THE SIGNIFICANCE OF INITIAL ADVENTITIOUS ROOTS IN POPLAR CUTTINGS AND THE EFFECT OF CERTAIN FACTORS ON THEIR DEVELOPMENT[1]

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ABSTRACT

In planted cuttings of Populus trichocarpa Torr. and Gray, P. x canadensis Moench 'Regenerata', and P. x canadensis 'Robusta Bachelieri', adventitious roots developed first along the cutting, then later at the basal end. Removal of the first roots, termed initial roots, resulted in decreased shoot growth during the early growth of the cuttings and a smaller root system at the end of the growing season. Mortality occurred only in those cuttings from which all initial roots had been removed. Poplar varieties differed significantly with respect to number, but not length of initial roots produced. In general, the number, length and weight of initial roots increased with the cutting moisture content and with temperature. Number of roots increased with increasing age of parent shoot up to a maximum at 10 months, with no further increase up to 16 months. Cuttings from the base of the shoot produced longer, and in the hybrids, heavier roots than cuttings from the top. At 50% moisture content, basal cuttings produced more roots than top cuttings, but at 100% moisture content, there was no significant difference between the shoot regions. The position in which cuttings were placed exerted a significant effect on the number of roots produced in the hybrids, but not in P. trichocarpa.

INTRODUCTION

During the course of investigations into poplar diseases, it was observed that within two weeks of being planted in early spring, poplar cuttings produced roots, herein referred to as initial roots, which were distributed chiefly along the cuttings (Fig. 1). Up to two months later, roots developed from the basal end of the cuttings, especially from the callus tissue surrounding

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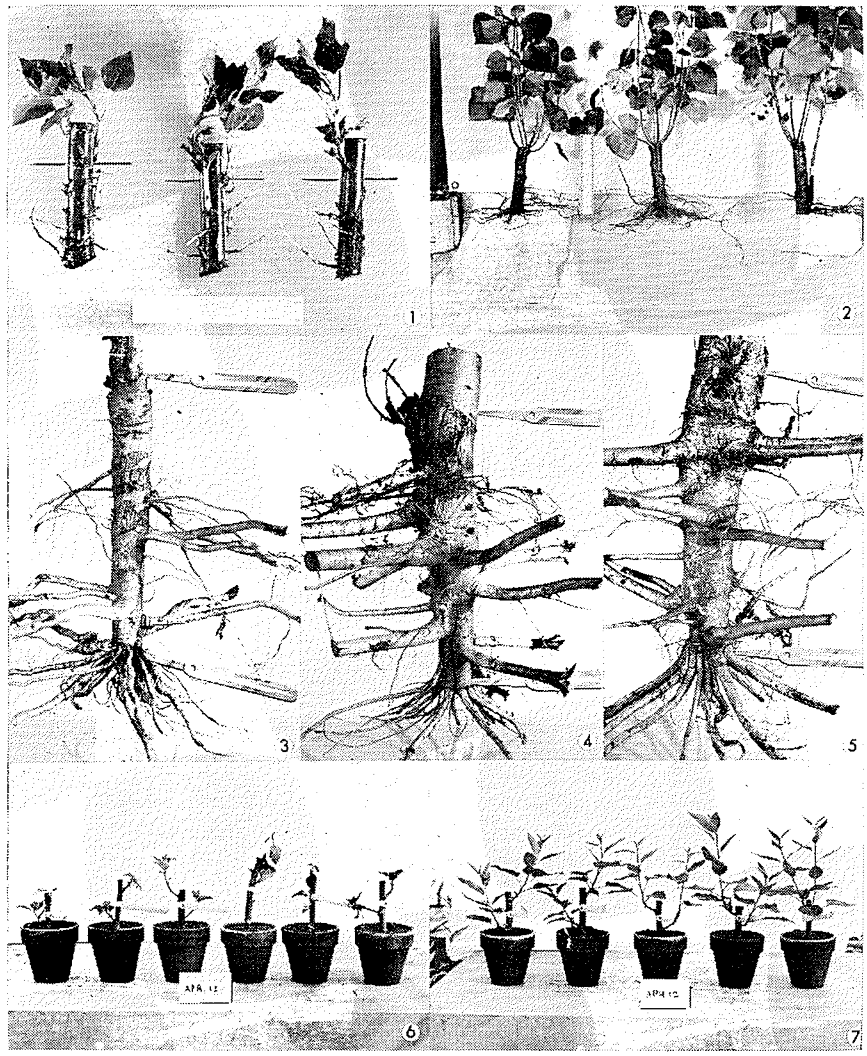

FIGURE 1. *Populus* 'Regenerata' cuttings, 1 month after being potted in soil in the greenhouse. Groundline is marked.

