Seven percent natural selfing in upper crowns is insignificant for most traits, but 34 percent natural selfing in lower crowns will cause noticeable inbreeding depression in several traits, especially yield of filled seed (FRANKLIN, 1969). For purposes of open-pollinated progeny testing, most biases due to natural inbreeding (NAMKOONG, 1966) can be avoided by making seed collections from upper crowns. The same applies to collections for provenance trials and to commercial seed collections. Conversely, when open-pollinated collections are used to locate trees heterozygous for recessive mutant alleles, as suggested by SNYDER *et* al. (1966), chances of finding such trees are increased by collecting cones from lower crowns.

The extremely low inbreeding coefficient for parent trees indicated that a very small proportion of selfed seedlings became established and reached sexual maturity in this stand, despite appreciable levels of inbreeding at fertilization. This trend was expected because severe inbreeding depression was found in controlled self-pollinated families from this same stand (FRANKLIN, 1969). These results firmly support the general assumption that mature stands of loblolly pine are largely outbred, even though appreciable amounts of self-fertilization occurs.

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An Instance of Clonal Incompatibility in Grafted Pinus radiata Seedlings

By R. J. CAMERON and GAIL V. THOMSON

Introduction

In tree improvement work at the New Zealand Forest Research Institute, a method has been developed for tip cleft grafting scions collected from adult trees of *Pinus* radiata on to seedling root-stocks (THULIN and FAULDS, 1966). Normally a rate of success better than 90 per cent can be expected. It has been observed, however, that scions taken from one particular tree, FRI Clone 104, show a high failure rate. The grafted seedlings appear healthy at first and grow quite vigorously, but soon after the seedling stocks are defoliated, usually early in January, a considerable proportion of the grafts become yellow, the needles droop and may fall, and many of the graft combinations die. Of the 50 per cent or so of grafted seedlings that do manage to survive the first growing season, many more die during the following spring.

The symptoms suggest that vascular transport between scion and stock is impaired. The movement of water and nutrients upwards through xylem tissues appears to be adequate for scion growth during the first growing season, but the dependence of some of the grafted seedlings, for healthy growth, upon the presence of live, functional foliage on the stock below the graft union gives the impression that in such plants photosynthates cannot pass from scion to stock. Under these conditions food reserves are soon exhausted in the stock which then, with its roots, dies of starvation. Death of the scion is concomitant. The second period of mortilaty, which occurs during the following spring when height growth is at a maximum, suggests, that in plants so affected the xylem connections in the graft are in some way inadequate; the stresses imposed at this time are too great and the plant dies.

The purpose of the present investigation was to study translocation of photosynthates within the grafted plants and thus investigate further the reason for graft failure.

The movement of photosynthates labelled with carbon-14 was used to follow phloem translocation in grafted seedlings.

From 200 plants of Clone 104 scion grafted on to 8-month-old seedling stocks in August 1966, 25 individuals were selected in February 1967, for detailed study. These comprised:

Group *A:* 5 apparently healthy grafted seedlings from which the foliage on the stocks had been removed four weeks previouslv.

Group B: 5 unhealthy grafted seedlings (foliage yellow or drooping) from which the foliage on the stocks had also been removed four weeks previously.

Groups *C,* D, *and* E: Each group consisting of five grafted seedlings, from which the foliage on the stock below the graft had not been removed.

For administration of $^{14}CO_2$ foliage zones of each grafted seedling were localised using polyethylene plastic bags, secured against the stem at open ends or ends with tight ties over cotton-wool pads, thus providing a firm seal without damaging the stem or restricting translocation. For Groups A, B, and E the polyethylene bags covered only the scion and were tied above the graft union; for Group C the whole plant stem, both stock and scion, was covered; and for Group D only foliage of the stock was covered using polyethylene tubes tied immediately below the graft union and again at ground level.

