SEASONAL CHANGES IN LIVE AND DEAD FINE ROOTS DURING TWO SUCCESSIVE YEARS IN A THINNED PLANTATION OF PINUS RADIATA IN NEW ZEALAND

D. SANTANTONIO* and E. SANTANTONIO*
Ministry of Forestry, Forest Research Institute,
Private Bag, Rotorua, New Zealand

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ABSTRACT

Previous studies in a 12-year-old plantation of **Pinus radiata** D. Don characterised seasonal changes in standing crops of fine (< 1 mm diam.) and small roots (1–2 mm diam.) in the thinned and control treatments. In the present study, standing crops of these roots were estimated from soil core samples for a second year to determine if the seasonal periodicity observed in the first year could be considered a general pattern. Results from Year 2 generally confirmed those from Year 1. With the exception of differences in late-winter/early-spring, standing crops of live fine roots indicated similar seasonal changes by treatment in the 2 years. Comparing the effect of treatment, we found no summer peak in the thinned treatment for either year. The over-all standing crop of live fine roots in the thinned treatment was 35% of the control. The seasonal periodicity of dead fine roots in the control was similar for both years, but in the thinned treatment, we found large differences by year. The over-all standing crop of dead fine roots was only 8% lower in the thinned treatment. Standing crops of small live roots did not change seasonally. The over-all standing crop of small live roots was lower in the thinned treatment but increased from Year 1 to Year 2. This increase may indicate an expansion of the networking system to which fine roots are attached. No similar expansion, however, was detected for fine roots in the thinned treatment.

Keywords: roots; periodicity; biomass; growth; mortality; herbivores; thinning; **Pinus radiata**.

INTRODUCTION

Biologically based models of tree growth are a useful, and necessary, tool to integrate understanding and explore relations among fundamental physiological processes underlying production at the whole-plant and stand level (Landsberg & McMurtrie 1985; Rook *et al.* 1985; Landsberg 1986). An important practical objective of such models is predicting the effects of site conditions and silvicultural practices on the amount, distribution, and quality of dry matter produced. From a theoretical point of view, these efforts also seek to define maximum potential production and factors that limit it.

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* Current address: Swedish University of Agricultural Sciences, Department of Ecology and Environmental Research, P.O. Box 7072, S-750 07, Uppsala, Sweden.

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Estimates of fine root production in boreal and temperate forests vary widely. Fine-root production has been estimated at between 1 and 12 Mg/ha/yr in boreal and temperate forests (Fogel 1985; Gholz *et al.* 1986; Santantonio in press). These estimates as a percentage of total net primary production (TNPP) range from 5% in a 12-yr-old plantation of *Pinus radiata* on a fertile site in New Zealand (Santantonio & Santantonio 1987) to 68% in a natural stand of 180-yr-old *Abies amabilis* (Loudon) Forbes in Washington, United States (Grier *et al.* 1981). The wide range in these estimates indicates greater variation in dry-matter partitioning to fine roots than to other tree components (Cannell 1985; Santantonio in press). Fine roots are an important component of forest production, and an essential component of a biological growth model.

Little, however, is kown about the mechanisms that control growth and development of fine roots in forests (Lyr & Hoffmann 1967; Hermann 1977; Bowen 1985; Fogel 1985; Santantonio & Hermann 1985; Coutts 1987). Less is known about how silvicultural practices influence these mechanisms and the extent to which these practices may be used to shift the distribution of dry-matter production to favour another component, such as stem wood.

Santantonio & Santantonio (1987) characterised monthly changes in standing crops of fine and small roots at Puruki during 1984–85. Thinning in 1983 significantly affected the standing crops and seasonal periodicity of live fine roots, but not dead fine roots. These data, along with information on fine-root decomposition and soil temperature, were used in a model (Santantonio & Grace 1987) to estimate fine-root production and mortality monthly. Results indicated that both processes could be generally represented as smooth, coincident, modal curves rising to highest values in late-winter/early-spring, and falling to lowest values in summer for the control and thinned treatments. Annual estimates of fine-root production were 2.2 and 1.9 Mg/ha/yr, respectively, and accounted for 4.6 and 6.1% of total net primary production. Thinning on this fertile site appeared to have only a small effect on dry-matter partitioning and production of fine roots on an area basis. Whether the observed periodicity and magnitude of fine-root growth and mortality could be considered a general pattern remained an open question.

