

ROOT CONFIGURATION AND ROOT REGENERATION IN *PINUS RADIATA* SEEDLINGS

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ABSTRACT

Root configuration of radiata pine (*Pinus radiata* D. Don) seedlings in the nursery was examined in relation to nutrient supply, and the configuration of the regenerated root system after transplanting was examined in relation to seedling treatment and soil temperature.

In the nursery an increase in shoot growth owing to high soil fertility was not accompanied by a similar response in root growth, resulting in a high shoot-root ratio. High soil fertility decreased mycorrhizas. Nitrogen and phosphorus deficiencies reduced the weights of the shoot and root but had little effect on root configuration. Changes in root weight can lead to faulty conclusions about root development. Even when nitrogen deficiency was extreme the root system possessed a remarkable ability to adjust the number and length of first and second order laterals, and so lessen the effect of stress on configuration. Similar, but lesser, effects were found under phosphorus deficiency. This ability may be important for the survival of seedlings in naturally regenerating forests. A decrease in the mean extension rate of root members seems to be the major reason for the reduction in root length in nutrient starved plants.

The configuration of roots regenerated after transplanting is closely related to the initial configuration of the planting stock, the number and length of the first order laterals capable of regeneration being the most critical basic framework for the new root network. However, the number of first order laterals appears to be not amenable to manipulation by nursery management practices.

Radiata pine seedlings developed strategies to cope partly with the effects of nutrient deficiency or low temperature on root configuration.

INTRODUCTION

The root systems form a network of filaments ramifying through the soil and the configuration they assume affects the paths of nutrient and water transfer from soil to root (Barley, 1970). Root configuration, particularly development of mycorrhizas, and the nutrient reserves in the seed are important factors governing the nutrient supply to tree seedlings in naturally regenerating forests in infertile soils (Barrow, 1977). In contrast to this, nursery seedlings are generally supplied with luxury amounts of nutrients and water and the dimensions of their root system may not be critical for their growth while in the nursery. However, it is well recognised that the size, form, and the physiological condition of the seedling root system can have a strong

influence on the survival and early growth of seedlings transplanted to many field environments.

The root growth of seedlings is influenced by several environmental factors such as temperature, light, and day-length (Barney, 1951; Cremer, 1968; Stahel, 1972), and in particular by soil factors such as temperature (Bowen, 1970; Heningen and White, 1974), bulk density (Sands and Bowen, 1978), and water content.

One of the main aims of conditioning the planting stock by root wrenching and other management practices is to lower the shoot-root ratio and also to alter the form of the root system (Rook, 1971; Bacon and Bachelard, 1978). Root regeneration, after wrenching or transplanting, is also greatly influenced by several factors such as light, air, and soil temperature, and soil water (Stone, 1967; Stone and Jenkinson, 1970; Abod *et al.*, 1979; Stupendick and Shepherd, 1979; Nambiar *et al.*, 1979). The configuration of the seedling root system developed while they are in the nursery would determine the size and form of the roots transplanted. The ability to grow new roots after transplanting has been considered as a measure of planting stock quality (Stone, 1967; Bacon and Bachelard, 1978; Burdett, 1979). The seedling physiological condition, particularly those influencing new root growth, drought or cold-hardiness, and dormancy, may also be critical in determining the performance of out-planted stock (Sutton, 1979).

Bowen *et al.* (1974) showed that the configuration of wheat root system was strongly influenced by phosphorus nutrition. Barrow (1977) suggested that the phosphorus supply had no great effect on the proportion of plants present as roots of seedlings of a number of tree species.

This paper examines the influence of nursery nutrition on the root configuration of radiata pine (*Pinus radiata* D. Don) seedlings and discusses how the root configuration of the planting stock is related to the configuration of the new root system developed after transplanting.

The constituent parts and principle geometric features are described according to Barley (1970) and followed in studies on wheat (Bowen *et al.*, 1974) and on radiata pine (Sands and Bowen, 1978; Nambiar *et al.*, 1979). For some days after germination, the pine seedling root system consists of an unbranched tap root (main axis), and as growth proceeds primordia develop on its pericycle and give rise to first order laterals (1°L), which in turn produce second order laterals (2°L) and so on.