FIGURE 2. *Populus* 'Regenerata' cuttings 4 months after being potted.

FIGURE 3. Roots of 2-year-old *P.* 'Robusta' dug up in the nursery. Pot labels mark top and bottom of original cuttings which are approximamtely 10 in. long and 1½ to 2 in. thick.

FIGURE 4. Roots of 3-year-old *P.* 'Robusta'.

FIGURE 5. Roots of 3-year-old *P.* 'Grandis'.

FIGURE 6. Cuttings with all initial roots removed, 1 month after planting.

FIGURE 7. Cuttings with no treatment, 1 month after planting.

the cut surface (Fig. 2). Three years after planting, both types of roots were well developed (Figs. 3 - 5) and appeared to be equally important. However, it seemed likely that the initial roots would be more important for the survival of the newly planted cuttings because they were the first to be produced.

Factors affecting the development of poplar root systems have been described by Van der Lek (1930), Shapiro (1957), and Bier (1961), while factors affecting the development of poplar root systems have been dealt with by Allen and McComb (1955), Schröck (1956), Larsen (1948, 1957), and Fröhlich (1961). The present paper describes the results of experiments which were carried out to assess the relative importance of initial roots, and to investigate the effects of the following factors on their development: moisture content of the cutting, temperature, location in the parent shoot from which the cutting was taken, date of collection of cuttings, poplar variety[3], and the position in which the cutting was placed.

Materials And Methods

Cuttings were obtained from the most vigorous shoots at the West Tree Farms Ltd. nursery at Lulu Island, B.C. They were collected freshly for each experiment. The following poplar varieties were tested: *Populus trichocarpa* Torr. and Gray; *P.* x *canadensis* Moench 'Regenerata'; and *P.* x *canadensis* 'Robusta Bachelieri'. Cuttings were 10-15 cm long and the cuts were made to include a node at either end of the cutting. Diameter varied from 1—2 cm.

Growth of initial roots was induced by placing the cuttings in polyethylene bags, moistening the enclosed atmosphere with an atomizer, then closing the bags and incubating in darkness. This procedure appeared to provide suitable conditions for root development and permitted observation without disturbance to the cuttings.

The number of roots was expressed as the number of root insertions per square decimeter of bark surface, excluding branch insertions, injured bark, and other areas from which roots might be prevented from developing. Dry weight of roots was determined by removing and drying all roots to constant weight at 75-80° C[4], then expressing the weight per dm^2. Average length of roots was obtained by removing roots, then laying them out straight on a sheet of glass.

The effect of initial roots on survival and growth of *P. trichocarpa* cuttings was determined by excising 75 and 100% of the initial roots after incubation in bags. The wounds and cut ends of the cuttings were covered with Braco tree emulsion[5]. The cuttings were then planted in 10-in. pots containing sandy loam, care being taken not to injure the roots. Cuttings were also planted without prior incubation, but with Braco applied to their cut ends. Treatments were replicated 16 times and the pots, which were watered from above, were set out randomly in the greenhouse. To simulate plantation moisture conditions

[3] Because the poplars were from one species and two cultivars, the term variety is not strictly speaking correct. However, it is used for convenience.

[4] All temperatures are in degrees centigrade.

[5] Brantford Roofing Company, Brantford, Ontario.

from early spring to late fall, the soil was kept rather dry for the first two months then watered abundantly until the end of the experiment, which lasted 9 months.

