ROOT REGENERATION OF ROOT-PRUNED *PINUS RADIATA* SEEDLINGS

II. EFFECTS OF ROOT-PRUNING ON PHOTOSYNTHESIS AND TRANSLOCATION

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ABSTRACT

Root-pruning of **Pinus radiata** D.Don seedlings resulted in a sharp increase in stomatal resistance and a concurrent drop in net photosynthesis. Eight days after root-pruning leaf water potential was restored to pre-pruning levels and within 12 days photosynthesis showed signs of recovery, accompanied by a decrease in stomatal resistance. Proliferation of new roots took place and thereafter the recovery process intensified. By day 32 photosynthesis was restored to about 60% of the initial rate prior to root-pruning. Translocation of ^{14}C assimilate was restricted by root-pruning. An hypothesis concerning the physiological processes involved in root-pruning and hardening of nursery stock is discussed.

INTRODUCTION

Pinus radiata D.Don has traditionally been planted in Australia as open root nursery stock, usually 1 + 0. Nursery practice was simple and cheap but in some circumstances the plants were not hardened when transferred to the field and frequently had only a very sparse root system after lifting. In difficult planting years of drought or severe frosts losses at planting were often high. More recently nursery stock has frequently been subjected to a programme of undercutting and root wrenching in the nursery bed (van Dorsser and Rook, 1972). The purpose of these operations is to improve the quality of planting stock by encouraging the development of a fibrous root system and a hardened shoot. Plants treated in this way are capable of establishing rapidly and growing well during the early establishment period, often under quite difficult field conditions (Benson and Shepherd, 1977).

In an earlier paper (Stupendick and Shepherd, in press) the effects of temperature on root regeneration of root-pruned, or wrenched, seedlings of *P. radiata* were examined as part of a programme of research to explore some of the physiological aspects of this regeneration process. The ambient air and soil temperatures were found to exert a considerable and independent influence over the subsequent regeneration of the seedling

root system. In this second paper the effects of root-pruning on some other physiological processes in the seedling, particularly net photosynthesis, are examined and related to the observed progress of root regeneration.

MATERIALS AND METHODS

The experimental procedures concerning the raising of plant material and maintaining these under controlled ambient and soil temperature conditions before and after root-pruning have been fully described in an earlier paper (Stupendick and Shepherd, in press). Briefly, the plants were raised in the glasshouses of the CSIRO CERES phytotron in Canberra, Australia, a controlled environment facility described in detail by Morse and Evans (1962). Many seedlings were raised to allow for ample selection for uniformity of plant size in the experiments, found to be essential to reduce variability in root regeneration. Plants were measured and allocated according to height and basal diameter into comparable groups. While the seedlings used in any one experiment were very uniform there was some variation in age and size of seedlings between experiments due to the difficulties of managing the large numbers required. Seedlings used range in age between 108 and 155 days from sowing in the experiments described. During the experimental period, both before and after root-pruning, the plants were maintained in an artificially-lit growth cabinet (Type LB) where the temperature of the ambient air and the rooting medium could be controlled separately. Some seedlings were maintained so that the soil temperature followed the air temperature.

At the beginning of the experimental period the seedlings to be root-pruned were removed from the root-medium, the roots carefully extended and pruned at a specified length from the cotyledon, usually 21 cm. All white roots were removed using forceps while the residual root system was kept moist. The seedlings were replanted as quickly as possible into a 1 : 1 perlite : vermiculite mixture before being replaced into the treatment conditions. An equal number of seedlings were left undisturbed until the final harvest. At the end of the observation period all the root systems were washed clean and the number and length of new white roots present were recorded.

