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Date of Shoot Collection, Genotype, and Original Shoot Position Affect Early Rooting of Dormant Hardwood Cuttings of *Populus*

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Abstract

Identifying superior combinations among date of dormant-season shoot collection, genotype, and original shoot position can increase the rooting potential of *Populus* cuttings. Thus, the objectives of our study were to: 1) evaluate variation among clones in early rooting from hardwood cuttings processed every three weeks from shoots collected throughout the dormant season and 2) evaluate variation among genomic groups in early rooting of the same cuttings while testing for differences among three parental shoot positions (apical, middle, basal). We tested 22 clones belonging to six genomic groups (*[P. trichocarpa* Torr. & Gray × *P. deltoides* Bartr. ex Marsh] × *P. deltoides* ‘BC’, *P. deltoides* ‘D’, *P. deltoides* × *P. maximowiczii* A. Henry ‘DM’, *P. deltoides* × *P. nigra* L. ‘DN’, *P. nigra* × *P. maximowiczii* ‘NM’, *P. trichocarpa* ‘T’). Cuttings, 20 cm long, were processed from shoots collected every three weeks beginning 1 Dec. 2003 until 9 Apr. 2004 from stool beds established at Hugo Sauer Nursery in Rhineland, Wisconsin, USA (45.6°N, 89.4°W). We measured number of roots and root dry weight from harvested cuttings after 14 days of growth. The interaction between date of shoot collection and clone governed both traits ($P < 0.0001$). In general, clones exhibited the best rooting when cuttings were processed from shoots collected on or after 23 Feb. 2004.

The interaction between date of shoot collection, genomic group, and shoot position governed number of roots ($P = 0.0348$) and root dry weight ($P = 0.0262$). There was broad variation in number of roots and root dry weight of apical, middle, and basal cuttings within and among genomic groups across dates of shoot collection, with 15 Mar. 2004 being an important date because differences among positions began to develop or changed relative to earlier dates. Thus, for increased plantation establishment potential with similar genotypes, we recommend collecting stool shoots no sooner than the end of February and matching cuttings of specific shoot positions to each genomic group.

Key words: *Populus* genomic groups, hybrid poplar, adventitious rooting, genotype × environment interaction, whip, stool bed.

Introduction

Evaluation of genetic variation among and within populations of genotypes belonging to the genus *Populus* has been conducted for over half a century in North America (PALLARDY and KOZLOWSKI, 1979; FARMER, 1970; ALLEN and MCCOMB, 1956). The potential of selecting promising genotypes for numerous end-uses (including bioenergy, fiber, phytoremediation, and agroforestry) has prompted breeding of intra- and inter-species hybrids, along with gathering of open-pollinated collec-

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Table 1. – Studies testing the effects of external factors on adventitious rooting of *Populus*.**Cutting size**

DESROCHERS and THOMAS, 2003; ROBISON and RAFFA, 1996; KRINARD, 1983; HANSEN and TOLSTED, 1981; DICKMANN et al., 1980; BOWERSOX, 1970; FARMER and WILCOX, 1968; ALLEN and MCCOMB, 1956

Planting date and methodology

ZALESNY et al., 2004; HANSEN, 1986; KRINARD, 1983; GILMORE, 1976

Environmental preconditioning

FARMER et al., 1989; 1988; 1986; WILCOX and FARMER, 1968

Storage and/or soaking

VOLK et al., 2004 (*Salix*); DESROCHERS and THOMAS, 2003; PURI and THOMPSON, 2003; HANSEN, 1986; HANSEN and PHIPPS, 1983; PHIPPS et al., 1983; CRAM and LINDQUIST, 1982; PHIPPS and NETZER, 1981; KRINARD and RANDALL, 1979; PETERSEN and PHIPPS, 1976

Chemical stimulation

DESROCHERS and THOMAS, 2003; SHIPMAN, 1974; NANDA and ANAND, 1970; FARMER, 1966; ALLEN and MCCOMB, 1956

Soil temperature

ZALESNY et al., 2005a; 2004; LANDHÄUSSER, 2003; LANDHÄUSSER et al., 2001

Date of shoot collection

HOULE and BABEUX, 1993; FARMER et al., 1989; CUNNINGHAM and FARMER, 1984; FEGE and BROWN, 1984; PHIPPS and NETZER, 1981; HANSEN et al., 1979; NANDA and ANAND, 1970; FARMER, 1966; BLOOMBERG, 1963; ALLEN and MCCOMB, 1956

Position along parent shoot

ZALESNY et al., 2003; SCHROEDER and WALKER, 1991; FEGE and BROWN, 1984; ERNST and FECHNER, 1981; HANSEN and TOLSTED, 1981; YING and BAGLEY, 1977; SMITH and WAREING, 1972; BLOOMBERG, 1963; 1959

tions (RIEMENSCHNEIDER et al., 2001; SCARASCIA-MUGNOZZA et al., 1997; WILCOX and FARMER, 1967). Four *Populus* species commonly used in North American breeding programs are eastern cottonwood (*P. deltoides* Bartr. ex Marsh), western black cottonwood (*P. trichocarpa* Torr. & Gray), European black poplar (*P. nigra* L.), and Japanese poplar (*P. maximowiczii* A. Henry). The result of such breeding and selection has led to the capture of a broad range of genetic material that exhibits exceptional promise for use as short rotation intensive forest crops (MCCAMANT and BLACK, 2000; ORLOVIC et al., 1998; YING and BAGLEY, 1976; MOHN and RANDALL, 1971). Adventitious rooting from dormant hardwood cuttings is an important trait for such systems.

In addition to the genetics involved, understanding genotype x environment interactions and the effects of pre-planting treatments on adventitious rooting are worthwhile given that poplars often are planted as

unrooted hardwood cuttings (RIEMENSCHNEIDER and BAUER, 1997; FEGE, 1983; ALLEN and MCCOMB, 1956). Adventitious rooting is biologically and economically important because it is the first biological requirement for plantation establishment (ZALESNY et al., 2005a; 2005b; 2004; TSCHAPLINSKI and BLAKE, 1989), and as such rooting warrants much research attention (HAISSIG et al., 1992; DAVIES and HARTMANN, 1988).

There have been recent reports about genotype x environment interactions as they related to rooting from dormant hardwood cuttings (ZALESNY et al., 2005a; 2005b; 2004). In addition, FEGE (1983) and HOWARD (1994) provided a detailed description of numerous economically-important pre-planting treatments. However, given budget and personnel shortfalls, along with accelerated focus on aboveground traits, interest in testing the effects of pre-planting treatments on rooting has waned in recent years. Nevertheless, there are reports

about the effects of numerous external factors on adventitious rooting from cuttings within the genus *Populus*, including but not limited to: cutting size, planting date and methodology, environmental preconditioning, storage and/or soaking, chemical stimulation, soil temperature, date of shoot collection, and shoot position along the parent shoot (*Table 1*).