$^{14}CO_2$ was generated in the laboratory by the action of concentrated H_2SO_4 on $BaCO_3$. One cubic centimetre of a $^{14}CO_2$/air mixture, containing approximately 25 microcuries of carbon-14, was injected into each bag at 3 p.m. on 28 February and the injection hole sealed. At 9 a.m. the following day the bags were removed and foliage samples taken for later analysis, to ensure that in each plant there had occurred a reasonable uptake of $^{14}CO_2$. The results are given in *Table 2.* A check measurement on samples of foliage taken from outside the bag showed no signs of radioactivity at this stage. Earlier measurements had shown that it takes approximately 72 hours after administration of $^{14}CO_2$ for photosynthates labelled with carbon-14 to attain maximum concentration in the growing tips of roots (see *Figure* 1). Excepting the plants comprising Group E from which only small samples of foliage and roots were taken and the seedlings then transplanted for further ob-

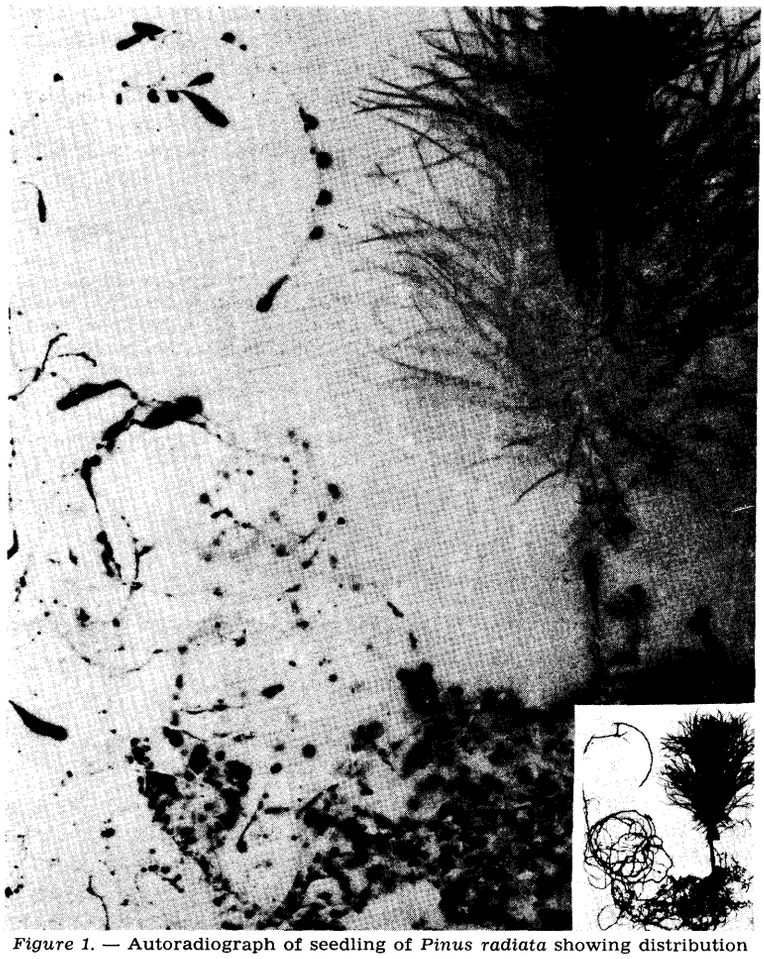

Figure 1. — Autoradiograph of seedling of *Pinus radiata* showing distribution of radioactivity after 72 hours exposure to $^{14}CO_2$. Inset is a photograph of the mounted seedling.

servation (see below), the labelled, grafted seedlings were, after 72 hours, dug up and removed to the laboratory for further investigation. The plants were washed clean and the following analyses made:

1. Two actively-growing roots from each seedling were autoradiographed on Kodirex film, using an 11-day exposure.
2. The remaining secondary roots on each plant were dried in an oven for 24 hours at 100° C, then ground in a Wiley Mill (40-mesh sieve). Samples of approximately 100 mg of the ground material were plated on planchets 2.5 cm in diameter, sealed with a minimal amount of cellulose lacquer (ca.a. 5 mg aerosol-packed lacquer per sample) and counted under a gas-flow-detector. The foliage samples mentioned above were similarly treated. The results are given in *Table 2.*
3. Longitudinal freehand sections were cut through the graft unions of a number of plants and autoradiographs, 9-days' exposure, prepared from them. These are shown in *Figures 2 and 3.*

At intervals from 14 March 150 of the surviving grafted seedlings of Clone 104 left in the nursery were examined for health and mortality. They were arbitrarily classified as:

1. Apparently healthy.
2. Foliage markedly yellow, or foliage being shed.
3. Plants yellow and desiccated, with dead tops, apparently dying.
4. Dead.

The results are given in *Table 1.* It should be noted that during the period of the observations the grafted seedlings were subjected to the normal practice (for our nursery) of fortnightly wrenching, using tractor-mounted equipment. In this operation the roots are undercut at a depth of 8 to 10 cm and the plants lifted and loosened in the soil; the first wrenching is primarily a pruning operation which severs the tap root and breaks the long lateral roots, whereas subsequent wrenching mainly achieve soil loosening and aeration. Wrenching may have affected the rate at which grafted seedlings became unthrifty and died.

Table 1. — Health and survival of 150 Clone-104 scions grafted on seedling stocks.

Date	Health classification as percentages			
	1 healthy	2 yellow or defoliating	3 dying	4 dead
14 March	56	41	3	0
6 April	51	29	17	3
20 April	48	28	14	10
2 May	55	21	13	11
17 May	51	20	12	17
30 may	51	16	11	22
23 June	49	13	9	29

Results and Discussion

The mortality of grafted seedlings:

Progressive morbidity and mortality of the grafts between scions of Clone 104 and stocks of seedling *Pinus radiata* are summarised in *Table 1*. No data are given which describe the behaviour of other clones but it is asserted that both stock defoliation and wrenching normally cause no mortality in grafted seedlings.

Assimilation of $^{14}CO_2$ and translocation of photosynthates:

The results of the measurement of carbon-14 in needle samples (18 hours after the introduction of $^{14}CO_2$) and in roots (after 72 hours) are summarised in *Table 2*. A 10-minute count was made of the activity of each sample and from these the values given in the table were calculated. Corrections have been made for sample thickness, self absorption, and for a counter efficiency of 14.3%.

Comparision of the measurements from Groups A and B, the 'healthy' and 'unhealthy' plants respectively, shows that whereas the foliage of both sets of plants possess similar rates of $^{14}CO_2$ assimilation (B 1 excepted) translocation to roots is considerably impaired in the plants assigned to Group B. An anomaly is grafted seedling A 3 in which radioactivity was not detected in the root sample. An

Table 2. — Measurement of the emission of beta particles from carbon-14 in photosynthates present in needles and in root tissues.