The purpose of this study was to determine whether estimates of standing crops from a second year of sampling (1985–86) would confirm results of the previous year. Confirmation would enable us to generalise fine-root growth, and attempt to model effects of thinning on the distribution of total dry-matter production at the present stage of stand development.

STUDY SITE

Puruki (38° 26′ S, 176° 13′ E) is a former pasture site 30 km south of Rotorua in the Purukohukohu Experimental Basin on the central volcanic plateau of the North Island, New Zealand. In 1973 the site was planted in *P. radiata* at 2200 stems/ha (1.8 m × 2.4 m spacing). The present study took place during 1984–86 in two sub-catchments – Tahi (5.9 ha) and Rua (8.7 ha). At the first closure of the canopy in 1979–80, branches of trees were removed to a height of 2.2 m before the stands were thinned to a nominal stocking of 550 stems/ha. By mid-1983 the canopy had closed again. During August and September 1983, Tahi was thinned to a nominal stocking of 140 stems/ha. This removed 60% of the basal area and generally left crowns of individual trees open on all sides. Re-establishment of understorey vegetation in the study plots was prevented by occasional spot applications of herbicide and weeding by hand. Rua remained at 550 stems/ha and served as the "control" or closed canopy treatment.

Former pasture sites on the volcanic plateau are the most productive sites currently planted in *P. radiata* in New Zealand (West *et al.* 1982; Beets & Pollock 1987). Soils were fine sandy loams of yellow-brown pumice, deep, well-drained, and with thick black A horizons. Their nutrient status was very favourable for pine growth. Results of foliar analyses and guidelines developed by Will (1985) indicated slight to moderate deficiencies for only magnesium and boron. Climatic conditions were also very favourable. Mean monthly temperatures of soil and air varied between 6° and 16°C (Fig. 1); rainfall was abundant and fairly evenly distributed throughout the year (Fig. 2). Site index was 34 m at 20 years according to equations of Burkhart & Tennent (1977). Stand characteristics of the study plots have been outlined in Table 1.

METHODS

The methods used to sample and extract fine roots were identical for both years (Santantonio & Santantonio 1987). Intact soil cores, 5 cm diameter, were extracted to a depth of 30 cm with a steel tubular device. Eight core samples were taken from each of two plots in each treatment (16 samples per month per treatment) by a randomised-block design from a sampling grid, 24 × 24 m, in the centre of each 36 × 36-m plot. Samples were taken every other month from May 1985 through March 1986. An additional sample was taken in October 1986 to confirm large changes in standing crops at this time in Year 1 (May 1984 through April 1985). Intact soil cores were cut into segments, 0–10 and 10–20 cm from the surface of the mineral soil, and kept in cold storage (2°C) until processed, a maximum of 7 days.

Processing of these samples consisted of two phases, the first to extract intact roots and the second to extract dead-root fragments (Santantonio & Santantonio 1987). In the first phase, live roots and larger dead roots were removed with forceps by starting at one end and carefully working through the nearly intact segment. These roots were cleaned and sorted by diameter size, species, and live *v.* dead, based on visual and mechanical criteria. Live roots consisted entirely of pine roots; the infrequent and extremely small contributions of herbaceous roots and fern rhizomes were not included. While live pine roots were being cleaned, the numbers of new mycorrhizal tips were counted as a means of assessing fine-root activity independently of changes in standing crop. After removal of all live roots, the soil from each sample was dried at 40°C in a forced-air oven. The second phase involved sieving and separating with a modified seed blower to extract organic material from the dry mineral soil. A combination of segregating techniques was used to separate dead roots from other organic fragments. All roots were dried to a constant weight in a forced-air oven at 70°C. These weights were recorded to the nearest 0.01 g and expressed as megagrams per hectare (Mg/ha = t/ha). Ash content of the samples, bulked to combine replicates and depths, was estimated as the weight remaining after ignition at 430°C for 24 h (Davies 1974). Fine roots (< 1 mm diameter) included mycorrhizal host and fungal mantle tissues.