Date of shoot collection and shoot position warrant further testing because of their influence/impact on rooting potential that ultimately contributes to the success of plantation establishment and subsequent development. Recent studies testing the effects of seasonal variation in root and shoot growth based on when cuttings were collected and of variation in root and shoot growth based on the location cuttings were taken from the original parent shoot are non-existent for poplars. Therefore, we seek knowledge combining collection date and position effects on adventitious rooting to understand the potential for establishment of current genotypes and associated genomic groups of poplar in the North Central United States. The broad variation in nursery practices for collection and storage of dormant hardwood cuttings of *Populus* highlights the practical need for such information in order to move closer to the development of a standardized testing and deployment protocol that can be applied to all genotypes, regardless of geographic location.

Our initial hypotheses for the current study were three-fold. First, an identical poplar genotype will exhibit different phenotypic responses when dormant hardwood cuttings are made from shoots collected throughout the dormant season (i.e. date of shoot collection x genotype interactions will exist). Second, phenotypic responses will differ among clones. Third, when clones are pooled into genomic groups based on their parentage

(ZALESNY et al., 2003), genomic groups will exhibit different phenotypic responses based on whether dormant hardwood cuttings are made from the apical, middle, and basal third of the parental stool shoots collected throughout the dormant season (i.e. date of shoot collection x genomic group x shoot position interactions will exist). Thus, the objectives of our study were to: 1) evaluate variation among hybrid poplar clones in early rooting of dormant hardwood cuttings that were processed every three weeks from shoots collected throughout the dormant season and 2) evaluate variation among genomic groups in early rooting of the same cuttings while testing for differences among the three aforementioned parental shoot positions.

Materials and Methods

Clone selection and cutting preparation

Twenty-two clones (*Table 2*) were sampled from six *Populus* genomic groups in November 2003 based on their growth potential and anticipated range of rooting abilities. Shoots were collected from stool beds established at Hugo Sauer Nursery in Rhinelander, Wisconsin, USA (45.6°N, 89.4°W) on 1 Dec. 2003, 22 Dec. 2003, 12 Jan. 2004, 2 Feb. 2004, 23 Feb. 2004, 15 Mar. 2004, and 9 Apr. 2004. Hardwood cuttings, 20 cm long, were prepared immediately following shoot collection on each of the aforementioned collection dates, with cuts made to position at least one primary bud not more than 2.54 cm from the top of each cutting. During processing, cuttings were separated according to one of three stem positions of the cutting on the stool plant (ZALESNY et al., 2003). Cuttings made from the upper third, middle third, and lower third of the parental stool plant are hereafter referred to as apical, middle, and basal posi-

Table 2. – Genomic groups, clones, and their origin in an experiment testing for differences in rooting ability among dormant hardwood *Populus* cuttings, based on the date of collection of the terminal shoots from stool beds and the cuttings' positions on the shoot system of the parental stool plant.

Genomic group	Origin	Clone
<i>P. trichocarpa</i> (T)	D. Riemenschneider, U.S. Forest Service	062, 065, 072, 322
(<i>P. trichocarpa</i> × <i>P. deltoides</i>) × <i>P. deltoides</i> (BC)	D. Riemenschneider, U.S. Forest Service	NC13568, NC13649, NC13670, NC13747
<i>P. deltoides</i> × <i>P. maximowiczii</i> (DM)	C. Mohn, Univ. of Minnesota and D. Riemenschneider, U.S. Forest Service	NC14103, NC14106, DM113, DM115
<i>P. deltoides</i> (D)	C. Mohn, Univ. of Minnesota	D105, D110, D124, D134
<i>P. deltoides</i> × <i>P. nigra</i> (DN ^a)	France, Europe, Europe, Netherlands (respectively)	DN17 'Robusta', DN182 'Raverdeau', DN34 'Eugenei', DN5 'Gelrica'
<i>P. nigra</i> × <i>P. maximowiczii</i> (NM)	Germany	NM2, NM6

^a Euramerican hybrids with the common designations of *P. x euramericana* Guin. and *P. x canadensis* Moench.

Note: Authorities for the species are: *P. deltoides* Bartr. ex Marsh; *P. trichocarpa* Torr. & Gray; *P. maximowiczii* A. Henry; *P. nigra* L.

Table 3. – Degrees of freedom, expected mean squares, and probability values from analysis of variance in an experiment testing for clonal differences in number of roots and root dry weight among dormant hardwood *Populus* cuttings, based on the date of collection of the terminal shoots from stool beds.

Source	df	Expected mean squares	P value	
			Number of roots	Root dry weight
Block	8	$\sigma^2 + 154\sigma_B^2$		
Collection Date	6	$\sigma^2 + 22\sigma_{BD}^2 + 198\Phi_D$	< 0.0001	< 0.0001
Block × Collection Date	48	$\sigma^2 + 22\sigma_{BD}^2$		
Clone	21	$\sigma^2 + 7\sigma_{BC}^2 + 63\Phi_C$	< 0.0001	< 0.0001
Block × Clone	168	$\sigma^2 + 7\sigma_{BC}^2$		
Collection Date × Clone	126	$\sigma_{BDC}^2 + 9\Phi_{DC}$	< 0.0001	< 0.0001
Block × Collection Date × Clone	1008	σ_{BDC}^2		
Total	1385			

tions, respectively. Cuttings were sealed in polyethylene bags and stored at 5 °C until each planting date. Cuttings were soaked in water to a height of 15 cm for 3 d before planting in book planters containing rooting medium consisting of equal parts of sand, peat, and vermiculite (v:v:v). Planting took place in a greenhouse at the Forestry Sciences Laboratory in Rhineland on 8 Dec. 2003, 29 Dec. 2003, 19 Jan. 2004, 9 Feb. 2004, 1 Mar. 2004, 26 Mar. 2004, and 16 Apr. 2004. The cuttings were grown in the greenhouse with a 16-h photoperiod and a constant temperature of 21 °C.

Data collection and analysis

Number of roots and root dry weight were determined at 14 d after planting. Individual trees were harvested on 22 Dec. 2003, 12 Jan. 2004, 2 Feb. 2004, 23 Feb. 2004, 15 Mar. 2004, 9 Apr. 2004, and 30 Apr. 2004. Trees were excavated and washed prior to dissection of stems, leaves, and roots. Following dissection, number of roots was recorded, and individual plant components were bagged and dried at 70 °C for 72 h for dry weight determination. A rooted cutting was defined as any cutting that exhibited a root > 1 mm in length, that is, any root clearly distinguishable from a nodule (ZALESNY et al., 2005b). Two separate analyses conducted to test the aforementioned hypotheses are described below.