EFFECT OF NUTRIENT SUPPLY ON THE SHOOT AND ROOT GROWTH OF RADIATA PINE SEEDLINGS

Effect of Nursery Fertility on the Shoot and Root Growth

Radiata pine seedlings were grown at Mount Gambier (South Australia) on a light textured sandy soil in a long-term fertility experiment. The high fertility seedlings referred to in Table 1 were from plots which had received annual applications of ammonium sulphate, superphosphate and potassium sulphate at the rates of 848, 436, and 108 kg ha⁻¹ respectively, before and during the year in which the seedlings used here were grown. The low fertility seedlings were from plots which received no fertiliser during the same period. Seed (open pollinated seed from seed orchard clone No. 50048 (Australian Plus Tree Register)) was sown in September 1976 and 1977 and the seedlings were sampled in August of the following year. In 1977 the seedlings

were lifted by inserting two spades vertically, 10 cm on either side of the seedling row and to a depth of 20 cm and lifting the block of soil and root. In the following year spade cuts were made at an angle so that the cutting ends met below the plant. The 1978 lifting procedure is comparable with field practice, but the volume of soil-root lifted was less than in the 1977 lifting. The shoots were harvested and the root system was carefully washed for measurement. The root lengths were measured either directly or by intercept counting (Tennant, 1975). Twelve seedlings were examined in each treatment, 3 seedlings for each of 4 replications.

The shoot and root characteristics of approximately 10-month-old seedlings are given in Table 1. The higher soil fertility increased the height and weight of the shoot as well as the weight of the root and to a less extent the root length. However, high fertility nearly doubled the shoot-root ratio. Furthermore, despite a two-fold increase in the shoot weight of seedlings grown under high fertility there was no significant increase in the number and total length of 1°L roots, but the length of 2° and 3°Ls increased nearly four-fold. The contribution of the tap root to the root weight was disproportionate to its contribution to root length particularly when fertility was high. There was a considerable decrease in the numbers of mycorrhizas on the roots of seedlings from high fertility plots.

The concentration of nutrients in the needles was similar in both years. In 1977, N and P (%) was 1.11 ± 0.03 (SE) and 0.167 ± 0.004 in low fertility seedlings, and 1.66 ± 0.07 and 0.200 ± 0.019 in high fertility seedlings.

Effect of Nutrient Supply on Root Development

The results from the above experiment stimulated interest to study the effect of individual nutrients on the growth of roots, and in particular to examine the configuration of roots developed under a specific nutrient stress, and under controlled conditions.

Radiata pine seedlings were grown, using seed from the same source as in the previous experiment, in wooden boxes (30 cm long, 10 cm wide, and 40 cm deep) with perspex plate fronts. Boxes were lined with polyethylene bags and filled with a white siliceous sand (A₂ horizon of Mount Burr sand complex) at a bulk density of 1.3 g cm⁻³.

All boxes received basal nutrient solutions to supply the following amounts of salts (mg per pot): K₂SO₄: 200; MgSO₄·7H₂O: 50; MnSO₄·4H₂O: 25; ZnSO₄·7H₂O: 25; CuSO₄·5H₂O: 25; Na₂BO₄: 1; Na₂MoO₄·2H₂O: 1; CoCl₂·6H₂O: 0.5; FeCl₃: 20; and CaSO₄·2H₂O: 300. The three nutritional treatments were: complete nutrients, nitrogen deficient, and phosphorus deficient. Complete treatments received 500 mg N per pot as NH₄NO₃ applied in five instalments during the experiment and 250 mg P per pot as KH₂PO₄ applied initially. The nitrogen deficient treatment received no N but the same amount of P, and the phosphorus deficient treatment received no P but the same amount of N, as in the complete nutrient treatment. There was one seedling per box. Plants were grown in a glasshouse from January (summer) to September (spring). Air temperature in the glasshouse was partly controlled and ranged between 28°C (mean maximum) and 15°C (mean minimum) during the first 13 weeks, 23 and 10°C during 13 to 20 weeks, and 19 and 7°C during 20 to 36 weeks. During the experiment the sand was watered to 12% (w/w) (equivalent to —10 kPa mean matric potential) as required, without allowing the water content to fall below 7%.