The experiments on moisture content, temperature, shoot region, collection date, and variety were of balanced, factorial design. Moisture content was adjusted to 50 and 100% saturation, using methods which have been described previously (Bloomberg, 1962). The cuttings were incubated at 15 and 25° for 10 days, and 5° for 60 days. Shoots were divided into four equal lengths; four cuttings were taken from the basal length, and four from the second length from the top of the shoot. Numbers of roots produced were determined in cuttings made from shoots collected in July, November, January, March, and the following July. The shoots were 4, 8, 10,12, and 16 months old, respectively. Weight and length of roots were determined only in the cuttings collected in March. Equal numbers of cuttings were used for all treatments, which were replicated at least 12 times.

The effects of the number of initial roots on survival and growth of cuttings, and the effects of the position of the cutting on initial root development, were examined in individual experiments.

All data were statistically treated by analysis of variance and covariance, and by transformation for anormality and heterogeneity of error, if necessary. Number and weight of roots in Tables II to V and VII are based on transformations; significant differences are obtainable by converting the table values to log $(x + 2)$. All differences referred to as significant and highly significant are at the 5% and 1% levels of probability, respectively.

Results

Mortality occurred only in those cuttings from which all initial roots had been removed (Table I). Compared to untreated cuttings, those with all roots removed had, at 1 month, about one-quarter of the leaf area; at 3 months they had significantly shorter roots; at 9 months their shoots were not significantly shorter, but the number and dry weight of their roots was significantly less. Cuttings with 75% of their initial roots removed suffered no mortality. Their leaf area at 1 month, shoot length at 3 months, and number of roots at 9 months were significantly less than in the untreated cuttings, but their leaf area at 1 month and root dry weight at 9 months were significantly greater than cuttings with all roots removed (Figs. 6 and 7). There was no sign that a pathogen had entered the cuttings as a result of excision of roots.

The results in Tables 2 - 7 are shown as means of all factorial treatments. For example, the effect of moisture content (Table 2) is shown as the average of all temperatures, collection dates, and shoot regions for each poplar variety. Unless specifically mentioned, none of the averaged factors showed significant interactions.

TABLE 1

THE EFFECT OF EXCISING INITIAL ROOTS ON SURVIVAL AND GROWTH OF *P. trichocarpa* CUTTINGS

Treatment	Mortality %	Shoot development: Leaf area at 1 mo. (sq. in.)	Shoot development: Length at 3 mo. (in.)	Shoot development: Length at 9 mo. (in.)	Shoot development: Dry wt. at 9 mo. (g)	Root development: Total No. at 9 mo.	Root development: at 9 mo. Dry wt. (g)
Control	0	17.3	18.9	151.7	13.7	15.1	27.8
75% of roots removed	0	9.9*	16.3**	138.9	13.2	11.0**	25.7
100% of roots removed	25	4.6*	15.3	137.0	12.7	11.0	20.0**
LSD		3.6	1.3	26.0	2.1	1.0	3.7

* significant difference
** highly significant difference

Cutting moisture content (Table 2) exerted a highly significant effect on the number, length, and weight of initial roots. Roots produced at 100% moisture content were 5 to 10 times more numerous and approximately twice as long as those produced at 50%. Weight of roots did not vary significantly with moisture content in cuttings from the top of *P. trichocarpa* or those from the base of *P.* 'Robusta', but in all other cuttings total weight of roots from cuttings at 100% was up to 9 times greater than those from cuttings at 50%.

TABLE 2

EFFECT OF MOISTURE CONTENT OF CUTTINGS ON THE DEVELOPMENT OF INITIAL ROOTS IN POPLARS

Variety	Moisture content % saturation	Root development: No./dm²	Root development: Length mm	Root development: Weight/dm² g
P. trichocarpa	50	4.8	7.6	6.4
	100	27.5**	12.4**	10.6
P. 'Regenerata'	50	1.6	6.7	3.1
	100	16.9**	15.0**	26.9**
P. 'Robusta'	50	7.2	6.2	9.2
	100	50.1**	12.8**	35.1**
LSD Moisture contents		.1307[1]	3.5	.2891[1]

[1] In tables 2 - 5 and 7, least significant differences are shown as logarithms, significant differences are obtainable by converting the table values to log (X+2).