Objective 1: Date of shoot collection and clone effects

Number of roots and root dry weight data were subjected to analyses of variance according to SAS® (PROC GLM; SAS Institute, Inc., 2004) assuming a split-plot design arranged in randomized complete blocks, with

nine blocks (i.e. replications), seven dates of shoot collection and 22 clones (n = 1386) (Table 3). Blocks were considered random in the analysis, while dates were fixed whole plots and clones were fixed sub plots. Clones were arranged in randomized complete blocks in order to minimize effects of any potential environmental gradients in the greenhouse, and clones were treated as fixed in the analysis in order to analyze means rather than variances. The significance of interaction terms between blocks and fixed main effects from the original all-effects model were tested to evaluate potential pooling with the residual error term to increase precision of F-tests. However, such interactions were significant ($\alpha < 0.25$) and, therefore, no pooling was conducted. The following linear additive model was used in the analysis:

$$Y_{ijk} = \mu + B_i + D_j + BD_{ij} + C_k + BC_{ik} + DC_{jk} + BDC_{ijk}$$

where: Y_{ijk} = response variable to be analyzed, μ = overall mean, B_i = main effect of i^{th} block, D_j = main effect of j^{th} date of shoot collection, BD_{ij} = effect of interaction between i^{th} block and j^{th} date of shoot collection, C_k = main effect of k^{th} clone, BC_{ik} = effect of interaction between i^{th} block and k^{th} clone, DC_{jk} = effect of interaction between j^{th} date of shoot collection and k^{th} clone, BDC_{ijk} = effect of interaction among i^{th} block, j^{th} date of shoot collection, and k^{th} clone.

Analyses of covariance were conducted to test for the effect of cutting size on both traits because of a broad variation in cutting dry weight at 14 d after planting (0.49 to 13.94 g). Cutting dry weight was a significant covariate for root dry weight ($P < 0.0001$); however, cut-

Table 4. – Degrees of freedom, expected mean squares, and probability values from analysis of variance in an experiment testing for clonal differences in number of roots and root dry weight among dormant hardwood *Populus* cuttings, based on the date of collection of the terminal shoots from stool beds and the cuttings' positions on the shoot system of the parental stool plant.

Source	df	Expected mean squares	P value	
			Number of roots	Root dry weight
Block	2	$\sigma^2 + 126\sigma_B^2$		
Collection Date	6	$\sigma^2 + 18\sigma_{BD}^2 + 54\Phi_D$	< 0.0001	< 0.0001
Block × Collection Date	12	$\sigma^2 + 18\sigma_{BD}^2$ (Error _A)		
Genomic Group	5	$\sigma^2 + 63\Phi_G$	< 0.0001	< 0.0001
Collection Date × Genomic Group	30	$\sigma^2 + 9\Phi_{DG}$	< 0.0001	< 0.0001
Pooled Error	70	σ^2 (Error _B)		
Stem Position	2	$\sigma^2 + 126\Phi_P$	0.1379	< 0.0001
Collection Date × Stem Position	12	$\sigma^2 + 18\Phi_{DP}$	< 0.0001	0.1732
Genomic Group × Stem Position	10	$\sigma^2 + 21\Phi_{GP}$	< 0.0001	0.0260
Collection Date × Genomic Group × Stem Position	60	$\sigma^2 + 3\Phi_{DGP}$	0.0348	0.0262
Pooled Error	1176	σ^2 (Error _C)		
Total	1385			

ting dry weight did not have a significant effect on number of roots ($P = 0.2422$). Therefore, only means for root dry weight were adjusted for the variation in cutting dry weight. Fisher's protected least significant difference (LSD) was used to compare adjusted and unadjusted means (CARMER and WALKER, 1985; 1982; CHEW, 1976).

Objective 2: Date of shoot collection, genomic group, and shoot position effects

Clones were pooled by genomic group for analysis (ZALESNY et al., 2003). Number of roots and root dry weight data were subjected to analyses of variance according to SAS® (PROC GLM; SAS Institute, Inc., 2004) assuming a split-split-plot design arranged in randomized complete blocks, with three blocks (i.e. replications), seven dates of shoot collection, six genomic groups, and three shoot positions (Table 4). There were 1386 experimental units, with four ramets for each combination of the aforementioned factors, except for the NM (*P. nigra* × *P. maximowiczii*) genotypes, which had two ramets per combination. Blocks were considered random in the analysis, while dates were fixed whole plots, genomic groups were fixed sub plots, and positions were fixed sub-sub plots. Nonsignificant ($\alpha > 0.25$) inter-

action terms from the original all-effects model were pooled with the residual error term to increase precision of F-tests. The following linear additive model was used in the analysis:

$$Y_{ijkl} = \mu + B_i + D_j + BD_{ij} + G_k + DG_{jk} + \text{Error}_B + P_l + DP_{jl} + GP_{kl} + DGP_{jkl} + \text{Error}_C$$

where: Y_{ijkl} = response variable to be analyzed, μ = overall mean, B_i = main effect of i^{th} block, D_j = main effect of j^{th} date of shoot collection, BD_{ij} = effect of interaction between i^{th} block and j^{th} date of shoot collection, G_k = main effect of k^{th} genomic group, DG_{jk} = effect of interaction between j^{th} date of shoot collection and k^{th} genomic group, Error_B = error resulting from pooling of BG_{ik} and BDG_{ijk} terms, P_l = main effect of l^{th} shoot position, DP_{jl} = effect of interaction between j^{th} date of shoot collection and l^{th} shoot position, GP_{kl} = effect of interaction between k^{th} genomic group and l^{th} shoot position, DGP_{jkl} = effect of interaction among j^{th} date of shoot collection, k^{th} genomic group, and l^{th} shoot position, and Error_C = error resulting from pooling of BP_{il} , BDP_{ijl} , BGP_{ikl} , and $BDGP_{ijkl}$ terms.

Analyses of covariance were conducted to test for the effect of cutting size on both traits because of the above-

mentioned variation in cutting dry weight at 14 d after planting. Cutting dry weight was a significant covariate for number of roots ($P = 0.0274$) and root dry weight ($P < 0.0001$). Therefore, all means were adjusted for the variation in cutting dry weight. Fisher's protected LSD was used to compare adjusted means (CARMER and WALKER, 1985; 1982; CHEW, 1976).

Results

Objective 1: Date of shoot collection and clone effects

There was broad genotypic variation for number of roots and root dry weight, based on the date of shoot collection. While the date and clone main effects were significant for both traits ($P < 0.0001$), their interaction governed number of roots and root dry weight

Table 5. – Number of roots for each combination of clone and date of shoot collection of 22 *Populus* clones belonging to six genomic groups when planted as dormant hardwood cuttings. Standard errors are listed in parentheses. Values for clones with the same letter in each row are not different according to Fisher's protected LSD ($\alpha = 0.05$; $n = 9$; $LSD = 3.6$).