Photosynthesis was measured using a Grubb-Parsons Model SB infra-red gas analyser (IRGA). The gas circuit was an open system with air drawn in from the roof of the building, stirred in a large drum then drawn off and divided into two streams, one for reference, one for the assimilation chamber. The flow rate of the gas stream through the chamber was regulated by a "Flostat" regulator at rates of 10-12 1/min, checked by using "Gapmeter" flowmeters. Air returning from the assimilation chamber was passed through a water bath at room temperature and a small portion of the air flowed to the IRGA as the sample air. Both reference and sample air were dried in $CaCl_2$ columns before entering the IRGA. The IRGA was calibrated to measure the CO_2 differential against a background of 200 p.p.m. CO_2 in nitrogen. The assimilation chamber was made of clear perspex (30 × 28 × 50 cm outside dimensions) and situated inside an artificially-lit LB growth cabinet. Illuminance of 635-835 $\mu E\ m^{-2}sec^{-1}$ was obtained from the lamps in the cabinet, fluorescent supplemented by incandescent. A 20 cm portion of the shoot only was carefully sealed into the chamber for the purposes of photosynthesis determinations. The shoot was maintained at the required ambient temperature by adjusting the temperature controller of the

LB cabinet. Fresh seedlings were involved with each measure as photosynthesis was calculated at mgCO_2 per gram needle dry weight per hour. Air was introduced near the top of the assimilation chamber and exhausted near the base. Adequate stirring of the air by a fan minimised air and water vapour gradients and ensured temperature uniformity, monitored by Cu-Con thermocouples connected to a recorder. The required soil temperature was maintained during the measured period by wrapping the seedling container in towels soaked with water at the required temperature and placing the whole in an 18 cm polyfoam pot positioned beneath the assimilation chamber.

Seedlings were fed $^{14}CO_2$ in a closed system where each received 5 μCi of aqueous sodium [^{14}C] carbonate (specific activity 1.0 mCi/mmol or 5.0 mCi/mmol). The $^{14}CO_2$ was generated by heating the sodium carbonate and a few mls of 88% lactic acid in a generating flask, the $^{14}CO_2$ was then pumped into the assimilation chamber at the rate of four litres per minute for ten minutes. Plant parts to be assayed were oven-dried and weighed, ground in aWiley mill, and one sample from each seedling component assayed following the method of O'Brien and Wardlaw (1961). Radioactivity was measured for a five minute period per sample with a Tracerlab-Omni/Guard Scaler, Model SC 520 M and corrections were made for background.

Leaf water potential was measured with a pressure bomb in the manner described by Scholander *et al.* (1965), Pierpoint (1967), and Waring and Cleary (1967). Measurements were made on single needle fascicles selected at mid-height of randomly chosen seedlings. Six determinations were made at each measurement time. Leaf potential was measured on intact seedlings and then at 1, 2, 5, 8, 16 and 20 days after root-pruning. The response of stomatal resistance (aperature) to root-pruning over time was measured with a ventilated diffusion porometer (Turner and Parlange, 1970; Waggoner and Turner, 1971). Determinations were made on intact seedlings and 1, 2, 5, 8, 12, 16 and 20 days after root-pruning. Estimations of the volumes of the needle portions used were made using a volumetric cylinder and needle area was determined by the method of Wood (1971).

Two sets of observations were carried out. In the first the observations were made at the end of a three-week period following root-pruning during which intact and root-pruned seedlings were maintained at various ambient air/root temperature combinations in a growth cabinet. The effects of these combinations on root regeneration was, in part, the subject of an earlier paper (Stupendick and Shepherd, in press). In addition, two intact and eight root-pruned seedlings were maintained in the cabinets at each ambient air temperature regime so that root temperature followed the air temperature very closely during the sixteen hour day, eight hour night. Photosynthesis measurements took place at the day air temperature but, as noted earlier, the roots were kept at the prescribed temperature.