The statistical analysis of the data followed that used for data from the first year (Santantonio & Santantonio 1987; Santantonio & Hermann 1985). Statistical tests were performed only on the categories of roots (type and diameter size) and segments of soil core samples where initial assumptions of parametric analyses were met. This determination was based on tests for normal distribution and homogeneity of variance of an intensive sample (n = 52) taken during the prethinning assessment in September

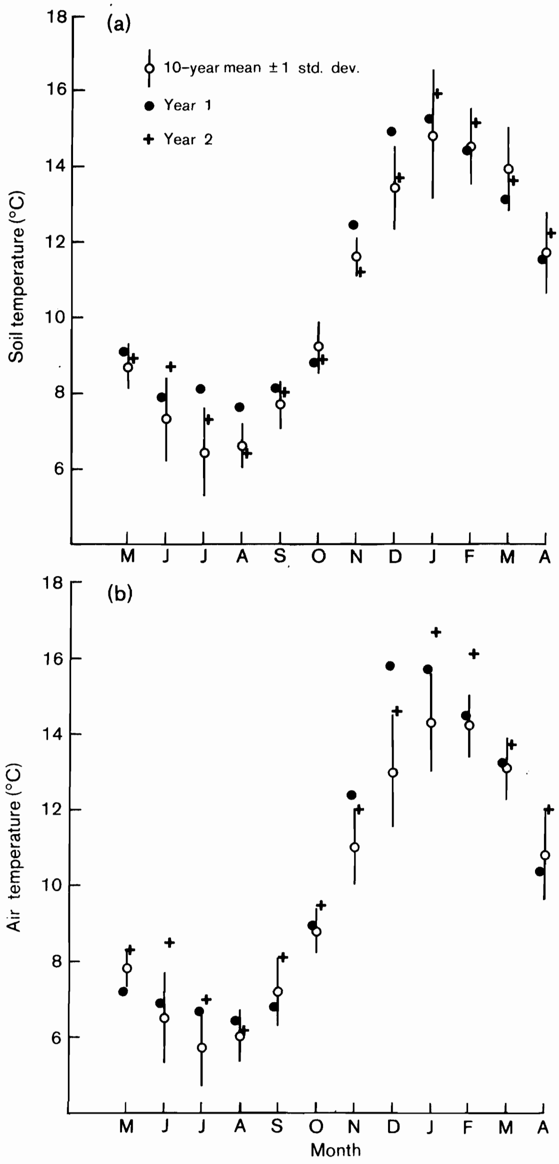

FIG. 1—Mean monthly temperature of soil at 10 cm depth (a) and air at 2 m above the canopy (b) measured on site in the Rua subcatchment. Values for Year 1 (May 1984 - April 1985) and Year 2 (May 1985 - April 1986) have been compared with the 10-yr mean (1976–85).

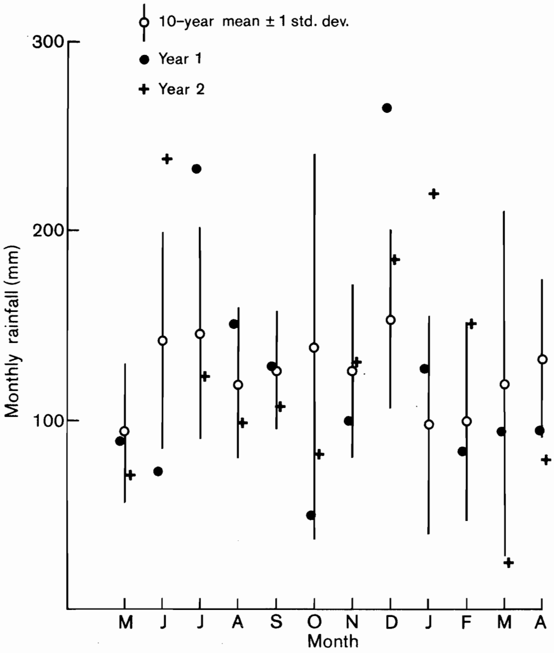

FIG. 2—Monthly rainfall measured on site in the Rua subcatchment. Values for Year 1 (May 1984 - April 1985) and Year 2 (May 1985 - April 1986) have been compared with the 10-yr mean (1976–85).