TABLE 1—Shoot and root characteristics of 10-month-old radiata pine seedlings grown under contrasting soil fertilities in the nursery

Time of Sampling	Soil Fertility level	Shoot Height (cm)	Collar Diam. (cm)	Dry weight (g/Plant)				Number and length (cm) of root members/Plant					
				Shoot	Root	Tap root	Shoot/Root	Tap root (cm)	All roots (cm)	1°L (number)	1°L (cm)	2°+3°L (cm)	Forked† (number)
August 1977	Low	22.8 *(0.59)	0.40 (0.01)	2.06 (0.16)	0.78 (0.06)	0.33 (0.02)	2.64	20.2 (1.4)	509.0 (32.5)	35 (1.9)	—	—	—
	High	41.4 (1.14)	0.54 (0.03)	6.10 (0.65)	1.20 (0.10)	0.62 (0.07)	5.08	20.9 (1.3)	723.6 (57.4)	31 (2.5)	—	—	—
August 1978	Low	26.0 (10.0)	0.42 (0.01)	2.76 (0.26)	0.82 (0.06)	0.31 (0.02)	3.37	18.2 (0.7)	318.0 (26.0)	26 (1.9)	218.5 (14.4)	79.4 (21.2)	217 (21)
	High	36.4 (1.5)	0.52 (0.02)	5.29 (0.39)	1.02 (0.09)	0.50 (0.06)	5.19	18.3 (1.8)	560.4 (49.9)	31 (3.0)	241.7 (20.1)	307.0 (47.2)	20 (5)

† Mycorrhizal forked apices.

* ± S.E. of mean of 12 seedlings.

Seedlings were harvested at 13, 20, and 36 weeks after sowing and intact root systems were obtained by dismantling the boxes and carefully washing the roots free of sand. The level of detail measured on the root system varied with each sampling, the most detailed being at the final harvest. Roots were not mycorrhizal throughout.

In N and in P deficient treatments, decreased growth of shoots was seen at 10 weeks after planting. At 13 weeks deficiency was severe, and the weight of shoot in nutrient deficient treatments was less than half of that in the complete nutrient treatment.

Allometric relationships between shoot and root (not presented) showed that the shoot-root distribution was strongly influenced by nutrition. The nitrogen or phosphate deficient plants had allocated relatively more photosynthate for root growth than had those under complete nutrition. For example, at 13, 20, and 36 weeks, root weight as a percentage of total plant weight was 28.0, 32.2, and 32.8 for complete nutrients, 31.9, 44.7, and 46.4, for N deficient, and 38.5, 46.4, and 50.6, respectively for P deficient plants.

Despite the large reduction in shoot and root weight due to N deficiency, the root length of N deficient plants was remarkably similar to that of complete nutrient plants (Table 2). Concentration of N (%) in the roots was 1.71 ± 0.11 (SE) and 1.18 ± 0.11 for complete nutrients and N deficient plants respectively. Although P deficiency reduced the root length, this effect was far less than that on shoot height and weight. Nutrient deficiency also reduced the mean diameter of the lateral roots. The preferential allocation of photosynthate to the root when plants are under nutritional stress and the remarkable ability of seedlings to sustain the total length of root are clearly seen.

TABLE 2—Shoot and root characteristics of 20-week-old radiata pine in relation to nutrition

Nutrient treatments	Shoot height (cm)	Collar diameter (mm)	Shoot Dry Wt. (g)	Root Dry Wt. (g)	Root length (cm)	Lateral† root diam. (mm)
Complete Nutrients	19.9 *(0.25)	2.68 (0.20)	1.22 (0.24)	0.56 (0.07)	405.7 (73.7)	0.96 (0.06)
N-Deficient	14.3 (1.82)	1.67 (0.23)	0.37 (0.09)	0.28 (0.05)	399.9 (48.5)	0.79 (0.06)
P-Deficient	11.6 (0.90)	1.78 (0.15)	0.30 (0.05)	0.21 (0.05)	299.5 (64.4)	0.63 (0.05)

* \pm S.E. of mean of 4 replications.

† Mean of 25-30 one-cm segments collected at random.