The second set of observations were made on seedlings at intervals over a thirty-two day period, from immediately prior to root-pruning until the end of the period. These seedlings were grown at 21°/16°C day/night and maintained throughout in a glasshouse under this regime. Soil temperature was not controlled separately but followed the air temperature within an hour. Rates of photosynthesis and dark respiration were measured for three seedlings from each treatment group, on the days stipulated in the results, during the period 1100 to 1400 hours, and at least one to one and a half hours

after watering. Following measurement of photosynthesis at 21°C the seedlings were transferred to a darkened cabinet and subsequently dark respiration was measured at 16°C.

RESULTS

Photosynthesis, Water Relations, and Growth

Net photosynthesis was observed in the first instance on plants which had either been root-pruned or left intact three weeks earlier and maintained for that period under stipulated air-soil temperature regimes (Table 1). Clearly the root-pruning operation had in some way impaired the photosynthetic efficiency of the seedlings as the intact plants, in general, maintained a higher rate of photosynthesis than root-pruned seedlings. Of the four exceptions, three were in the highest day temperature regime, 30°C/20°C, and all were from relatively high air-soil temperature combinations. In each instance the difference between the two readings was slight and in agreement with a general trend for all the higher temperature combinations to have high readings for root-pruned seedlings relative to intact seedlings.

TABLE 1—The value in mg CO_2 per gram needle dry-matter for net photosynthesis of intact (0) and root-pruned (P) seedlings after three weeks at various air and soil temperature combinations. The values are the means of two replicates

Soil temperature regime (°C)	Ambient air temperature day/night (°C)							
	15/5		20/10		25/15		30/20	
	0	P	0	P	0	P	0	P
5	4.6	3.2						
10	7.8	4.6	9.2	7.3	7.6	3.1		
15/ 5 (i)	10.8	6.8						
15/ 5 (ii)	10.7	5.3						
15	12.8	6.8	7.1	5.5	9.7	3.5	8.7	9.7
20/10			9.5	6.1				
20 (i)	9.3	6.9	11.2	9.5	10.0	3.5	7.1	7.5
20 (ii)					9.5	6.9		
25/15					10.3	3.7		
25 (i)			13.8	11.1	10.9	3.9	9.7	7.2
(ii)					6.2	6.5	7.7	4.5
30/20							9.6	7.3
30 (i)					5.9	5.0	9.0	6.3
(ii)							9.3	7.7
35					7.3	5.3	7.4	7.6
40							5.8	4.5

(i) and (ii) are repeat experiments at the same temperatures.

Photosynthetic rates for intact seedlings were high at a daytime air temperature of 25°C and at 20°C air when the soil was 25°C or 20°C. At 15°C air there was a trend to reduced photosynthesis as soil temperature decreased from 15° to 10° to 5°C. Similarly at high air temperatures photosynthesis declined as the soil temperature rose from 30° to 35° to 40°C. Only at these extremes of the range of temperature combinations tested was there any clear indication for much reduced photosynthesis in intact

plants, and the root-pruned seedlings tended to follow the intact seedlings in this respect. Root regeneration (length and weight) had been observed to follow much the same pattern (Stupendick and Shepherd, in press), and was favoured most at temperature combinations within the range of 20° to 30° and not favoured at the extremes of the combinations tested.

At the higher temperature combinations the rate of photosynthesis of root-pruned seedlings was frequently comparable with that of intact seedlings from the same treatment. This suggests these seedlings had tended to regain lost photosynthetic capacity more quickly than was so at lower temperature combinations. This hypothesis is supported by a similar result obtained in our laboratory with root-pruned seedlings of *Pinus caribaea* Morelet (Abod, Shepherd and Bachelard, 1979).

The second series of observations was designed to throw some light on the time sequence of events leading to this discrepancy between photosynthesis of intact and of root-pruned seedlings three weeks after the roots were removed. The air temperature regime employed, 21°C day/16°C night, had been found favourable for root regeneration in a number of earlier trials. The results for net photosynthesis are shown in Fig. 1 and compared statistically between day zero and days eight and 32, and between day eight and 32 (Table 2). The first two of these comparisons are on a total needle dry weight basis, whereas the third is on the basis of green needle material only (see Fig. 1). A proportion of the needle material died due to desiccation following root-pruning and these adjusted photosynthesis values exclude this dead material.