TABLE 1—Stand characteristics on 31 July 1985. Values are means of data from two 0.13-ha plots within each treatment.

Characteristic	Control	Thinned
Age (yr)	13	13
Stocking (stems/ha)	567	166
Number of stems in plot	74	22
Basal area (m^2/ha)	40.5	18.1
Diameter at breast height (cm)	29.9	36.6
Height of dominants (m)	19.6	19.2
Leaf area (all sides) (m^2/m^2)	20	13
Above-ground biomass (Mg/ha)	168	76

1983 (Santantonio & Santantonio 1987). A square-root transformation of data was required to satisfy the assumption of homogeneity of variance. A "repeated measures" analysis of variance for a nested randomised-block design (SAS Institute 1985, pp. 112 and 478) was conducted on the transformed data to determine whether changes in standing crops were significant. The Student-Newman-Kuels (SNK) test of means

(Sokal & Rohlf 1969, p. 239) was used to identify seasonally high and low monthly values of the transformed data. Student's t test was used to determine whether the mean standing crop in a given month differed from one year to the next. By pooling data on cores within plots and averaging across sample periods, we were able to develop statistically valid annual means for categories of roots and core segments which we were unable to test for monthly changes. These means of untransformed data constitute the best estimate of overall standing crops. Test results at the 95% confidence level have been accepted as statistically significant.

RESULTS

Standing crops of fine roots changed seasonally and were affected by thinning during Year 2. Repeated measures analysis of variance indicated significant interactions between treatment and date of sampling for live and dead roots < 1 mm diameter (Table 2). According to this analysis, differences in the seasonal periodicity of fine-root standing crops between treatments can be attributed to thinning. For live fine roots the main effects were also significant. Seasonal changes in standing crops of live and dead fine roots were generally limited to the 0–10 cm segment. The exception to this was a significant decline in the standing crop of dead fine roots from July to September in the 10–20 cm segment. Although this drop occurred in both treatments, no consistent seasonal periodicity was apparent in the data for this segment. Standing crops of small roots 1–2 mm in diameter did not change with date of sampling. Further analysis of seasonal periodicity was limited to fine roots in the 0–10 cm segment.

With the SNK test of means we identified seasonally high and low monthly estimates within Year 2. This *a posteriori* test confirmed effects of thinning on seasonal periodicity which were indicated by the repeated measures analysis of variance. The standing crop

TABLE 2—Results of F-tests in the repeated measures analysis of variance on transformed data. The F statistic and degree of freedom are given for each test. The distribution of the number of degrees of freedom reflects the nesting of the randomised block design.

Type and diameter (mm)	Segment† (cm)	Effect‡						
		T	P	S	D	TxD	PxD	SxD
Pine <1	0–10	46.6*	1.9	1.1	2.3*	3.6*	1.2	1.2
	10–20	44.7*	0.4	1.1	0.9	2.2	1.0	1.0
Pine 1–2	0–10	19.8*	1.9	0.6	1.9	1.6	0.8	1.2
Dead <1	0–10	3.5	2.4	2.6*	1.8	7.6**	0.5	1.1
	10–20	0.1	4.7*	1.3	2.8*	1.5	0.8	0.8
Degrees of freedom								
Numerator		1	2	12	5	5	10	60
Denominator		2	12	16	80	10	60	80

* Significant at 95% confidence level

** Significant at 99% confidence level

† Segments are core lengths; to convert to approximate soil depths multiply by 1.1

‡ T, treatment; P, plots within treatment; S, subplots within plot; D, date of sampling; TxD, PxD, and SxD are interactions with date of sampling

of live fine roots in the control peaked in January (summer) from a low in October (spring), but no peak could be detected by this test in the thinned treatment (Fig. 3). The appearance of new mycorrhizal root-tips paralleled changes in standing crop; in the control it ranged between 2 and 5 × $10^5/m^2$ and also peaked in January, while in the thinned treatment it remained unchanged at about 1 × $10^5/m^2$. The standing crop of dead fine roots in the control peaked in July (winter) and in November (spring), but in the thinned treatment there was no peak in spring (Fig. 4).