The effect of nutrition on root configuration was examined in more detail at 36 weeks and the main features are presented in Table 3. Severe N deficiency caused a 10-fold reduction in shoot weight, but only 4.5-fold reduction in root weight. By this time, in contrast to the 20-week sampling, nitrogen deficiency had resulted in a significant reduction in the number of root apices and root length. Nevertheless the magnitude of the effect on the number and length of root members was far less than that on shoot height and weight. Also, nitrogen deficient plants had considerably longer tap roots and more 1°Ls, but the same length of 1°Ls compared to complete nutrient

TABLE 3—Shoot characters and root configuration of 36-week-old radiata pine in relation to nutrition

Nutrient Treatment	Shoot Characters/Plant			Root Characters/Plant						
	Height (cm)	Dry Wt. (g)	Collar Diam. (mm)	Dry Wt. (g)	Total length (cm)	Apices 1°-5°L (number)	Tap Root length (cm)	1°L Longer than 1 mm		
								(number)	Length (cm)	Diameter (mm)
Complete Nutrients	45.9 *(0.60)	15.29 (1.06)	7.2 (0.31)	7.40 (0.36)	4837 (311)	3416 (381)	59.1 (8.4)	57.0 (12.9)	981.0 (112.6)	1.51 (0.06)
N-Deficient	20.9 (0.58)	1.55 (0.13)	2.8 (0.22)	1.63 (0.22)	1586 (188)	1613 (345)	102.6 (23.7)	89.0 (11.6)	993.0 (86.9)	0.91 (0.03)
P-Deficient	15.1 (0.74)	0.88 (0.99)	2.5 (0.13)	0.87 (0.08)	733 (80)	653 (28)	55.2 (9.5)	68.2 (8.2)	440.5 (61.5)	1.04 (0.03)

* ± S.E. of mean of 5 replication.

plants. The effect of acute P deficiency on root configuration was more severe, but it is worth noting that P deficiency caused no reduction in the number and only a 2.2-fold reduction in the length of 1°Ls, compared to a 17-fold reduction in shoot weight. This striking adjustment in the growth of the root system in nutrient-starved plants, particularly the initiation and growth of 1°Ls, seems to be achieved, at least in part, by growing laterals considerably thinner than those under complete nutrition.

The distribution of root apices (>1mm) on different root members and the frequency of 1° and 2°Ls are given in Table 4. Nitrogen deficiency, despite being severe, did not affect the initiation of 1° and 2°Ls, but did affect the number of 3° and 4°Ls. The greater number of 1°Ls on N-deficient plants compared to other treatments should be seen in relation to length of tap roots (Table 3). Severe P deficiency resulted in a decrease in the number of all laterals except 1°Ls. However, the nutrient deficiencies had little effect on the frequency of 1° and 2°Ls on their respective higher order root members. While the frequencies of 1° and 2°Ls were similar in complete and N-deficient treatments, in P-deficient treatments the frequency of 2°Ls appears to be considerably lower than that of 1°Ls.

TABLE 4—Distribution of root members on the root network of 36-week-old radiata pine

Root member	Nutrient treatments		
	Complete Nutrients	N-Deficient Number/Root System	P-Deficient
1°L	57 *(8)	89 (11)	68 (8)
2°L	1088 (89)	1089 (251)	395 (28)
3°L	2042 (284)	423 (95)	159 (17)
4°L†	225 (74)	10	23
	Mean Frequency		
1°L cm ⁻¹ Tap Root	1.01 (0.13)	0.96 (0.12)	1.34 (0.24)
2°L cm ⁻¹ 1°L	1.15 (0.16)	1.09 (0.12)	0.95 (0.12)

* ± S.E. of mean of 5 replicates.

† Only 2-3 replicates produced 4°Ls in N- and P-deficient treatments.

The number and length of the 1°Ls and the number of 2°, 3°, and 4°Ls in the basal 20 cm segment of the main axis (tap root) of seedlings grown under complete nutrition and under N deficiency are given in Table 5. The pattern of root growth in this zone will largely determine the configuration of the planting stock. In both treatments, the number and length of the 1°Ls and the number of other laterals declined rapidly along the main axis. Although the N deficiency did not affect the number of 1°Ls, the total length of 1°Ls was reduced so that the mean length of 1°Ls in the 0-10 cm section was 26.4 cm in complete nutrient plants compared to 14.4 cm in N-deficient plants. In complete nutrient plants the difference in the number of 1°Ls between the two depths was relatively small, but the difference became greater with the successive orders of root member.