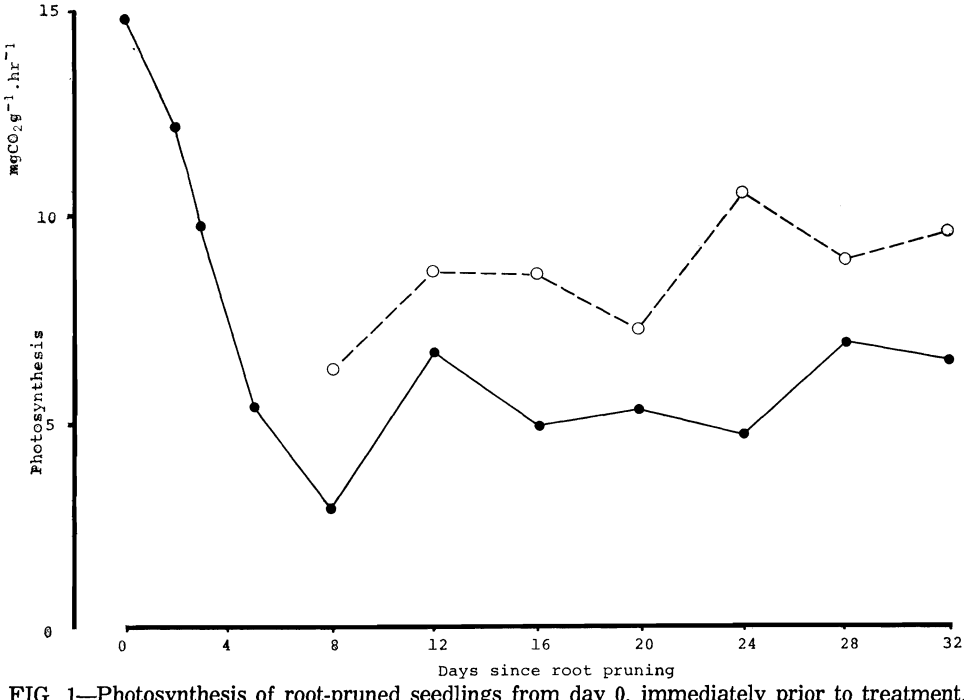

FIG. 1—Photosynthesis of root-pruned seedlings from day 0, immediately prior to treatment, to day 32. The solid line is pphotosynthesis based on the dry weight of all needles as at day 0, the dotted line isadjusted photosynthesis where the needle material which died due to desiccation following root-pruning has been excluded. Each point is the mean for three seedlings.

TABLE 2—The value in mg CO_2 per gram needle dry matter per hour for net photosynthesis of seedlings measured over a 32-day period following root-pruning. The seedlings were held at 21°/16°C day/night for shoot and root. Values are the means of three replicates expressed on a basis of all needles (1 and 2) and green needles (3). Bracketed values represent the number of days after root-pruning at which measurements were taken. '0' represents intact seedling immediately prior to root-pruning. Values underlined are not significantly different (P = 0.05)

Measurement period	Photosynthesis (day of measure)										
1. Day 0 to Day 8	2.9 (8)			5.4 (5)		9.7 (2)		12.3 (1)		14.8 (0)	
2. Day 0 to Day 32	2.9 (8)	4.7 (24)	5.0 (16)	5.3 (20)	5.4 (5)	6.4 (32)	6.7 (12)	6.9 (28)	9.7 (2))	12.3 (1)	14.8 (0)
3. Day 8 to Day 32	6.3 (8)			7.2 (20)	8.6 (16)		8.6 (12)	8.9 (28)	9.6 (32)		10.5 (24)

There was a sharp decline in photosynthetic values during the first few days following root-pruning which was reversed after the eighth day, followed by a very gradual recovery over the remaining 24 days of observations. Thirty-two days after root-pruning the photosynthetic rate had recovered from a low of about 20-45% of the original rate. Dark respiration did not change markedly, it rose slightly immediately after root-pruning then slowly declined to a steady level after eight days.