Student's t test of the difference in estimates from Years 1 and 2 indicated significant differences in seasonal periodicity during successive years. Standing crops

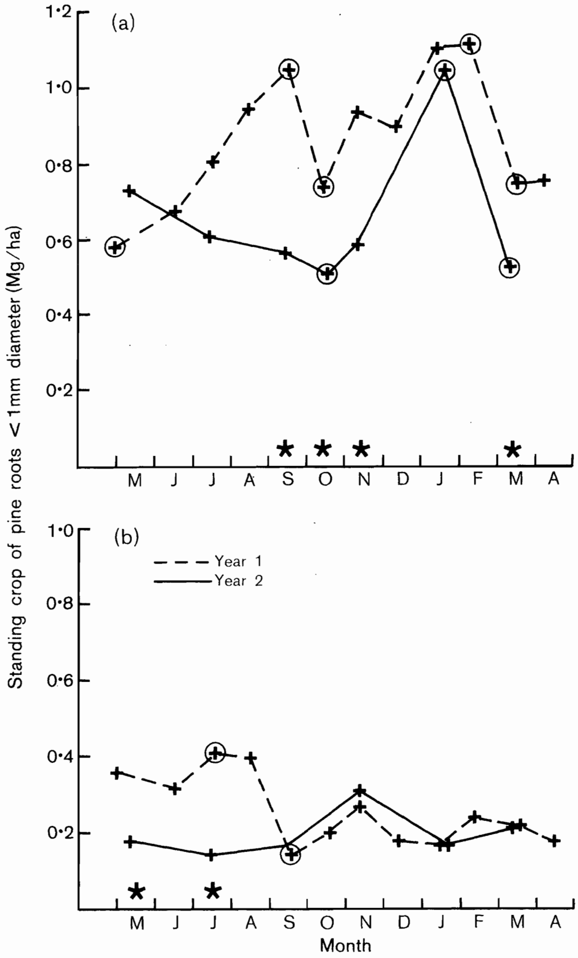

FIG. 3—Standing crop of live fine roots in the 0–10 cm segment for Year 1 (broken line) and Year 2 (solid line) in the control (a) and thinned (b) treatments. Statistically different high and low monthly values within each year as identified by SNK tests of transformed data have been circled. Months where estimates in Year 1 differ from Year 2, as determined by t tests, are indicated with an asterisk.

of live fine roots showed no late-winter/early-spring peak during the second year for either treatment (Fig. 3). Otherwise, the seasonal patterns were similar within treatments; the effect of thinning was consistent in the absence of a peak in summer during both years. Seasonal changes in standing crops of dead fine roots in the control were