Clone	Date of shoot collection						
	1 Dec. 2003	22 Dec. 2003	12 Jan. 2004	2 Feb. 2004	23 Feb. 2004	15 Mar. 2004	9 Apr. 2004
062	5.4 (0.7) c	8.9 (1.1) bc	8.4 (1.4) bc	9.7 (0.9) b	10.0 (1.5) b	13.6 (2.2) a	8.2 (1.1) bc
065	6.0 (0.3) x	8.4 (0.7) xy	10.8 (0.8) yz	9.0 (0.7) xy	9.9 (0.9) yz	10.1 (1.1) yz	13.1 (1.4) z
072	10.1 (1.0) bc	9.6 (0.7) bc	7.7 (0.9) c	10.4 (1.0) abc	12.0 (1.1) ab	13.8 (0.8) a	12.8 (0.9) ab
322	7.2 (0.8) yz	5.8 (0.8) y	8.7 (1.4) yz	7.8 (1.5) yz	8.2 (1.2) yz	10.2 (1.7) z	9.6 (1.5) z
NC13568	5.2 (0.8) d	8.4 (1.2) d	18.0 (3.2) bc	16.2 (1.6) c	19.7 (1.8) bc	24.4 (1.2) a	20.9 (1.3) ab
NC13649	3.2 (0.5) x	4.3 (0.6) x	3.0 (0.7) x	8.9 (0.9) y	15.1 (1.7) z	16.3 (2.2) z	13.2 (2.4) z
NC13670	4.4 (0.8) c	5.4 (1.2) c	7.0 (1.4) bc	9.2 (1.8) b	20.0 (1.7) a	23.3 (1.3) a	21.7 (2.4) a
NC13747	2.7 (0.3) x	3.6 (0.9) xy	5.1 (0.8) xy	6.8 (1.5) y	10.4 (1.1) z	12.0 (1.5) z	12.2 (0.8) z
NC14103	6.4 (1.2) c	8.8 (1.0) c	12.9 (0.8) b	12.4 (0.9) b	13.3 (0.9) b	17.4 (1.9) a	12.8 (0.7) b
NC14106	9.1 (1.2) v	8.9 (0.5) v	11.4 (1.2) vw	12.9 (1.0) wx	15.8 (0.6) xy	19.8 (2.5) z	18.3 (1.3) yz
DM113	7.8 (0.9) d	7.2 (1.3) d	12.1 (1.1) c	13.8 (1.5) c	18.2 (2.5) b	27.8 (5.4) a	21.6 (3.9) b
DM115	9.1 (0.9) x	9.7 (0.6) x	14.8 (1.2) y	14.6 (0.6) y	15.3 (1.2) y	25.4 (2.3) z	16.3 (1.5) y
D105	3.2 (0.5) c	5.0 (0.8) c	5.3 (0.8) c	5.3 (0.9) c	11.8 (1.3) b	13.0 (1.4) ab	15.8 (1.0) a
D110	5.8 (0.9) w	9.9 (0.6) x	11.1 (0.9) x	12.1 (0.6) xy	16.0 (0.7) z	17.1 (1.1) z	14.8 (1.4) yz
D124	4.4 (0.8) c	5.4 (1.0) c	7.4 (1.3) bc	9.8 (0.9) ab	12.8 (1.1) a	10.0 (2.0) ab	10.3 (1.4) ab
D134	2.0 (0.5) w	3.8 (0.6) wx	4.1 (0.9) wx	7.3 (1.6) xy	9.7 (1.4) yz	9.1 (1.8) z	10.9 (0.7) z
DN17	6.1 (1.0) c	6.7 (0.6) c	9.0 (1.4) bc	12.3 (1.4) ab	13.9 (1.0) a	14.6 (1.3) a	14.3 (0.9) a
DN182	3.0 (0.6) x	4.0 (0.7) x	7.9 (0.8) y	11.2 (1.0) yz	13.0 (0.8) z	11.1 (0.9) yz	11.9 (1.1) z
DN34	4.7 (0.5) c	6.2 (0.3) bc	9.7 (1.1) ab	11.2 (0.8) a	11.8 (1.0) a	11.1 (0.6) a	12.9 (0.5) a
DN5	4.1 (0.6) x	5.6 (0.8) x	6.7 (1.7) x	6.9 (1.0) x	17.4 (1.5) yz	20.9 (1.3) z	14.3 (1.6) y
NM2	11.1 (1.0) b	11.0 (0.7) b	13.1 (0.9) ab	11.9 (0.7) ab	13.1 (1.5) ab	14.7 (1.3) a	9.9 (0.7) b
NM6	11.2 (0.8) z	11.7 (0.8) z	11.4 (0.7) z	12.1 (0.7) z	13.3 (1.0) z	12.8 (1.0) z	12.9 (1.0) z
Overall	6.0 (0.3) d	7.2 (0.2) cd	9.3 (0.4) cd	10.5 (0.3) bc	13.7 (0.3) ab	15.8 (0.5) a	14.0 (0.4) ab

($P < 0.0001$) (Table 3). There was a general trend across clones of greater number of roots when shoots were collected on 23 Feb. 2004 and later (Table 5). However, with the exception of clones in the T (*P. trichocarpa*) genomic group that did not display a discernible pattern

for number of roots across collection dates, clones within specific genomic groups exhibited unique trends. Root initiation for clones of the BC [*P. trichocarpa* × *P. deltoides*] × *P. deltoides* and D (*P. deltoides*) genomic groups followed the general trend of the greatest num-

Table 6. – Root dry weight (mg) adjusted for cutting dry weight for each combination of clone and date of shoot collection of 22 *Populus* clones belonging to six genomic groups when planted as dormant hardwood cuttings. Standard errors are 4.9 and 1.1 for adjusted and overall means, respectively. Values for clones with the same letter in each row are not different according to Fisher's protected LSD ($\alpha = 0.05$; $n = 9$; LSD = 13.8).

Clone	Date of shoot collection						
	1 Dec. 2003	22 Dec. 2003	12 Jan. 2004	2 Feb. 2004	23 Feb. 2004	15 Mar. 2004	9 Apr. 2004
062	2.3 b	6.3 b	11.8 b	4.7 b	7.6 b	35.1 a	14.9 b
065	2.5 w	5.0 wx	16.7 xy	7.5 wx	13.8 wxy	22.8 yz	32.7 z
072	13.2 a	13.1 a	8.1 a	9.1 a	15.7 a	17.5 a	18.6 a
322	1.8 y	3.0 y	6.8 y	2.7 y	8.2 yz	12.6 yz	21.2 z
NC13568	4.8 e	16.5 de	32.2 bc	19.4 cd	25.8 bcd	37.5 ab	48.9 a
NC13649	2.2 y	4.4 y	7.1 y	6.0 y	22.6 z	21.6 z	23.0 z
NC13670	5.4 c	9.4 c	5.0 c	7.2 c	35.3 b	60.7 a	63.3 a
NC13747	0.7 y	1.7 y	1.6 y	1.4 y	10.6 yz	23.2 z	22.8 z
NC14103	17.3 d	23.1 cd	44.3 b	33.4 bc	41.0 b	69.1 a	65.8 a
NC14106	4.1 x	12.9 x	10.7 x	8.2 x	31.8 y	28.9 y	48.0 z
DM113	10.2 c	5.6 c	19.0 c	12.9 c	45.6 b	45.3 b	75.4 a
DM115	14.6 v	31.8 w	41.9 wx	36.8 wx	48.4 x	78.8 y	92.9 z
D105	3.3 b	3.0 b	5.2 b	1.9 b	23.2 a	26.3 a	34.8 a
D110	4.4 x	8.2 x	7.8 x	7.8 x	27.4 y	33.1 yz	43.0 z
D124	4.5 c	6.9 c	10.1 abc	8.9 bc	21.7 ab	15.0 abc	23.7 a
D134	2.9 z	4.4 z	5.0 z	6.7 z	13.8 z	12.8 z	16.3 z
DN17	4.6 c	4.4 c	20.0 b	18.1 bc	43.7 a	47.6 a	35.5 a
DN182	2.7 x	3.9 x	14.4 xy	18.3 y	24.6 y	27.7 yz	38.5 z
DN34	6.3 b	5.7 b	7.6 b	9.4 b	32.8 a	31.6 a	37.7 a
DN5	3.5 y	6.8 y	6.1 y	5.3 y	34.7 z	40.8 z	29.5 z
NM2	7.8 c	10.4 bc	17.9 abc	15.5 abc	16.3 abc	23.1 ab	28.8 a
NM6	14.0 x	20.3 xy	22.6 xy	10.1 x	21.9 xy	28.7 y	82.9 z
Overall	6.0 d	9.4 d	14.6 cd	11.4 d	25.7 bc	33.6 ab	40.8 a