Concurrent movements in observed values for stomatal resistance and leaf water potential (Fig. 2) suggest that photosynthesis was severely restricted during the eight days following root-pruning through stomatal closure induced by water deficit. Leaf water potential declined dramatically up to the fifth day after root-pruning but by the eighth day had returned to a point comparable with the initial value. Stomatal resistance rose rapidly and continued to rise to the eighth day but declined during the next four days. However, stomatal resistance remained at a value higher than the initial rate from the twelfth to the twentieth day, when the observations were discontinued. These observations are in considerable agreement with those of Bacon and Bachelard (1978) on *P. caribaea* seedlings. A further study of their results also suggests the increased stomatal resistance observed in the present work on *P. radiata* at 20 days after root-pruning could most likely be sustained and thus constitute part of the hardening process leading to maintenance of good water relations in root-wrenched seedlings after lifting and field planting (Rook, 1969).

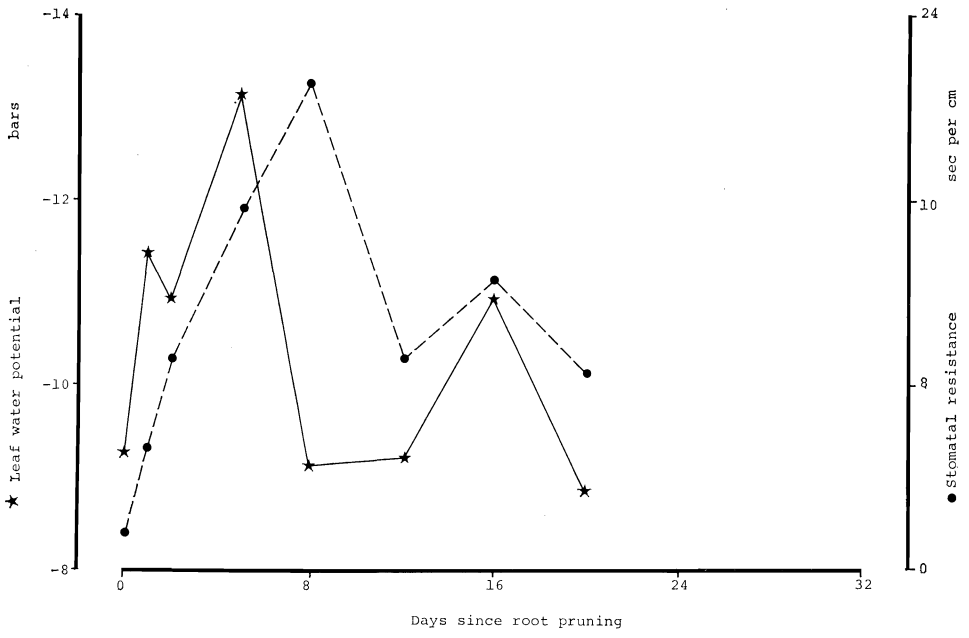

FIG. 2—Observed values for stomatal resistance (.) and leaf water potential (*) of root-pruned seedlings from day 0, immediately prior to treatment, to day 20. Each point is the mean for ten replicates for stomatal resistance and six for leaf water potental.

Root regeneration and height increment of these seedlings are given in Table 3 for the 32-day observation period. Height growth almost ceased during the first eight days following root-pruning but then resumed, and continued at a fairly steady rate of about 0.25 cm per day until the end of the observations. There was little regeneration of new roots at the eighth day although, on average 38 new roots per plant had been formed and one of these was more than 1.5 cm long. The dry weight of these roots was, however, very low. It was not until the sixteenth to the twentieth day that root extension and active growth increased markedly. Most of our earlier observations on root regeneration were made at 21 days as it had been found the new root system proliferated very rapidly after this time and observations became very time consuming. By the thirty-second day in this trial the seedlings, on average, had almost 900 new roots with a mean length of just on 2 cm.