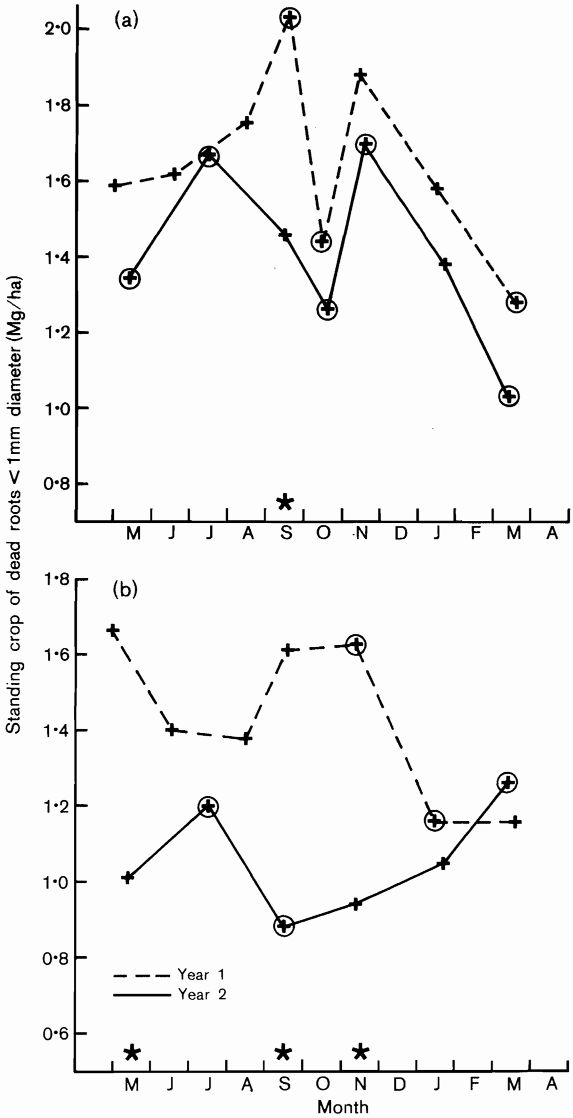

FIG. 4—Standing crops of dead fine roots in the 0–10 cm segment for Year 1 (broken line) and Year 2 (solid line) in the control (a) and thinned (b) treatments. Statistically different high and low monthly values within each year as identified by SNK tests of transformed data have been circled. Months where estimates in Year 1 differ from Year 2, as determined by t tests, are indicated with an asterisk.

similar during both years; estimates differed significantly only for September (Fig. 4). For dead fine roots in the thinned treatment, the seasonal periodicity changed in successive years; three of six estimates during Year 2 were statistically different (lower), and the seasonal pattern was nearly opposite that for Year 1. Standing crops of live and dead fine roots were generally lower during Year 2.

Differences in standing crops of live and dead fine roots during the late winter and spring of Year 2 coincided with dramatic changes in the physical appearance of pine roots. Samples taken during July through October showed extensive, apparently recent, damage to roots. This damage consisted of deep gouging along the surface, "chewed" nubs where clusters of root-tips would be expected, few new mycorrhizal root-tips, and loss of turgor. Damaged roots were found in all cores from both treatments, with nearly all roots showing some damage. Numbers of macrolarvae and damage to roots fell sharply in November. By January, pine roots were nearly back to normal with regard to vigorous appearance. Production of new mycorrhizal root-tips was extensive and peaked at this time in the control.

Comparisons of annual means by the t test indicated that overall standing crops of roots < 1 mm diameter were significantly lower during Year 2, while those of small roots 1–2 mm diameter generally remained unchanged (Table 3). The exception was small roots in the 0–10 cm segment of the thinned treatment; live ones increased 59% and dead ones decreased 35%. With regard to the effect of treatment, thinning reduced the over-all standing crop of pine roots < 1 mm diameter to 30% and 58% of the control for segments 0–10 cm and 10–20 cm, respectively. Thinning had a much smaller impact on the over-all standing crop of dead fine roots; it was 80% of the control in the 0–10 cm segment, and unchanged in the 10–20 cm segment.

Live fine roots were more evenly distributed within the treatments than dead fine roots during Year 2. Tests for the effects of plot and subplot were significant for pine roots only at confidence < 82% (Table 2). In contrast, results for dead fine roots indi-

TABLE 3—Comparison of over-all standing crops from Year 1 to Year 2 for live and dead roots in segments 0–10 and 10–20* cm by treatment; annual mean ± one standard error.

Type and diameter (mm)	Segment (cm)	Control			Thinned		
		Year 1 (kg/ha)	Year 2 (kg/ha)	Change†	Year 1 (kg/ha)	Year 2 (kg/ha)	Change
Pine <1	0–10	858 ± 36	656 ± 62	–	251 ± 18	198 ± 23	–
	10–20	245 ± 14	182 ± 16	–	144 ± 11	104 ± 13	–
Pine 1–2	0–10	217 ± 17	230 ± 22	0	71 ± 6	113 ± 14	+
	10–20	75 ± 5	80 ± 6	0	55 ± 5	54 ± 7	0
Dead <1	0–10	1636 ± 58	1405 ± 73	–	1377 ± 56	1057 ± 57	–
	10–20	1118 ± 42	985 ± 54	–	1193 ± 53	990 ± 73	–
Dead 1–2	0–10	73 ± 12	61 ± 7	0	82 ± 9	53 ± 7	–
	10–20	53 ± 6	63 ± 10	0	74 ± 6	71 ± 10	0

* Segments are core lengths from the surface of the mineral soil. To convert to approximate soil depths multiply by 1.1

† Changes in standing crop as indicated by t test of difference between means for Years 1 and 2 with the pooled error estimate at 95% confidence.

cated significant main effects of plot in the 10–20 cm segment and subplot in the 0–10 cm segment. No interactions of plot or subplot with date of sampling were significant. These results agree with repeated measures analysis of data from Year 1.