ber of roots with shoots collected on and following 23 Feb. 2004. In contrast, clones of the DM (*P. deltooides* × *P. maximowiczii*) genomic group exhibited the greatest number of roots when shoots were collected on 15 Mar. 2004. With the exception of clone DN5 that followed the general trend, clones of the DN (*P. deltooides* × *P. nigra*) genomic group exhibited the greatest number of roots when shoots were collected on 2 Feb. 2004 and later. Clones of the NM (*P. nigra* × *P. maximowiczii*) genomic group performed similarly for number of roots regardless of collection date.

In general, root dry weight was greatest when shoots were collected on 15 Mar. 2004 and later (Table 6). The T clones did not exhibit a clear trend for root dry weight across collection dates. In contrast, root dry weight for BC clones followed the general trend of the greatest root dry weight with shoots collected on and following 15 Mar. 2004. Clone NC14103 also had the greatest root dry weight from shoots collected on 15 Mar. 2004 and later, while the other clones of the DM genomic group exhibited the greatest root dry weight when shoots were collected on 9 Apr. 2004. This trend was similar for NM clones, although differences in root dry weight were negligible for shoots collected on 12 Jan. 2004 and later for clone NM2. The greatest root dry weight for cuttings belonging to the D and DN genomic groups was for shoots collected on 23 Feb. 2004 and later, with the exception of clone D134 that exhibited similar root dry weight regardless of collection date.

Objective 2: Date of shoot collection, genomic group, and shoot position effects

Genomic groups performed differently for number of roots and root dry weight, based on shoot position effects. There was an interaction between genomic group and shoot position for number of roots ($P < 0.0001$) and root dry weight ($P = 0.0260$) (Table 4). Differences for number of roots existed for apical, middle, and basal cuttings of the BC, D, and DM genomic groups (Fig. 1). Basal cuttings of the BC genomic group exhibited the greatest number of roots and middle cuttings exhibited the fewest number of roots, while the apical cuttings were not different from either of the other positions. For the D genomic group, basal cuttings were superior to apical and middle cuttings. Cuttings of the DM genomic group exhibited the greatest variation among shoot positions, in addition to having a trend opposite that of the BC and D genomic groups. Specifically, apical cuttings exhibited the greatest number of roots, while middle and basal cuttings were second best and fewest, respectively. Moreover, differences for root dry weight existed for the DM, NM, and T genomic groups (Fig. 1). Cuttings of the DM and NM genomic groups performed similarly, with comparable root dry weight for apical and middle cuttings being superior to that of basal cuttings. For the T genomic group, apical cuttings exhibited the greatest root dry weight that was different from similar root dry weight for middle and basal cuttings.

In addition, genomic groups performed differently for number of roots and root dry weight, based on date of shoot collection and shoot position effects. There was an interaction between date of shoot collection, genomic

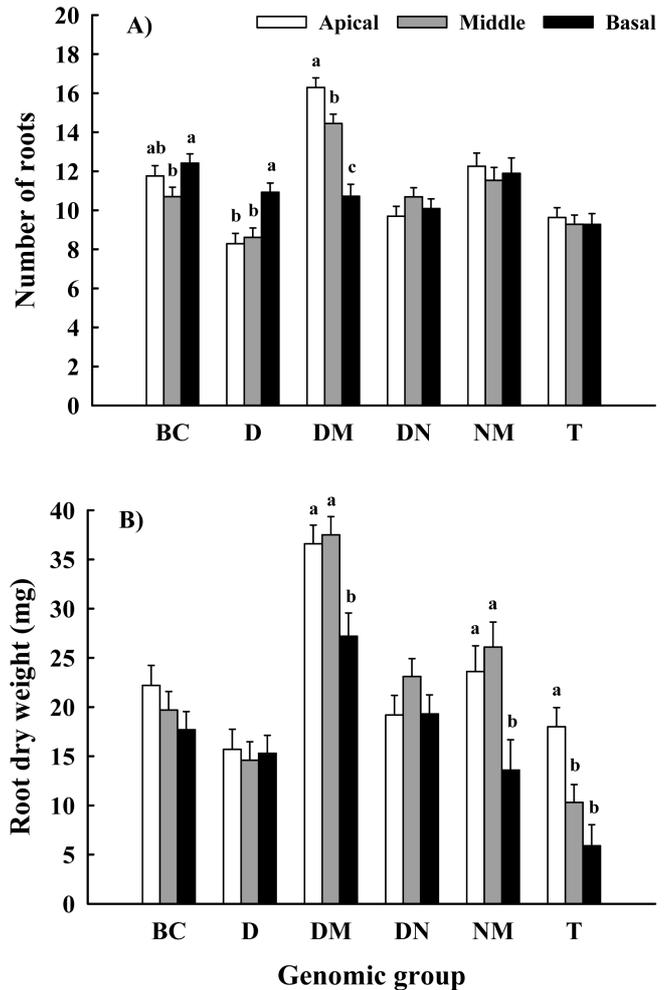


Figure 1. – Number of roots (A) and root dry weight (B) of *Populus* cuttings belonging to six genomic groups, based on the cuttings' positions on the shoot of the parental stool plant. Each bar represents the mean adjusted for cutting dry weight with one standard error, across collection dates. Positions with different letters above bars within each genomic group are different according to Fisher's protected LSD [$\alpha = 0.05$, LSD: number of roots – BC, D, DM, DN, and T = 1.3 ($n = 84$), NM = 1.8 ($n = 42$); root dry weight – BC, D, DM, DN, and T = 5.1, NM = 7.3], where non-labeled comparisons are negligible.