Translocation of Photosynthate

The effects of various air and soil temperatures on the translocation of ^{14}C-labelled photosynthates in both intact and root-pruned seedlings from the first series of observations are given in Table 4. Here the proportion of the ^{14}C-label translocated to the root is given as a percentage of the total in the seedling. The shoot of each seedling was exposed to $^{14}CO_2$ immediately after root-pruning and repotting and prior to the replacement of containers into the various temperature treatment conditions. Statistical comparisons were possible between means for intact seedlings within experiments,

TABLE 3—Root regeneration and shoot growth of seedlings grown at 21°C/16°C day/night for shoot and roots and observed over a 32-day period following root-pruning. Bracketed values represent the number of days after root pruning. Values underlined are not significantly different ($P > 0.05$). Values for day 8, 16, 24 and 32 are the means for eight replicates, other values are means of four replicates

Parameter	Root regeneration and shoot growth — Days subsequent to root-pruning (bracketed)						
Number of new roots > 0.1 cm	38 (8)	100 (12)	114 (16)	254 (20)	506 (28)	700 (24)	888 (32)
Number of new roots > 1.5 cm	1 (8)	2 (12)	14 (16)	123 (20)	155 (28)	233 (24)	410 (32)
Length of new roots > 0.1 cm	21 (8)	55 (12)	91 (16)	450 (20)	877 (28)	1069 (24)	1832 (32)
Average length of roots > 0.1 cm	0.52 (8)	0.59 (12)	0.59 (16)	1.45 (20)	1.47 (24)	1.78 (28)	1.99 (32)
Dry weight of new roots mg	6 (8)	16 (12)	30 (16)	127 (20)	337 (28)	363 (24)	716 (32)
Height increment cm	0.25 (8)	2.01 (16)	2.10 (12)	3.28 (20)	4.09 (24)	4.62 (32)	5.22 (28)

and similarly for root-pruned seedlings, but not for comparisons between intact and root-pruned seedlings, or between experiments, because of the nature of the experimental procedures. Substantial plant to plant variation in readings of ^{14}C-label was evident in both root-pruned and intact seedlings but, nevertheless, some interesting trends are apparent in these data.

In the intact seedlings about 25-35% ^{14}C-labelled photosynthate was found in the root system after three weeks under the various temperature combinations tested. The only apparent difference in these figures is for a higher proportion of labelled material to be translocated to the roots under the lowest air temperature regime of 15°C day/5°C night. This result may well reflect the natural seasonal pattern for autumn in *P .radiata* nurseries when stock tend to cease height growth and to produce proportionately more root material (Benson and Shepherd, 1977). Within this day/night temperature regime there is an indication of less translocation to the roots at lower soil temperatures, just as 10° and 15°C soil temperatures appear less favourable at higher air temperature regimes. At these higher temperature regimes more translocation took place when the soil temperature was at or above 20°C for all or part of 24 hours.

In the root-pruned seedlings far less translocation to the roots of ^{14}C-labelled photosynthate has taken place over the 21 days than is apparent for intact seedlings. There

TABLE 4—Effects of various air and soil temperature combinations on the distribution of ^{14}C-photosynthate to the root system of intact (I) and root-pruned (P) seedlings three weeks after both ^{14}C-labelling and root-pruning. Bracketed values indicate soil temperatures in °C, (A) is where soil temperature followed closely the air temperature. Values underlined are not significantly different ($P > 0.05$), intact seedlings the mean of two, root-pruned the mean of three replicates