TABLE 5—Number and length of root apices on the basal part of the main axis of 36-week-old radiata pine

Treatments	Distance from the Collar (cm)	1°L Length (cm)	Root Apices (Number/Plant)			
			1°L	2°L	3°L	4°L
Complete Nutrients	0-10	480.6 *(63.3)	18.0 (2.9)	605 (46.9)	1558 (252.7)	190 (74.6)
	10-20	232.6 (51.6)	12.0 (3.0)	240 (56.7)	345 (117.4)	51 (25.0)
N-Deficient	0-10	316.0 (56.6)	22.0 (1.1)	389 (69.4)	171 (43.7)	Nil
	10-20	156.9 (50.5)	13.0 (3.0)	180 (67.4)	62 (29.6)	Nil

* \pm S.E. of mean of 5 replications.

In field practice the amount of root "lifted" and carried with the seedlings would be considerably less than that shown in Table 5, since the lateral roots are normally pruned at about 10 cm radial to the plant row during lifting. I have found that seedlings transplanted to the field generally have 15-18 cm tap root and 400-500 cm lateral root of which the 1°Ls may account for about 200 cm, and the remainder largely by 2°Ls. The length of individual 1°Ls may range widely from 2 to 20 cm. Third order laterals are generally negligible on seedlings grown at usual plant densities.

EFFECT OF SEEDLING TREATMENT AND SOIL TEMPERATURE ON NEW ROOT GROWTH

So far the effect of nutrition on the configuration of seedlings in the nursery has been considered. When seedlings are lifted and transplanted, most of the roots are mutilated and the length of root transferred is unlikely to exceed 25% of the original. Considerable damage to the root can also occur while handling the planting stock during lifting, transporting and planting out, the apices of the second and subsequent order laterals being most susceptible. The ability of the transplants to produce adequate amounts of new root is critical for their survival and establishment.

Nambiar *et al.* (1979) have described in detail the patterns of new root growth in transplanted pines in relation to soil temperature. It was found that the initiation and elongation of new roots are severely restricted at 5°C soil temperature, increased significantly at 10°C, and dramatically increased between 10 and 15°C. It was also concluded that, in southern Australia, the low soil temperature in the winter planting season restricts early root regeneration and causes water stress in out-planted seedlings. Some of the results which are related to the present discussion are given here, mainly to highlight the relationship between the configuration of the initial root system and that of the newly grown root.

Table 6 shows the distribution of new root on the root networks of radiata pine seedlings after transplanting. Seedlings were raised in the nursery from polycross orchard seeds, and were 8 months old and dormant at transplanting. Seedling

TABLE 6—Number and length of new roots and their distribution on radiata pine seedling root system after transplanting, in relation to seedling treatment and soil temperature

Root members	Soil temperature at which roots regenerated for 55 days					
	10°C			20°C		
	Normal	Normal + Nutrients	Root Wrenched	Normal	Normal + Nutrients	Root Wrenched
New apices > 5 mm (Number/Plant)						
1°L	3 (0.9)*	4 (1.9)	10 (1.3)	7 (1.3)	5 (1.3)	7 (1.6)
2°L	12 (1.7)	30 (10.1)	25 (8.1)	134 (12.4)	131 (18.9)	45 (9.1)
3°L	3 (0.8)	14 (5.8)	10 (5.1)	15 (7.7)	22 (10.6)	36 (14.7)
4°L	—	—	—	—	14†	—
Length of new apices > 5 mm (cm/Plant)						
1°L	15.1 (5.6)	26.7 (12.9)	55.1 (8.5)	179.2 (32.2)	125.1 (39.6)	205.5 (57.9)
2°L	16.7 (3.8)	50.1 (22.7)	55.4 (14.5)	1130.0 (101.8)	1004.2 (154.7)	370.3 (51.9)
3°L	2.3 (0.8)	14.4 (6.0)	12.7 (7.2)	115.1 (23.5)	344.0 (77.2)	99.3 (20.4)
4°L	—	—	—	—	38.3†	—

* ± S.E. of mean of 6 replications.