group, and shoot position for number of roots ($P = 0.0348$) and root dry weight ($P = 0.0262$) (Table 4). There was broad genotypic variation in number of roots, with 15 Mar. 2004 being an important collection date because differences among positions began to develop or changed relative to earlier dates (Fig. 2). For shoots of the BC genomic group collected on 12 Jan. and 2 Feb. 2004, basal cuttings exhibited superior number of roots to apical and middle cuttings, which were similar to one another. A reversal of this basal superiority occurred in cuttings from shoots collected on 15 Mar. and 9 Apr. 2004. Specifically, apical cuttings exhibited the greatest number of roots and basal cuttings exhibited the fewest number of roots, while the middle cuttings were not different from either of the other positions. For the D genomic group, basal cuttings processed from shoots collected on 15 Mar. 2004 exhibited the greatest number of roots and apical cuttings exhibited the fewest number of

roots, while the middle cuttings were not different from either of the other positions. Differences among shoot positions for the DM genomic group existed for shoots collected on 2 Feb. 2004, whereby apical and middle cuttings exhibited similar and greater number of roots than basal cuttings. The apical superiority increased with

later collection dates. Apical cuttings processed from shoots collected on 23 Feb. 2004 exhibited the greatest number of roots and basal cuttings exhibited the fewest number of roots, while the middle cuttings were not different from either of the other positions. In contrast, differences in order from greatest to fewest number of

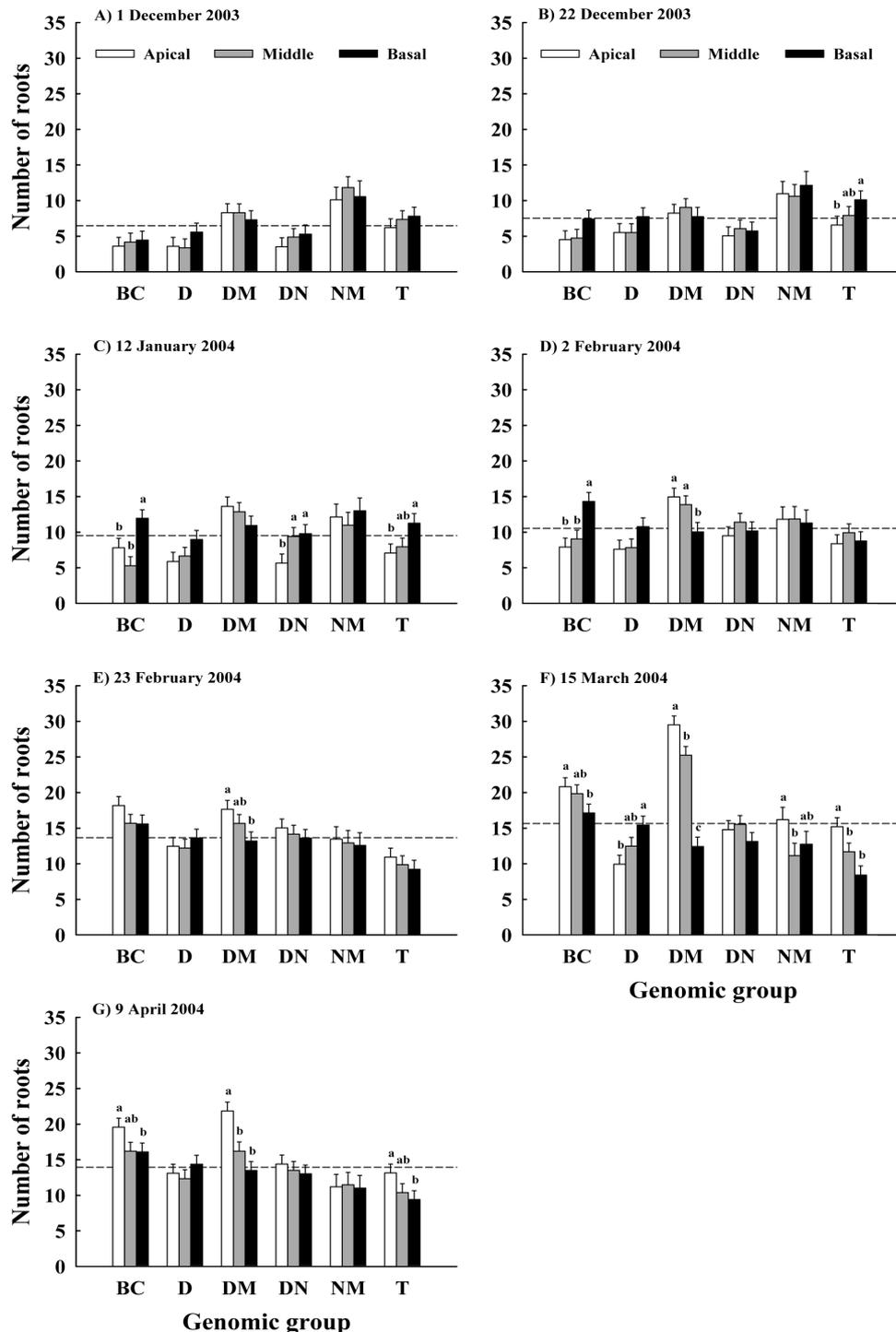


Figure 2. – Number of roots of *Populus* cuttings belonging to six genomic groups, based on the date of collection of the terminal shoots from stool beds and the cuttings' positions on the shoot of the parental stool plant. Each bar represents the mean adjusted for cutting dry weight with one standard error. Positions with different letters above bars within each genomic group are different according to Fisher's protected LSD [$\alpha = 0.05$, LSD: BC, D, DM, DN, and T = 3.4 ($n = 12$), NM = 4.9 ($n = 6$)], where non-labeled comparisons are negligible. The dashed line is the overall mean.

roots on 15 Mar. 2004 were apical, middle, and basal, respectively. Apical cuttings exhibited the greatest number of roots on 9 Apr. 2004, while middle and basal cuttings were different than apical yet similar to one another for this trait. Differences among shoot positions for the DN genomic group existed for shoots collected on 12 Jan. 2004, when middle and basal cuttings exhibited similar number of roots that was superior to that from apical cuttings. Differences among shoot positions for the NM genomic group existed for shoots collected on 15 Mar. 2004, when apical cuttings exhibited the greatest number of roots, middle cuttings exhibited the fewest number of roots, and basal cuttings were not different from either of the other positions. For the T genomic group, basal cuttings processed from shoots collected on 22 Dec. 2003 and 12 Jan. 2004 exhibited the greatest number of roots and apical cuttings exhibited the fewest number of roots, while the middle cuttings were not different from either of the other positions. Apical cuttings exhibited the greatest number of roots for shoots collected on 15 Mar. 2004, with middle and basal cuttings having similar number of roots. Apical cuttings processed from shoots collected on 9 Apr. 2004 exhibited the greatest number of roots and basal cuttings exhibited the fewest number of roots, while the middle cuttings were not different from either of the other positions.