Day/night air temperature °C	Expt.	% Total ^{14}C photosynthate in roots — Soil temp. °C (bracketed)									
		Intact					Root-pruned				
15/5	1		29.9 (10)	34.0 (A)	39.0 (15)			20.7 (A)	22.3 (10)	25.4 (15)	
15/5	2		32.6 (5)	41.6 (20)				10.1 (5)	21.3 (20)		
20/10	3		20.0 (10)	24.7 (15)	27.0 (A)			7.7 (10)	12.2 (A)	18.0 (15)	
20/10	4		29.2 (25)	34.2 (20)				16.9 (20)	21.9 (25)		
25/15	5	20.7 (10)	21.8 (15)	24.4 (A)	26.1 (20)	28.2 (25)	6.0 (10)	8.1 (15)	10.1 (A)	11.7 (25)	12.5 (20)
25/15	6	16.0 (20)	25.9 (25)	26.8 (30)	27.7 (35)		8.8 (25)	10.5 (20)	14.7 (35)	14.9 (30)	
30/20	7	25.6 (30)	27.5 (20)	28.3 (A)	31.0 (15)	34.1 (25)	11.4 (15)	11.7 (A)	12.1 (20)	12.3 (30)	16.0 (25)

is less indication in these data for an increased proportion of the labelled photosynthate to be translocated at the lowest air temperature regime of 15°/5° although there is still the indication of reduced translocation at the lowest soil temperatures.

In the experiments, root-pruned seedlings have translocated a lower proportion of ^{14}C-labelled photosynthate to the roots than intact seedlings over a 21-day period during which photosynthesis markedly declined for about eight days and then only slowly returned to about 45% of the original rate. Intact seedlings maintained the original high level of photosynthesis and translocated maintained the original high level of photosynthesis and translocated 25-35% of ^{14}C assimilate to the roots. These plants suffered no physiological disruption, being maintained undisturbed in the container and in the same environmental conditions. In a study of nursery stock of *P. caribaea* followed transplanting Bacon and Bachelard (1978) found that root-wrenched plants, particularly those treated weekly, translocated a greater proportion of ^{14}C assimilate to the roots over a short period (seven days) than untreated nursery stock.

The root-wrenched plants also possessed a greater capacity for survival, shoot extension, and root regeneration and growth than unwrenched controls. There is then an apparent transformation in the physiological capability of a root-wrenched seedling during the period in the nursery bed from the day of initial wrenching to the day of lifting.

CONCLUSION

In summary, we suggest the physiological processes involved in the production of hardened root-wrenched nursery stock possessing a mass of fibrous roots are as follows. When the root system is first severed the plant suffers from water stress for some days resulting in stomatal closure and a reduction in photosynthesis, accompanied by reduced translocation to the root system. The plant gradually regains turgor and leaf water potential returns to normal levels; in the present experiments this took from 8 to 12 days under near-ideal conditions of controlled environment with abundant soil moisture. Photosynthesis gradually strengthens, accompanied by a massive proliferation of the root system. This active metabolic activity in the root system acts as a preferential sink, channelling assimilates to that part of the plant as the root regeneration process gathers momentum (Rook, 1971; Wardlaw, 1976). Stomatal resistance in the needles remains higher than in unwrenched seedlings and this enhanced level of stomatal resistance is retained, especially if the nursery bed wrenching treatment is repeated, for example at weekly intervals as reported in Bacon and Bachlard (1978). On lifting, the root-wrenched seedling is able to maintain a more favourable water status through a high stomatal resistance and a high root-soil surface contact area. The active and relatively large root system attracts adequate assimiltes to enable rapid contact with soil moisture and nutrient reserves to maintain the plant, ensure survival and rapid early growth (Bacon and Hawkins, 1977; Benson and Shepherd, 1977; Rook, 1969). The process of readjustment by the seedling in the nursery bed is favoured by soil temperature above 15°C and in most instances root regeneration and restoration of photosynthetic capacity appears to be favoured by similar air and soil temperatures within the 20° to 30°C range.