Sample number	Disintegrations per minute per mg dry wt of foliage	Disintegrations per minute per mg dry wt of root tissue
A. Apparently healthy grafted seedlings, stock defoliated:		
A 1	1634	111
A 2	1127	132
A 3	1697	0
A 4	2327	190
A 5	1611	555
		Mean value .... 247 ± 1.8* (value for A 3 omitted)
B. Unhealthy grafted seedlings, stock defoliated, $^{14}CO_2$ applied to scion only:		
B 1	68	15
B 2	1737	2
B 3	1921	8
B 4	1825	3
B 5	2081	1
		Mean value .... 6 ± 0.4*
C. Grafted seedlings, stock not defoliated, $^{14}CO_2$ applied to foliage of both stock and scion:		
C 1a (above graft union)	531	
C 1b (below graft union)	1720	402
C 2a	1237	
C 2b	534	116
C 3a	1932	
C 3b	1305	121
C 4a	2863	
C 4b	497	79
C 5a	1020	
C 5b	485	31
		Mean value .... 150 ± 1.4*
D. Grafted seedlings, stock not defoliated, $^{14}CO_2$ applied to foliage of stock only:		
D 1a (above graft union)	0	
D 1b (below graft union)	3131	145
D 2a	9	
D 2b	1652	361
D 3a	0	
D 3b	2382	387
D 4a	0	
D 4b	1265	178
D 5a	0	
D 5b	628	189
		Mean value .... 252 ± 1.8*
E. Grafted seedlings, stock not defoliated, $^{14}CO_2$ applied to foliage of scion only:		
E 1a (above graft union)	964	
E 1b (below graft union)	12	567
E 2a	2139	
E 2b	3	2
E 3a	2070	
E 3b	2	5
E 4a	780	
E 4b	1	1
E 5a	1727	
E 5b	1	8
		Mean value .... 4 ± 2.7* (value for E 1 omitted)

* indicates counting errors in measurements of carbon-14, P = 0.05.

obvious conclusion is that this plant has been wrongly categorised and should have been included in Group B.

The data for Groups C and D, when compared, show clearly that the foliage of both stock and scion can contribute photosynthates which are translocated to the root sink. The experimental conditions do not allow, for these two groups, any identification of the seedlings in which passage of photosynthates from scion to stock has been restricted. The data for Group E show that whereas plants E2, E3, E4 and E5 show inhibited translocation, plant E1 appears to possess a graft union through which photosynthates can move.

So that further information could be obtained to confirm that foliage on the stock was actually responsible for the maintenance of the grafted seedlings E2, E3, E4 and E5 all the needles were stripped from the below-graft portions of each plant after the seedlings had been transplanted, and their subsequent growth was followed. Within a short time the scion sections E2a, E3a, E4a and E5a became yellow and within three months the plants died. Plant E1 remained healthy.

The rates of CO_2 fixation and quantitative translocation of labelled photosynthates in apparently healthy grafted seedlings of Clone 104 (plants A1, A2, A3, A4 and A5 of *Table 2)* were compared with measurements made of apparently healthy grafts from a selection of other clones. The differences were small and not significant ($P = 0.05$).

The autoradiographs of the root samples provide a quantitative assessment of the movement of labelled photosynthates into secondary roots. The developed films were compared visually. So that a tabular comparison could be made they were given the following assessment rating:

0 = no blackening of film
1 = faint traces only of film blackening; no clear image
2 = slight blackening of the film, giving an identifiable root image
3 = clear root image
4 = dark image

The results are summarised in *Table 3.* Once more it is quite clear that the unhealthy appearance of the grafted seedlings assigned to Group B can be correlated with impairment of the translocation of photosynthates from scion to stock. The results are consistent in that Plant A3 shows up, again, as having been wrongly classified. The distribution of radioactive materials in Plant E1, as apparent in

Table 3. — Comparison of autoradiographs of root samples.

Group and plant number	Sample 1	Sample 2
A 1	3	3
A 2	3	3
A 3	0	0
A 4	3	3
A 5	3	4
B 1	0	0
B 2	0	0
B 3	0	0
B 4	0	0
B 5	0	0
C 1	2	2
C 2	4	4
C 3	2	3
C 4	3	3
C 5	2	2
D 1	4	3
D 2	2	2
D 3	2	0
D 4	3	0
D 5	1	1
E 1	3	4
E 2	0	0
E 3	0	1
E 4	0	0
E 5	1	1