Mineral material remaining after ignition of roots < 1 mm diameter from the different sample periods varied little. Ash as a percentage of the dry weight was 12.4% ± 0.3% in the control and 14.6% ± 0.6% in the thinned treatment for pine roots. For dead roots it was 28.2% ± 0.6% and 29.4% ± 0.8%, respectively. These results agree with values from Year 1.

DISCUSSION

Results from Year 2 generally confirm those from Year 1. A major difference, however, appeared in the absence of a late-winter/early spring peak in the standing crop of live fine roots during Year 2. This occurred in both treatments. Another large difference appeared in the nearly opposite seasonal periodicity of dead fine roots in the thinned treatment. We do not know what caused these differences. Environmental conditions during both years were favourable for growth, and were generally in agreement with 10-yr averages of temperature and rainfall data measured on the site. Monthly observations and measurements of needle development and shoot growth indicated that growth above-ground was within 2 weeks of being in phase during the 2 years (unpubl. data). As far as we can tell, no unusual factors affected tree growth.

We can only speculate about what may have caused these differences in seasonal periodicity when climate and the growth of other tree components were similar. At least two possible explanations exist: the seasonal periodicities were, in fact, different for reasons which we were unable to discern within the context of our studies; or the seasonal periodicities were actually similar, but the effects of some other factor made them appear different. The simultaneous occurrence of high numbers of soil macrolarvae, extensive damage to roots, and low standing crops of fine roots during the period July to November has led us to consider that grazing on roots may account for the differences in seasonal periodicity and the decrease in the overall standing crops of live and dead fine roots. High numbers of larvae of species in the Bibionidae (marsh fly) and Tipulidae (crane fly) families of the Order Diptera were also found in these samples. These larvae were more numerous in the 0–10 cm segment than the 10–20 cm segment. As many as 14 macrolarvae were found in one 0–10 cm segment. On the average we found five macrolarvae in segments 0–20 cm, which would be about 13 per litre soil volume, or 2500 per square metre. However, we have no direct observations or data to prove that the damage we observed was the result of feeding on roots by larvae of Bibionidae and Tipulidae. Although these are large and diverse families with species living in a wide range of habitats, we have been unable to find information regarding their feeding behaviour in pine forests. Species of Tipulidae, at least, have been reported to damage roots of conifers (Oosterbroek 1984; Shrimpton 1985). Thus, the evidence we have is circumstantial; the presence of Diptera larvae may be only coincidental, but grazing on roots may be a possible explanation for the differences in seasonal periodicity we observed.

Extremely little information exists on which to evaluate the occurrence and importance of grazing on roots in forests (Fogel 1985). Studies by Ausmus *et al.* (1977) in a mesic hardwood stand dominated by *Liriodendron tulipifera* L. indicated that phytophagous nematodes and cicada larvae annually consumed 8.5% and 1.1% of the mean biomass of roots < 5 mm diameter, respectively, or about 720 kg/ha/yr. This amounts to 8% of root production < 5 mm diameter based on estimates of Harris *et al.* (1977). Magnusson & Sohlenius (1980) found root consumption by nematodes in a young stand of *Pinus sylvestris* L. in Sweden was much lower, about 4 kg/ha/yr or 0.3% of root production < 2 mm diameter. We made no attempt to estimate consumption by herbivores. If differences in standing crop from Year 1 to Year 2 are an indication of the amount of grazing that may have occurred, then consumption by herbivores could represent a significant loss of fine roots. It is clear that the potential impact of grazing on standing crops and production of fine roots deserves further investigation, and should not be dismissed as negligible.

Data on standing crops of fine roots during successive years have not been analysed to evaluate specific differences in seasonal periodicity from one year to the next in other studies. Good general agreement in seasonal standing crops of fine roots from one year to the next can be seen in data for *Liriodendron tulipifera* in Tennessee, United States (Harris *et al.* 1977), *Picea sitchensis* (Bong.) Carr. in Scotland (Alexander & Fairley 1983), and *Pinus elliottii* Engelm. in Florida, United States (Gholz *et al.* 1986). Obvious differences in seasonal periodicity can be seen in data for *Pinus sylvestris* in England (Roberts 1976) and *Pseudotsuga menziesii* (Mirb.) Franco in Oregon, United States (Fogel & Hunt 1983; Santantonio & Hermann 1985). In part, these differences reflected different levels of environmental stress in successive years. Direct effects of soil temperature and water explain many aspects of fine-root growth, but attempts to correlate changes in standing crop of fine roots with environmental conditions have yielded inconclusive results (Santantonio & Hermann 1985).