Data from E. K. S. Nambiar, G. D. Bowen and R. Sands (unpubl.);

† Only 3 replications produced 4°Ls.

Nambiar, Bowen and Sands (1979)

treatments referred to are normal seedlings transplanted to unfertilised soil (Normal), normal seedlings transplanted to soil fertilised with nitrogen and phosphorus (Normal + Nutrients), and seedlings which were conditioned by root wrenching and transplanted to unfertilised soil (Root wrenched). Seedlings were transplanted into pots filled with infertile sandy forest soil and the pots were kept in water baths maintained at 10 or 20°C. Other details of this experiment have been described elsewhere (Nambiar *et al.*, 1979). Regardless of seedling treatment and soil temperature, a great majority of the new roots were present either as 1°Ls (directly on the tap root) or as 2°Ls (on 1°Ls). Together (1° + 2°Ls) they accounted for 77 and 63% of the new apices and 89 and 85% of new root lengths at 10 and 20°C respectively. Although the mean length of root members decreased successively from 1°L to 3°L (e.g., from 26.7 to 2.9 cm at 20°C), the 2°L were the major constituent of the regenerating root system. Both the supply of nutrients and root wrenching stimulated new root production at the lower temperature.

As Nambiar *et al.* (1979) pointed out radiata pine seem to adopt distinctly different strategies for producing new roots in response to soil temperature (Table 7). At 20°C the weight of individual new roots was less than half of that at 10°C. At warmer soil temperatures rapid elongation of 1°Ls to form a framework and the production of 2° and 3°Ls on them is a major regeneration strategy but at low temperature where regeneration of 1°Ls is decreased, the production of 2°Ls on the existing 1°Ls at a greater frequency seems to be the strategy. The diameters of the apical region of the 1°Ls were not significantly affected by soil temperature, but the diameters of 2°Ls were. This is important considering the importance of 2°Ls in achieving the full development of new root system, because depending on soil temperature, 2°Ls may produce 1.4 to 2.1 times the length g^{-1} root compared to 1°Ls.

TABLE 7—Strategy for new root growth in radiata pine seedlings transplanted to different soil temperatures

Soil Temperature (°C)	New 1°L				New 2°L			
	Dry Weight (mg cm^{-1})	Apices > 5 mm (number)	Mean Length (cm)	Diam. (mm)	Frequency on Old 1°L (cm^{-1})	New 1°L	Mean Length (cm)	Diam. (mm)
10	1.12	5.7	5.7	1.51	1.65	5.3	1.8	0.93
20	0.46	6.3	26.7	1.39	0.30	0.9	5.9	0.67

(From Nambiar *et al.*, 1979)

GENERAL DISCUSSION

Configuration of the Root System Developed under Nutrient Stress

The results from the nursery experiment with radiata pine showed that when seedling nutrition is manipulated in the nursery a large shoot growth response was accompanied by only a relatively small response in the root system, particularly in relation to the root configuration—number, distribution, and length of different root members. Consequently, high fertility in the nursery can lead to an undesirably high

shoot-root ratio in seedlings. The use of root weight as a criterion for evaluating changes in root development can be misleading, for the tap root may account for nearly 50% of the root weight, but only 3-6% of the root length (Table 1). Similarly, even a 2-fold difference in root weight may not be accompanied by a significant difference in root length (Table 2). Bowen *et al.* (1974) also had shown that simple root weight to length conversion can result in erroneous conclusions regarding root development in phosphate deficient wheat plants. The observation that high soil fertility decreased mycorrhizas has practical implications because the rates of fertilisers used in the experiment were comparable to those recommended for local nurseries. Mycorrhizas can be considered as an extension of the root network and their abundance on seedlings grown under low fertility would have compensated to a large extent for the difference in total length of root filaments.

