl. Gregorius und G. Müller, 1975). Übersteigt aber die Selbstbefruchtungswahrscheinlichkeit diesen Wert, so stehen potentiell zwar alle Paarungspartner zur Verfügung, jedoch wird der Anteil der durch Fremdbefruchtung zustandegekommenen Paarungen zugunsten des Anteils der Selbstbefruchtungen reduziert. Durch diesen gegenüber der Zufallspaarung zusätzlichen Beitrag an Verwandtenpaarung (Verwandschaft eines Individuums mit sich selbst) wird zwingend Inzucht induziert, da das Entstehen von Inzucht von der Existenz verwandtschaftlicher Beziehungen zwischen den Paarungspartnern abhängig ist.

Selbstbefruchtungsraten, die den für Zufallspaarung maßgeblichen Wert überschreiten, bedingen somit einen Zuwachs der mittleren Abstammungs- und Inzuchtkoeffizienten der Individuen der Nachkommenpopulation (Definitionen siehe z. B. Crow und Kimura, 1970, Kap. 3) und bewirken konsequent eine Erhöhung des Anteils homozygoter Genotypen gegenüber den korrespondierenden Hardy-Weinberg-Proportionen. Durch die Funktionsidentität der Allele an einem Genlocus können sich auf diese Weise bei Homozygoten rezessive Allele auswirken, deren Effekt bei Heterozygoten durch dominante Allele überlagert würde. Handelt es sich dabei um Allele mit nachteiligen Wirkungen auf bestimmte Leistungsmerkmale, so bewirkt ein überproportionaler Anteil an Homozygoten eine verstärkte phänotypische Präsenz solcher Merkmale, infolgedessen das Mittel einer Pflanzenpopulation bezüglich dieser Leistungsmerkmale nachteilig beeinflußt werden kann, solange diese Genotypen in der Population verbleiben. Es sei hier nur angemerkt, daß von diesen Wirkungen das gesamte Genom betroffen ist, also z. B. auch alle Allele, die an der Ausprägung von Resistenzeigenschaften beteiligt sind. Definiert man die genische Vielfalt eines Individuums als die Gesamtzahl verschiedener Allele an allen polymorphen Genloci (Gregorius 1977), so bewirkt jede Erhöhung des Anteils homozygoter Genloci den Verlust an genischer Vielfalt dieses Individuums.

Daß Selbstbefruchtung und die daraus resultierenden Wirkungen für Fichte und Kiefer bedeutsam sind, ist nachgewiesen. So ist weder bei diesen beiden Baumarten noch sonst einer der bisher untersuchten Gymnospermenarten irgendeine Form der Selbstinkompatibilität gefunden worden (Hagman, 1975). Eine Reduzierung der Selbstbefruchtungswahrscheinlichkeit ist in geringem Umfang allenfalls durch die Anordnung der männlichen und weiblichen Blüten zu erwarten, da sich insbesondere in Fichtenkronen die weiblichen Blüten bevorzugt in den oberen bzw. äußeren Kronenpartien befinden und deshalb besonders für Fremdbefruchtung exponiert sind. Ein ähnlicher Effekt kann durch das von Sarvas (1962) an einigen Individuen beobachtete frühere Einsetzen der weiblichen Blüte hervorgerufen werden.

Die als Folge von Selbstbefruchtung bzw. Verwandtenpaarung allgemein zu erwartenden nachteiligen Wirkungen lassen sich leicht mit Hilfe von Kreuzungsexperimenten nachweisen. So zeigt Franklin (1970 und 74 a) am Beispiel verschiedener Kiefernarten, daß sich die Vollkornerträge nach künstlicher Selbstbestäubung im Vergleich zur Fremdbestäubung um durchschnittlich über 50% verringern, daß lebensfähige Nachkommen aus Selbstbefruchtung signifikant geringere Wuchsleistungen zeigen (siehe auch Kriebel 1975) und zu diversen Abnormalitäten neigen können. Anhand der Analyse des Wuchsverhaltens von Nachkommen aus Verwandtenkreuzungen weisen z. B.

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