There was broad genotypic variation in root dry weight, with 15 Mar. and 9 Apr. 2004 being important dates because differences among positions began to develop or changed relative to earlier dates (Fig. 3). Differences among shoot positions for the D genomic group existed for shoots collected on 9 Apr. 2004, where basal cuttings exhibited superior root dry weight to that which was similar for apical and middle cuttings. For the DM genomic group, middle cuttings processed from shoots collected on 22 Dec. 2003 exhibited the greatest root dry weight and basal cuttings exhibited the least root dry weight, while the apical cuttings were not different from either of the other positions. Apical and middle cuttings performed similarly for shoots collected on 2 Feb. 2004, and these cuttings were superior to those of the basal position. All cutting positions processed from shoots collected on 15 Mar. 2004 were different for root dry weight, with the greatest to least being from middle, apical, and basal positions, respectively. The trend from 15 Mar. 2004 reversed with cuttings processed from shoots collected on 9 Apr. 2004, with basal cuttings exhibiting the greatest root dry weight and middle cuttings exhibiting the least root dry weight, while the apical cuttings were not different from either of the other positions. Differences among shoot positions for the NM genomic group existed for shoots collected on 23 Feb. 2004, when apical and middle cuttings performed similarly and were superior to basal cuttings. Apical cuttings processed from shoots collected on 15 Mar. 2004 exhibited the greatest root dry weight and basal cuttings exhibited the least root dry weight, while the middle cuttings were not different from either of the other positions. Middle cuttings from 9 Apr. 2004 were superior to apical and basal cuttings that exhibited similar root dry weight. Differences among shoot positions for the T genomic group existed on 15 Mar. and 9 Apr. 2004, when

apical cuttings exhibited the greatest root dry weight that was superior to similar root dry weight for middle and basal cuttings.

Discussion

The broad genotypic variation for number of roots and root dry weight among and within our genomic groups corroborated the need for detailed evaluation of pre-planting treatments. Our data supported the assertion that genotypic superiority for these traits was dependent upon the date of shoot collection during the dormant season and original shoot position from which the cuttings were made.

The date of shoot collection during the dormant season is important for rooting of dormant cuttings because the shoots must pass through an adequate chilling period of physiological dormancy (rest) before rooting will commence (quiescence) (COLEMAN et al., 1993; CHANDLER and THIELGES, 1973; NANDA and ANAND, 1970). SMITH and WAREING (1974) reported for cuttings of *Populus x canadensis* Moench 'Robusta' (*P. deltoides* x *P. nigra* 'DN17') that physiological dormancy ended 5 to 6 weeks before the buds began to swell. CUNNINGHAM and FARMER (1984) tested balsam poplar (*Populus balsamifera* L.) and reported that percent rooting and number of roots per cutting increased for cuttings collected later in the dormant season, from November through April. These results are similar to those in our study. In general, shoots collected before the end of February rooted relatively poorly compared with those collected on 23 Feb. and later. Likewise, FARMER (1966) tested *P. deltoides* in the southern United States and reported the best rooting from cuttings collected in late January, after chilling requirements were met but before depletion of nutritional reserves for bud growth decreased rooting in late February and March. The design of our experiment did not support testing of shoots collected later than 9 Apr. However, even by this date, number of roots and root dry weight began decreasing for our cuttings. Thus, we speculate, based on these results and those from other researchers, that cuttings made from shoots collected after 9 Apr. would have exhibited even less rooting because the shoots came out of dormancy and began translocation to buds for aboveground growth instead of keeping necessary reserves within the shoot itself (COLEMAN et al., 1993; DREW and BAZZAZ, 1978).

Our results lead us to assert shoots should be collected following the breaking of physiological dormancy. The effect of the date of shoot collection on the rooting of the genotypes studied may have been the result of seasonal variation in the physiology of cambial activity. NANDA and ANAND (1970) reported for *P. nigra* control cuttings tested throughout the year that the greatest percent rooting and number of roots was from cuttings collected in February and March, respectively. Likewise, FARMER et al. (1989) reported the greatest number of roots for *P. balsamifera* was from cuttings collected in April (compared with those collected in November through January), when physiological dormancy was released by chilling, and cambial activity was elevated. Similarly, HOULE and BABEUX (1993) reported the greatest rooting percent, number of roots, and root length of five *P. balsam-*