Standing crops of small roots 1–2 mm diameter did not change seasonally in either year, which probably reflects their different functional role from that of fine roots. They appear to be a longer-lasting component of the networking system to which fine roots are attached. The over-all increase in standing crop of these roots from Year 1 to Year 2 in the thinned treatment may be a response to expand the networking system of trees remaining after thinning. The decrease in the over-all standing crop of dead small roots in this treatment probably reflects lower mortality associated with such an expansion and less inter-tree competition.

Thinning resulted in lower standing crops of fine roots and a change in seasonal periodicity that carried through Year 2, the third year after thinning. In a study of the effects of thinning on fine and small roots of *Pinus sylvestris* in Finland, Kalela (1955) assessed standing crops from soil core samples taken in two plantations during the first and second years after thinning. Thinning resulted in lower standing crops, but only small differences in periodicity during the first year. By the end of the first growing season, however, standing crops of fine roots in the thinned treatments were equal to or greater than those in the control. Roots were sampled fewer times during the second year; standing crops were similar, though periodicities may have been a little different. The standing crop of small roots was also lower in the thinned treatment and did not change seasonally. Kalela ascribed the differences in fine-root periodicity to year-to-year differences in environmental conditions. This is what we would expect when the growing season is short and seasonal variation is severe as in Finland. We believe the high nutritional status and favourable soil water at Puruki may be the reasons why the thinned treatment has not quickly re-established the pre-thinning levels of fine-root standing crops as did the stands of Kalela.

In our report of results from Year 1, we used data on standing crops, fine-root decomposition, and soil temperature as inputs to a compartment-flow model (Santantonio & Grace 1987) to estimate monthly production and mortality of fine roots. These results showed that, although we found differences in the periodicity of standing crops, the periodicities of fine-root production and mortality were quite similar in both treatments. This was because changes in standing crop of dead fine roots were similar and had a more important effect than the smaller changes in live fine roots when run in the model. Annual estimates of fine-root production and mortality were only slightly lower for the thinned treatment. Thinning shortened the mean longevity of fine roots (calculated as the annual mean standing crop of live fine roots divided by the annual mortality times 12 months). Monthly fine-root production and mortality for Year 2 were not estimated with the model because we were unable to assume a negligible loss to grazing. The high amount of dead fine roots relative to live fine roots (Table 3), however, indicates that the mean longevity remained much lower in Year 2, regardless of possible effects of grazing on roots. Although smaller standing crops of live fine roots were maintained on the thinned site with little seasonal periodicity, these roots had a shorter mean longevity and this accounted for the similar estimates of fine-root production and mortality for Year 1. Thus, changes in standing crop alone may not adequately represent fine-root production and mortality. These processes, along with decomposition, occur simultaneously. So, it is possible for fine roots to be produced while others are dying and dead ones are decomposing. Responses to perturbation may variously affect structure (state variables) or process rates (flows), or both.

We conducted our studies at Puruki in order to represent a very favourable site for the growth of *P. radiata* with relatively little environmental stress and a minimum of year-to-year variation. *Pinus radiata* there do not become dormant, but grow throughout the year; we do not expect environmental conditions to limit fine-root growth. Unless we accept the hypothesis that the seasonal periodicities of fine roots were actually similar in both years and some other factor like grazing accounts for the differences in Year 2, we must explain why the seasonal periodicities of fine-root standing crop varied so much in successive years when growth of other tree components was similar and environmental conditions were favourable. We have no such explanation. Given these two choices and our present understanding, we are inclined to believe that grazing accounted for the differences in fine-root standing crops. For the present, we accept the results from Year 1 as being representative. Obviously a better understanding of the factors causing short- and long-term changes in standing crops of live and dead fine roots is needed. Future studies need to focus on the extent to which whole plants and stands respond to specific perturbations and environmental stresses by changes in structure or changes in process rates.

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