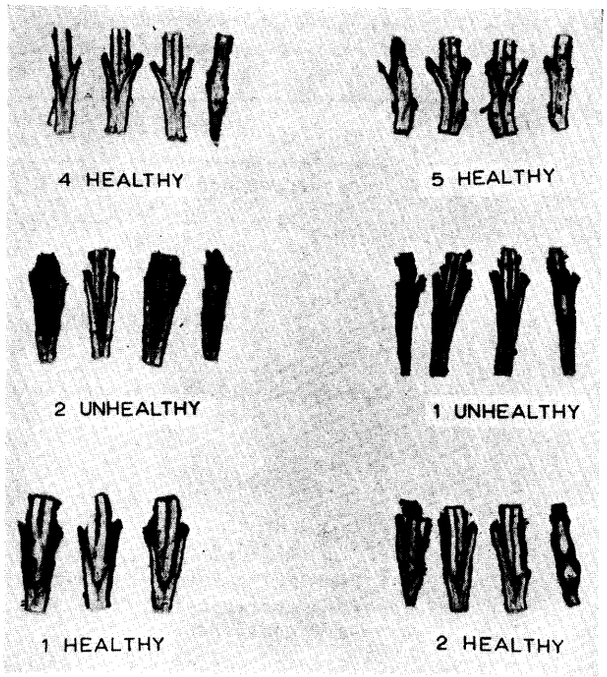

Figure 2. — Photograph of hand sections cut through the graft unions of: — plant A 4 (above left); — plant A 5 (above right); — plant B 2 (midst left); — plant B 11 (midst right); — plant A 1 (below left); — plant A 2 (below right).

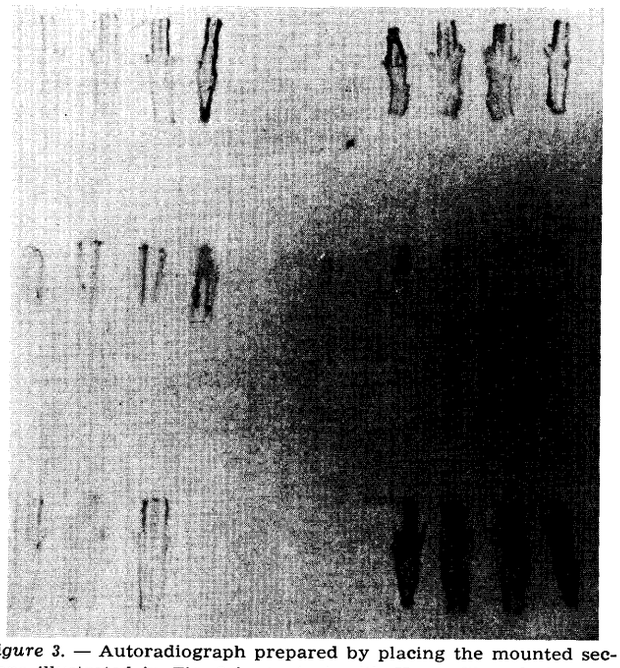

Figure 3. — Autoradiograph prepared by placing the mounted sections illustrated in *Fig. 2* in contact with X-ray film; dark areas indicate the presence of carbon-14.

the measurements summarised in *Table 2*, also agrees well with the autoradiographic assessment for this plant.

Examination of graft unions:

Autoradiographs were prepared from the hand sections cut through the graft unions of plants A1, A2, A4, A5, B1 and B2. Photographs of the sections are shown in *Figure 2* and of the autoradiographs from these in *Figure 3*. It can be seen that whereas the autoradiographs for the healthy plants (A1, A2, A4 and A5) show a blackening corresponding with zones of phloem tissue, both above and below the actual graft union (due to the presence of photosynthate labelled with carbon-14) the sections of the unhealthy plants show that the phloem below the graft union carries little or no detectable carbon-14. Thus the data given in *Tables 2 and 3*, and the characteristics indicated in *Figure 3*, are all highly consistent.

Conclusions

There is good evidence that for seedlings grafted with scions of Clone 104 the low rate of survival is due to the secondary phloem of the scion failing to form a functional union with the secondary phloem of the seedling stock. The second period of mortality, which could be due to inadequate xylem transport, has yet to be investigated.