None of the poplar varieties produced roots after 10 days' incubation at 5°. *Populus trichocarpa* produced as many roots after 60 days at 5° as after 10 days at 15° (Table 3). Both hybrids, even after 60 days' incubation at 5°, produced significantly fewer roots than at 15°. There was no significant difference between 15 and 25° with respect to the number of roots produced by any variety. In all varieties, root length was significantly shorter at 5° after 60 days than at 15° after 10 days. In *P.* 'Regenerata', root length was significantly shorter at 15° than at 25°, but the other two varieties showed no difference in this respect. In all varieties, the weight of roots after 60 days at 5° was significantly less than at the higher temperatures. The differences in root length between 15° and 25° did not attain significance in *P. trichocarpa*, but the higher temperature resulted in greater weight of roots in both hybrids.

TABLE 3
EFFECT OF TEMPERATURE ON THE DEVELOPMENT OF INITIAL ROOTS IN POPLAR CUTTINGS

Variety	Temperature °C	Incubation period (days)	Root development		
			No./dm^2	Length mm	Weight/dm^2 g
P. trichocarpa	5	60	11.1	1.0	<1
	15	10	11.7	8.6**	6.9**
	25	10	13.1	11.3	9.9
P. 'Regenerata'	5	60	1.8	<1	<1
	15	10	6.6**	7.8**	7.0**
	25	10	6.0	14.0**	12.9**
P. 'Robusta'	5	60	0.7	<1	<1
	15	10	17.9**	8.7**	13.7**
	25	10	21.9	10.3	23.8
LSD temperatures			.2094	3.1	.3067

At 100% moisture content, there were no significant differences between regions of the parent shoot from which cuttings had been taken with respect to the number of roots produced. At 50% moisture content, basal cuttings from both hybrids produced significantly more roots than top cuttings (Table 4.) The same relationship held in *P. trichocarpa* with the exception of cuttings collected in March, when it was reversed. Basal cuttings of both hybrids

TABLE 4
EFFECT OF SHOOT REGION ON THE DEVELOPMENT OF INITIAL ROOTS IN POPLAR CUTTINGS AT 50% MOISTURE CONTENT

Variety	Shoot region	Root development		
		No./dm^2	Length mm	Weight/dm^2 g
P. trichocarpa	Top	3.2	5.4	9.6
	Base	6.8**	9.7**	4.3
P. 'Regenerata'	Top	0.7	0.5	0.8
	Base	2.7**	12.9**	8.5**
P. 'Robusta'	Top	3.7	2.8	1.4
	Base	15.3**	9.5**	47.4**
LSD Shoot regions		.2440	3.8	.4094

produced a greater weight of roots than did the top cuttings, regardless of moisture content. In *P. trichocarpa,* shoot region did not have any effect on the weight of roots. Basal cuttings of all varieties produced longer roots than did the top ones.

In all varieties, the number of roots reached a maximum in the 10-month-old cuttings, collected in November, then did not change significantly in the 12- and 16-month-old cuttings (Table 5). In both hybrids, but not in *P. trichocarpa,* 8-month-old cuttings produced significantly more roots than 4-month-old ones.

TABLE 5

EFFECT OF COLLECTION DATE ON THE NUMBER OF INITIAL ROOTS IN POPLAR CUTTINGS

Collection date	Age months	No. of roots/dm^2		
		P. trichocarpa	P. 'Regenerata'	P. 'Robusta'
July	4	3.5	0.4	0.8
			**	**
November	8	6.5	3.3	14.5
		**	**	**
January	10	13.9	6.1	28.0
March	12	17.9	10.8	17.4
July	16	19.3		
LSD dates		.2770		

Cuttings of *P.* 'Regenerata' produced significantly more roots when placed in an upright position than in the inverted or the horizontal positions (Table 6). The number of roots produced by cuttings placed in the other two positions did not differ significantly. When the cuttings were placed in upright or