The wide adoption of root-wrenching techniques in nursery practice will be governed by the circumstances of plantation establishment. The simple techniques for producing open-root nursery stock of *P. radiata,* as practiced in much of Australia for many years, is adequate where field planting conditions are not severe. But in many parts of S.E. Australia the winters are quite cold with frequent frosts and consequently low soil temperatures. Short periods of drought following planting are not uncommon. Under these circumstances the use of root-wrenched nursery stock which is adequately hardened and possesses an ample fibrous root system is likely to result in better establishment. This possibility assumes greater importance where expensive site preparation and fertiliser practices are adopted to provide conditions conducive to rapid growth of an established seedling.

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REFERENCES

ABOD, S. A., SHEPHERD, K. R. and BACHELARD, E. P. 1979: Effects of light intensity, air and soil temperatures on root regeneration potential of **P. caribaea** var. **hondurensis** and **P. kesiya** seedlings. **Aust. For. Res. 9**: 173-84.

BACON, G. J. and BACHELARD, E. P. 1978: The influence of nursery conditioning treatments on some physiological responses of recently transplanted seedlings of **Pinus caribaea** Mor. var. **hondurensis** B & G. **Aust. For. Res. 8**: 171-83.

BACON, G. J. and HAWKINS, P. G. 1977: Studies on the establishment of open root caribbean pine planting stock in southern Queensland. **Aust. For. 40**: 173-91.

BENSON, A. D. and SHEPHERD, K. R. 1977: Effect of nursery practice on **Pinus radiata** seedling characteristics and field performances. II. Nursery root wrenching. **N.Z. J. For. Sci. 7**: 68-76.

MORSE, R. N. and EVANS, L. T. 1962: Design and development of CERES — an Australian phytotron. **J. Agric. Eng. Res. 7**: 128-40.

O'BRIEN, T. P. and WARDLAW, I. F. 1961: The direct assay of ^{14}C in dried plant materials. **Aust. J. Biol. Sci. 14**: 361-7.

PIERPOINT, G. 1967: Direct measurement of internal moisture deficits in trees. **For. Chron. 43**: 145-8.

ROOK, D. A. 1969: Water relations of wrenched and unwrenched **Pinus radiata** seedlings on being transplanted into conditions of water stress. **N.Z. J. For. 14**: 50-8.

——— 1971: Effect of undercutting and wrenching on growth of **Pinus radiata** D.Don seedlings. **J. Appl. Ecol. 8**: 477-90.

SCHOLANDER, P. F., HAMMEL, H. T., BRADSTREET, E. D. and HEMMINGSEN, E. A. 1965: Sap pressure in vascular plants. **Science 148**: 339-46.

STUPENDICK, J-A. T. and SHEPHERD, K. R.: Root regeneration of root-pruned **Pinus radiata** seedlings. 1. Effects of air and soil temperature. **Aust. For. 42(3)**: (in press).

TURNER, N. C. and PARLANGE, J-Y. 1970: Analysis of operation and calibration of a ventilated diffusion porometer. **Plant Physiol. 46**: 175-7.

VAN DORSSER, J. C. and ROOK, D. A. 1972: Conditioning of radiata pine seedlings by undercutting and wrenching: description of methods, equipment, and seedling response. **N.Z. J. For. 171**: 61-73.

WAGGONER, P. E. and TURNER, N. C. 1971: Transpiration and its control by stomata in the pine forest. **Bull. Conn. Agric. Expt. Sta. 726**: 1-87.

WARDLAW, I. F. 1976: Assimilate partitioning: cause and effect. P381-91 **In** Wardlaw, I. F. and Passioura, J. D. (eds.). Transport and transfer processes in plants. Academic Press, New York, 484p.

WARING, R. H. and CLEARY, B. D. 1967: Plant moisture stress: evaluation by pressure bomb. **Science 155**: 1248-54.

WOOD, G. B. 1971: Shape of **Pinus radiata** fascicles and the implications for estimating needle surface area. **Aust. For. Res. 5**: 31-6.