The writers are uncertain whether to term such incompatibility histological or physiological; nor do they attempt any further explanation of the phenomenon.

Acknowledgements

We are grateful to Mr. T. Faulds who performed the grafting work and who first identified the incompatibility peculiar to grafted scions of Clone 104; also to Mr. I. J. Thulin who recognised the nature of the problem and suggested that it could be profitably investigated using radiotracer techniques.

Summary

Translocation studies in which carbon-14 labelled photosynthates were used as tracer substances, confirmed that the failure of graft combinations is due primarily to the secondary phloem of stock and scion failing to form a functional union. A secondary cause of mortality, possibly resulting from xylem transport being inadequate, has yet to be investigated.

Reference

Thulin, I. J., and T. Faulds: Outdoor grafting of *Pinus radiata*. FRI Internal Report (Forest Tree Improvement No. 33, 1966).

Comparative Qualitative Relationships of Wood Properties of Euramerican Poplars

Dimensions of Wood Fibres and Specific Gravity*)

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Forestry and wood industry are steadily strengthening their demands for more exact and detailed information on the forest resources and the properties of various species.

In the USA serious attention has been devoted in recent years to the problem of juvenile wood, since its low specific gravity, short wood fibres etc. make it unsuited to industrial processing (Polge, 1965). However, the use of juvenile wood in poplars has yielded good results (Jayme *et al.*, 1943; Cech — Kennedy — Smith, 1960; Babicki, 1963; Masirević-Oblak, 1966); as regards its degree of usefulness, poplar juvenile wood equals the wood of older plantations.

This study was designed to provide data on juvenile wood variation and inheritance.

*) From a paper read at 13th Session of International Poplar Commission, Montreal 23—28. 9. 1968. The text has been revised and illustrations added. This research has been financed in part by Grant-FG-YU-127 made by USDA, Agricultural Research Service.

Materials: At the "Tungla" plantation near Novi Sad, set up on normal carbonate alluvial soil with eight clones in a randomized block design with five replications in very dense stand (2 × 2 m.). One tree per plot (five trees in all) were harvested from each clone at age four years. Two years after thinning, 40 sample trees in all were selected again, according to the same principle as in the previous case. Thus in both cases 10 model trees were selected from each clone and cultivar. The chief taxonomic data for these trees are presented in *Table 1.*

Methods: For wood property determination samples were taken at breast height (1.30 m).

Alter defibration the dimensions of the wood fibres were measured by screen projection, using an A. O. Spencer microscope.

Table 1.

Nr.	Clones	D.b.h. in the age — cm		Height in the age — m.	
		4	6	4	6
1.	*Marilandica*	8.0—*10.5*—12.7	14.0—*14.6*—16.0	10.8—*12.2*—13.3	14.0—*14.8*—15.4
2.	*Serotina*	6.4— *9.1*—11.5	10.5—*12.1*—14.0	10.1—*11.4*—14.0	14.1—*14.9*—15.8
3.	*Robusta*	8.0—*10.4*—12.7	14.0—*14.7*—15.0	12.2—*14.0*—15.1	14.1—*14.9*—15.8
4.	*Istra*	8.6—*10.6*—12.1	13.0—*13.5*—14.5	11.5—*12.3*—13.0	13.3—*14.5*—15.2
5.	*Ostia*	9.2—*10.9*—12.1	13.5—*15.4*—16.5	13.8—*14.2*—14.6	14.4—*17.1*—17.8
6.	*Jacometti*	11.5—*12.6*—13.7	15.0—*15.6*—17.0	13.8—*14.4*—14.6	16.8—*17.1*—17.3
7.	*I-154*	10.5—*11.7*—15.9	13.0—*13.8*—15.0	13.0—*14.0*—15.4	14.8—*16.7*—16.8
8.	*I-214*	11.5—*13.2*—15.0	15.5—*17.3*—18.5	14.4—*14.9*—15.2	17.3—*17.8*—18.3