TABLE 6

EFFECT OF POSITION OF CUTTING AND THE REGION WITHIN THE CUTTING ON THE NUMBER OF INITIAL ROOTS IN POPLARS

Variety	Region of cutting	No. of roots/dm^2			LSD positions (av.)
		Upright position	Inverted position	Horizontal [a] position	
P. trichocarpa	Upper	17.1	18.4	17.8	6.1
	Lower	22.0	18.4	15.5	
	Av.	19.6	18.4	16.7	
P. 'Regenerata'	Upper	11.0	11.8	5.5	
		**		**	
	Lower	30.6	8.2	14.1	
	Av.	20.8	10.0	9.8	
		**			
P. 'Robusta'	Upper	12.9	16.1	33.5	
		**			
	Lower	23.0	13.9	36.9	
	Av.	17.9	15.0	35.2	
			**		
LSD region	8.2				

[a] Upper and lower regions in horizontal cuttings refer to the morphologically upper and lower regions, respectively.

horizontal positions, more roots were produced in the lower than in the upper half of the cutting. The morphologically lower half was taken as the lower half in horizontal cuttings. There was no significant difference between halves when the cutting was inverted.

Populus 'Robusta' cuttings in the horizontal position produced more roots than inverted or upright cuttings, which did not differ from each other. When the cuttings were upright, the lower half produced more roots than the upper half; there were no differences in this respect when the cuttings were kept horizontal or inverted. *Populus trichocarpa* showed no differences either between cutting positions or between halves of the cutting.

The average number, length, and weight of roots from all experiments is shown in Table 7. *Populus* 'Robusta' had significantly more roots than *P. trichocarpa* which, in turn, had significantly more than *P.* 'Regenerata'. *Populus* 'Robusta' had significantly greater weight of roots than the other two varieties; the latter did not differ significantly from each other. There were no significant differences between varieties with respect to root length.

TABLE 7

EFFECT OF POPLAR VARIETY ON THE DEVELOPMENT OF INITIAL ROOTS IN CUTTINGS

Variety	Root development		
	No./dm²	Length mm	Weight/dm² gr.
P. 'Regenerata'	11.8	10.0	10.4
	**		
P. trichocarpa	5.7	10.9	11.0
	**		**
P. 'Robusta'	19.2	9.5	21.5
LSD	.2274	3.8	.1506

DISCUSSION

The occurrence of mortality and the severe reduction of early shoot growth in cuttings which were devoid of initial roots indicates that these roots are very important to the survival and early growth of the cutting. However, in 6 months, shoot length differences between treatments had diminished and by 9 months were no longer significant. With time, therefore, the cuttings evidently became less dependent on initial roots. However, cuttings from which all initial roots were removed had a smaller root system at 9 months than those in the other treatments. These developments may have been due to meagre production of callus roots during the first period of the experiment when the soil was kept dry, followed by an increase in callus root growth in the final period when the soil was watered abundantly. Traumatic differences between the 75 and 100% root removal treatments were so small that little, if any, of the growth difference can be attributed to this cause. Presumably, the superior growth of the untreated cuttings can be credited mainly to their possession of a full complement of roots.

Heimburger[6] has found some batches of Braco tree emulsion to be carcino-

[6] Heimburger, C. Division of Research, Ontario Department of Lands and Forests, Personal communication.

genic when used in poplar grafting. No evidence of this effect was observed in the rooting experiment. Furthermore, Braco was used to cover cut ends in all treatments, therefore its effect, if any, would be fairly constant.

Bier (1961) found that "morphological" roots were not related to survival when basal cuttings from weaker shoots were grown in vermiculite with a constant supply of water. Assuming his "morphological" roots to be equivalent to initial roots, as defined in this paper, it is possible that the results obtained may not be applicable to cuttings from vigorous shoots grown in soil and subjected to dry, as well as moist, soil conditions.

Moisture deficit is known to reduce growth (Ashton, 1956; Helmerick and Pfeifer, 1954; Upchurch *et al,* 1955; and Wadleigh and Gauch, 1948) and it appears that reducing the moisture content of a cutting to 50% saturation causes a sufficient stress to affect development of the roots adversely. It has been shown that there is a correlation between soil moisture content and root production in poplar cuttings (Allen and McComb, 1955; and Larsen, 1957) and that there is a correlation between soil moisture content and shoot moisture content (Bloomberg, 1962a).