Despite the large difference in the environment there was a remarkable uniformity in the spacing of 1°Ls (6 to 8 mm) on the roots grown in the field and in the glasshouse (Tables 1 and 3). Thus the frequency of 1°Ls on the basal 20 cm of the main axis (tap root) was independent of soil nutrient supply and was 1.58 cm^{-1} in the nursery plants and 1.55 cm^{-1} in the glasshouse plants. The mean frequency across the entire length of the main axis was less than that at the basal part and ranged from 0.96 to 1.34 cm^{-1} . These values compared well with the value of 1.10 cm^{-1} reported by Sands and Bowen (1978) in a similar soil and at a comparable bulk density of 1.35 g cm^{-3} . No clear pattern was found in the distribution of 1°Ls below the basal 20 cm on the main axis. The distance from the youngest 1°L to the tip of the main root apex varied considerably between replicates and was not consistently affected by the treatments in the two sampling times. In general the distance of the youngest 1°L from the apex of the main axis was 4.9 and 8.5 cm at 20 and 36 weeks respectively.

In 3-week-old seedlings, soil temperature within the range of 11 to 25°C increased the initiation and elongation of the 1°Ls (Bowen, 1970), but in 8-month-old seedlings transplanted to a similar range of temperatures the number of 1°Ls was not affected by soil temperature even after 55 days (Nambiar *et al.*, 1979). Other observations show that seedling conditioning techniques such as root wrenching do not influence the number of 1°Ls, even though wrenching increases the production of 2°Ls considerably (Rook, 1971; Nambiar, unpubl.). It is interesting to note that Sands and Bowen (1978) found that a decrease in soil bulk density from 1.48 to 1.38 g cm^{-3} decreased the frequency of 1°Ls from 1.45 to 1.11 cm^{-1} , but doubled the frequency of 2°Ls from 0.82 to 1.65 cm^{-1} . One of the main effects of most root pruning techniques, wrenching in particular, is to loosen the surface soil. It is not uncommon to find a relatively compact surface soil layer in heavy textured nurseries and it is likely that wrenching increases 2°Ls production and produces a "fibrous root system" partly by lowering the bulk density of the surface soil. It would also appear that mechanical stress has a greater influence on lateral root production than nutrition has.

Localised external supply of nitrogen and phosphorus are known to induce a strictly localised stimulation in root growth in barley (Drew, 1975) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.) (Philipson and Coutts, 1977) even though nitrogen and phosphorus are readily translocated internally from one part of the root system to another. It remains to be seen whether the initiation and extension of 1°Ls on the

main root axis of tree seedlings can be manipulated in this way. If so, it may have practical value.

In general, it would appear that the number of 1°Ls on the basal part of the tap root on the radiata pine seedling is surprisingly constant and is not readily amenable to manipulation. This has important practical implications because 1°Ls, as discussed later, provide the most important framework for the new root production after transplanting and are important for mycorrhizal production. Furthermore, in field practice only 20-45% of the 1°Ls regenerate new roots after transplanting even under the relatively moderate environment of southern Australia.

Results from both field and controlled experiments show that nutrient deficiencies, unless severe, had considerably less effect on root configuration than on shoot growth. The root system, even when low in nutrient concentration, seems to be capable of adjusting the configuration so that detrimental effects on root length are avoided or lessened (Tables 2 and 3). The nutrient-starved plants studied here would have been short of assimilates at least from the 9th week after planting, when the height of N and P deficient plants was found to be significantly less than normal plants. Healthy plants produced 53% more shoot dry weight than deficient plants after 13 weeks, and 72% more after 20 weeks. Nevertheless the ability of the nutrient-starved pine seedlings to make the best use of the very limited assimilate allotted to the root, to produce the most effective root system (configuration) is clearly seen.