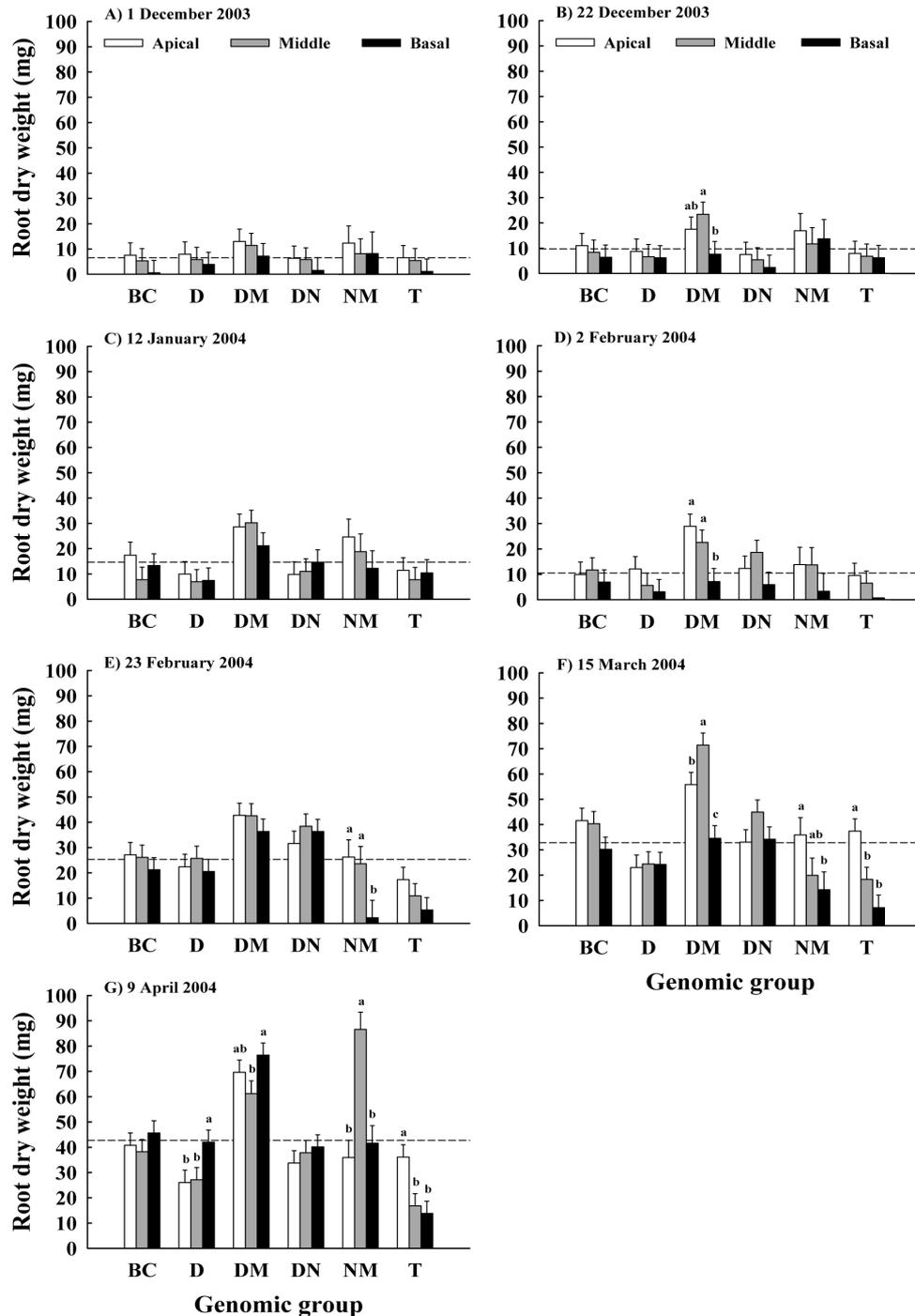


Figure 3. – Root dry weight of *Populus* cuttings belonging to six genomic groups, based on the date of collection of the terminal shoots from stool beds and the cuttings' positions on the shoot of the parental stool plant. Each bar represents the mean adjusted for cutting dry weight with one standard error. Positions with different letters above bars within each genomic group are different according to Fisher's protected LSD [$\alpha = 0.05$, LSD: BC, D, DM, DN, and T = 13.6 ($n = 12$), NM = 19.2 ($n = 6$)], where non-labeled comparisons are negligible. The dashed line is the overall mean.

ifera clones when shoots were collected following the break of dormancy but before bud break and subsequent development.

In addition to seasonal variation in the physiological status of cambial activity, the effect of collection date on rooting of our genotypes may have been the result of changes in the allocation of starch and sugar to above-

ground and belowground plant components during the release of physiological dormancy. The quantity and composition of carbohydrate reserves in cuttings has been positively correlated with increased levels of rooting (TSCHAPLINSKI and BLAKE, 1989; FEGE and BROWN, 1984; OKORO and GRACE, 1976). NGUYEN et al. (1990) tested allocation of starch and sugar to shoots and roots

of two poplar clones [*P. xcanadensis* Moench 'Eugenei' (*P. deltoides* × *P. nigra* 'DN34'); *Populus tristis* Fisch. × *P. balsamifera* 'Tristis #1'] during the onset of dormancy. In both clones, the conversion of starch to sugar increased with decreasing temperatures, with the greatest proportion of starch and sugar stored in the large roots (> 1 mm diameter). FEGE and BROWN (1984) reported the greatest levels of sucrose, raffinose, and stachyose in two poplar clones [(*P. xjackii* Sargent) × (*P. xberolinensis* Dippel)] 'NC5262'; *P. deltoides* var. *angulata* × *P. trichocarpa* 'NC5334' occurred in cuttings collected in March. These sugars were used for rooting after the breaking of dormancy and before substantial quantities of stored carbohydrates were used for above-ground growth.

Great demands for fiber, energy, and environmental benefits of *Populus* deem it necessary to match shoot position to the specific genotype in order to increase the potential for successful plantation establishment. The variation in rooting of the current genotypes largely was due to shoot position effects, which may have been the result of translocation and distribution of carbohydrates throughout the parent shoot (FEGE and BROWN, 1984; SMITH and WAREING, 1972). Most recently, ZALESNY et al. (2003) explained position effects within our genomic groups in terms of size of cuttings, existence of preformed root primordia, and organogenic activity within the cuttings.

In general, our current results corroborated those of ZALESNY et al. (2003) that rooting increased with cuttings made closer to the base of the parent shoot. However, this trend did not exist for all combinations of dates of collection and genomic groups. In the current study, a reversal of the basal superiority was exhibited for the DM cuttings collected on and after 2 Feb. for number of roots and on 2 Feb. for root dry weight. In both cases, apical cuttings outperformed basal cuttings. Similar apical superiority was exhibited for BC and T cuttings collected on 15 Mar. and 9 Apr. for number of roots, while NM and T apical cuttings collected on 15 Mar. and T apical cuttings collected on 9 Apr. had the greatest root dry weight. Superiority of middle NM cuttings collected on 9 Apr. also agreed with results from ZALESNY et al. (2003). Overall, the deviation from the general trend further supported our aforementioned assertion that date of shoot collection along with shoot position is important for enhanced rooting.

Additional shoot position effects previously have been reported by several investigators for different genomic groups of poplar (SCHROEDER and WALKER, 1991; ERNST and FECHNER, 1981; HANSEN and TOLSTED, 1981; YING and BAGLEY, 1977; SMITH and WAREING, 1972; BLOOMBERG, 1963; 1959). In the current study, with the exception of number of roots from cuttings processed 22 Dec. and 12 Jan., all other significant differences in rooting resulted in apical cuttings being superior to middle and basal cuttings. Furthermore, these differences were found within the BC, DM, NM, and T genomic groups, which leads to speculation that genotypes from the section *Tacamahaca* (i.e. those with *P. maximowiczii* or *P. trichocarpa* parentage) contributed to the apical superiority. In contrast, genotypes with parentage exclu-

sively from the section *Aigeiros* (i.e. D and DN genomic groups) failed to exhibit any apical superiority, regardless of collection date. Thus, detailed physiological and anatomical studies testing the differences in root initiation and development among all of the genomic groups is necessary.

Conclusion

We contend the practice of simply using a specific genotype because of its previous superior performance, without consideration for the response of the genotype to current pre-planting treatments, is used too often and contributes to less-than-optimal plantation success. Where possible, we recommend consideration of a genotype's response to pre-planting treatments based on empirical observation before broad-scale deployment is convened. Thus, for increased plantation establishment potential with similar genotypes, we recommend collecting stool shoots no sooner than the end of February, and matching cuttings of specific shoot positions to each genotype.

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Early Selection of Radiata Pine

I. Trends over Time in Additive and Dominance Genetic Variances and Covariances of Growth Traits

Ensis, Joint Venture between CSIRO (Australia) and Scion (formerly Forest Research, New Zealand)

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Abstract

Additive genetic, dominance genetic and phenotypic variances and corresponding correlations were estimated

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for growth data collected from disconnected half-diallel progeny trials involving 25 *Pinus radiata* D. DON parents and replicated across two sites in central North Island, New Zealand. Sectional area of stem was measured at three, seven, 10 and 13 years after planting at both sites, and height at three and 10 years at one site.

Sectional area at three years exhibited similar levels of estimated additive (σ_A^2) and dominance (σ_D^2) genetic variance. However, levels of σ_D^2 remained approximately constant between three and 13 years while σ_A^2 increased substantially. Thus, sectional-area growth changed from