At 5°, roots developed at a greatly reduced rate compared to 15°. After a sufficent incubation time at 5°, *P. trichocarpa* produced as many roots as at 15° but they were shorter and weighed less. In the hybrids, the number of roots at 5° after 60 days was less than at 15°. It is concluded that in *P. trichocarpa,* as many root primordia will start growth at 5° as at 15°, but the growth is slower at the lower temperature. In the hybrids it appears that a smaller proportion of primordia will initiate growth at 5° than at 15°. Root length and weight were influenced more strongly by 25° in the hybrids than in *P. trichocarpa.* Apparently, the hybrids were generally more sensitive to temperature than was *P. trichocarpa.*

At 100% moisture content, there was no significant difference between the basal and top cuttings with respect to number of roots produced per dm^2 of bark surface. This relationship could result from the number of root primordia in both shoot regions being proportional to the size of the cutting. There is other evidence to this effect in the findings of Van der Lek (1930) that the primordia occur at the intersection of the rays with the cambium, and of Bloomberg (1962a) that the number of these intersections per cm is the same for both shoot regions.

At 50% moisture content, the number of roots per dm^2 of bark surface was greater in cuttings from the basal as against those from the upper part of the shoot; this relation was consistent in the hybrids and there was only one exceptional month in *P. trichocarpa.* By implication, the roots in the upper region were more sensitive to moisture reduction than those in the base, or, what is equally probable, the moisture in the basal cuttings was more favorably distributed for root growth than in the top cuttings. It has been shown that the anatomy of the basal region of the shoot of poplar is more favorable for water storage, retention, and translocation than the top (Bloomberg, 1962a). *Populus trichocarpa* appeared to be more variable than the hybrids in the relationship between shoot regions, partly due no doubt, to the greater heterozygosity in the cuttings.

It has been suggested that the reduction of root development may be caused by the presence of phloem fibres which obstruct the emergence of the root (Beakbane, 1961). However, it has been shown that in the three poplar varieties, the basal shoot region has more bands of fibres than the top (Bloomberg, 1962a). The fact that the basal region of the shoot produced roots which were heavier and longer than those from the top, suggests that the two regions differ with respect to the distribution of food reserves within the shoot. These results agree with the findings of Schröck (1956) and Bloomberg (1959) that rooting capacity of poplar cuttings decreased with distance from the base of the stem.

The fact that the number of initial roots increased with age up to 10 months, then remained about the same, indicates that the number of root primordia laid down, or their ability to initiate growth, increases up to this age. Evidently, the relative paucity of roots in 4-month-old *P. trichocarpa* shoots was not related to the fact that they were collected in July, for the 16-month-old shoots were collected at the same time of year, yet their roots were much more numerous. This conclusion is in contrast with Shapiro's findings (1957) that in Lombardy poplar shoots the number of roots which can be caused to emerge by dark treatment decreases after the parent tree breaks dormancy.

It was apparent that the position in which cuttings were placed resulted in characteristic rooting responses by the three varieties. In the hybrids, the average number of roots for the whole cutting was reduced by inversion, but in *P. trichocarpa* there was no effect. The hybrids also showed polarization of root development within the cutting, in that the morphologically lower part produced more roots than the upper part. In *P. trichocarpa* there was no difference in this respect. It is concluded that the polarization effect was confined to the lower part of the cutting, because the upper part was not significantly affected by inversion. Shumulina (1949) has reported that horizontally-planted cuttings were superior to vertically-planted ones with respect to root growth.

The practical value of the results lies in the guidance they give for the selection of varieties, type of cuttings, and date of collection for the best survival and growth when planted out. The importance of ensuring that cuttings have a high moisture content, by soaking them if necessary, and that soil temperature is sufficiently high to promote good root growth, is also obvious from the results. The effect of the position in which unrooted cuttings are planted deserves further investigation under field conditions. Incubation of cuttings in polyethylene bags is suggested as a method of assaying rooting ability analogously to germination testing in seeds.

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