As the assimilate supply worsens further, the elongation of root members would suffer. Thus the mean extension rate, MER (May *et al.*, 1965) between 20 and 36 weeks for all root apices was 0.23, 0.10, and 0.07 mm root⁻¹ day⁻¹ for complete nutrients, N deficient, and P deficient plants respectively. MER of the 1°Ls which were more than 5 cm long was 1.7, 1.8, and 1.2 mm root⁻¹ day⁻¹. The MER of all apices observed for pine seedlings here is about one-fifth of that reported by May *et al.* (1965) for barley seedlings, but MER of the 1°Ls (> 5 cm) found here is similar to that reported for the same root order (referred to as "secondary" roots by the authors) in barley. Nitrogen deficiency did not seem to affect the MER of 1°Ls, but decreased the overall MER of the root system. The lower MER of P-deficient roots and the fact that they had significantly more 1°Ls shorter than 5 cm (56% of the total 1°Ls compared to 38% in complete nutrient plants) would explain why the effect of P deficiency on root length was more detrimental than N deficiency. The nutrient deficiencies had surprisingly little effect on the frequency of root members and the net decrease in the number of any order of root seems to be related to the decrease in length of the preceding order. For example, when the length of 1°Ls was unaffected by N deficiency the number of 2°Ls also remained unaffected. Thus, the decrease in total root length resulting from nutrient deficiency seems to be due largely to the slower root elongation rather than the decrease in root initiation. Production of lateral roots which are up to 65% thinner is an obvious strategy to maintain the root configuration when plants are nutritionally stressed.

The importance of maintaining an adequate internal concentration of nutrients to sustain root elongation is not clear. The youngest member of the root system was found to have the highest nutrient concentration. The N % in the tap root, 1°L, and the remaining laterals of complete nutrient plants was 0.39 ± 0.01 (SE), 0.86 ± 0.05 , and

1.37 \pm 0.06 respectively compared to 0.42 \pm 0.04, 0.67 \pm 0.05, and 0.94 \pm 0.06 in N deficient plants. Evidently, even when N deficiency was extreme, the N concentration in higher order laterals was twice that in the tap root. Similar trends were found with phosphorus. It was also found that when the supply of nutrients was restored, nutrient deficient roots readily reassumed higher growth rate (data not presented) demonstrating the remarkable plasticity of the root system (Coutts and Philipson, 1977).

It will be valuable to know the effect of nutrient deficiencies on the seedling root configuration of plant species in naturally regenerating vegetation and forests, for the plant's ability to sustain an adequate root length to explore more soil may be critical for survival in infertile and drought-prone soils.

Root Configuration and Root Regeneration

The effects of soil temperature on the regeneration of roots in several species of tree seedlings have been studied by a number of workers (Stone and Schubert, 1959; Stone *et al.*, 1962; Stupendick and Shepherd, 1976; Abod *et al.*, 1979; Nambiar *et al.*, 1979). These studies show the critical importance of soil temperature for the regeneration of roots, either under conditions simulating root wrenching or lifting and transplanting in the field. The critical temperature below which root regeneration is restricted is different among species. For example, in *Pinus radiata* the critical temperature may lie between 11 and 14°C, new root growth being prolific at 15°C (Nambiar *et al.*, 1979), whereas in tropical pines (*Pinus caribaea* Morelet and *Pinus kesiya* Royle ex Gard.) negligible root regeneration occurs at a soil temperature of 15°C and below (Abod *et al.*, 1979).

The results presented here highlight two important aspects. Firstly, they show the importance of 1°Ls in determining the configuration of a regenerating root system either by extending themselves or by being the necessary framework for the initiation of 2°Ls, regardless of seedling treatment and temperature. Secondly, even in root wrenched seedlings, which at transplanting had more than twice the 2°Ls than normal plants (Nambiar, unpubl.), new root growth was essentially made up of 1° and 2°Ls. Evidently the presence of large numbers of second and subsequent order laterals may not be major contributors to new root lengths, but may be important for the absorption of water by seedlings immediately after transplanting. Root wrenched seedlings had a greater proportion of 1°Ls capable of regeneration (Nambiar *et al.*, 1979) and regenerated more new roots after transplanting (Bacon and Bachelard, 1978; Nambiar *et al.*, 1979). This is likely to be due to the plants' ability to avoid plant water stress during the critical post-planting period (Bacon and Bachelard, 1978; Nambiar *et al.*, 1979). As in the case of roots under nutritional stress, pine seedling root systems seem to develop strategies to cope with the effect of soil temperature on root regeneration. There is a close inter-relationship between the constituent parts of the root system.

As understanding of the factors that govern the development of the seedling root system in the nursery phase, and the relationship between the root configuration of the planting stock and root regeneration during the critical post-planting period, is essential for the production of planting stock of maximum quality.

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