

Root Growth of *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora* on Mount Stirling, Southeastern Australia

Abstract

This present study was undertaken in order to further understand the role of root physiology of subalpine *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora* in relation to belowground temperature in Victoria, Australia. Root growth of *E. pauciflora* was examined for 31 months (December 1992-June 1995) in a mature stand at an elevation of 1545 m with a southerly aspect on Mt Stirling. Shoot growth was monitored from April 1994 to June 1995. It was found that root growth commenced in the spring at soil temperatures $\leq 1.5^{\circ}\text{C}$, under 550 mm of snow, at least one month before the onset of shoot growth and continued at least one month longer than shoot growth during the autumn. A one-month period of root dormancy occurred in August. The seasonal variation in root numbers of *E. pauciflora* appeared to be related mainly to soil temperature and to a lesser extent to soil water content. Moreover, there appeared to be some periodicity in root growth which was independent of the external environment on Mt Stirling.

Introduction

Soil temperature is of paramount importance in determining when tree roots are able to grow (Romberger 1963). Root growth of many coniferous and deciduous seedlings and trees usually commences and ceases at soil temperatures between 2 and 4°C (Harris 1926, Ross 1932, Wardle 1968, Hilton 1978). However, root elongation has been recorded at 0°C soil temperatures for seedlings of *Carya illinoensis* (Wangenh.) K. Koch grown in a controlled environment (Woodroof and Woodroof 1934). Also, winter root growth has been documented in *Acer saccharum* (Marsh.) (Morrow 1949) and at a soil temperature of 0.5°C under 2000 mm of snow in *Abies amabilis* (Dougl.) Forbes (Keyes 1982). A soil temperature of 35°C is evidently the upper limit for root growth in most temperate tree species (Lyr and Hoffmann 1967, Bowen 1991).

Theophrastus of Lesbos (372-284 BC) was evidently the first to report that root growth began before the onset of shoot growth (Dengler 1927). Duhamel du Monceau (1758) was first to note that root growth continued after autumn leaf-fall. Numerous studies have corroborated these early observations (e.g. Goff 1898, Woodroof and Woodroof 1934, Bhar et al. 1970, Kuhns et al. 1985). A variety of tree species have been shown to have two main periods of root growth; one during

the spring and the other during the autumn (e.g. Resa 1878, Kinman 1932, Riech et al. 1980, Teskey and Hinckley 1981, Dell and Wallace 1983). There are, however, some exceptions to this general pattern. For example, root growth of Alaskan taiga trees had only one short growing period prior to the soil freezing in autumn (Tryon and Chapin 1983), and seedlings of *Larix decidua* Mill. exhibited only one surge of root growth during the limited growing season in the European Alps (Tranquillini 1979).

The summer depression between vernal and autumnal root growth has been correlated with moisture stress (Rogers 1939, Morrow 1949, Leshem 1965, Yaroslavtsev and Kuznetsov 1982). Merritt (1968) worked with stressed and unstressed seedlings of *Pinus resinosa* Ait. in a controlled environment and observed the bimodal (spring/autumn) pattern first identified by Resa (1878). She suggested that even though environment influences root growth intensity and timing, that the basic pattern of root growth was the expression of an identifiable 'endogenous rhythm'. By contrast, Romberger (1963 p.77) believed that "there is no reason for supposing that root growth follows an endogenous cycle, nor is there any strong evidence suggesting it." Yet, individual roots have been shown to exhibit 'endogenous seasonal rhythms' (see Wilcox 1962, Johnson-Flanagan and Owens 1985).

The objective of this research was to gain a better understanding of root physiology of *Eucalyptus pauciflora* Sieber ex Sprengel ssp. *pauciflora*

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in Victoria, Australia. This study: 1) examined the relationship between soil temperature and soil moisture on monthly and seasonal root numbers of mature *E. pauciflora* ssp. *pauciflora* trees, and 2) compared the period of onset and cessation of shoot growth with that of root growth.

Materials and Methods

The Study Area

Mt Stirling in the Victorian Alps, southeastern Australia (37°07'S, 146°48'E) has an elevation of 1747 m and is classified as a steep alpine-subalpine mountain (Costin 1957). The climate is characterized by warm, dry summers and cold, wet winters. The mean maximum air temperature of January is 19°C; the mean maximum of June is -1°C. Temperature extremes of -12°C to 31°C have been recorded and frosts can occur in any month (Anon. 1992). Annual precipitation ranges from 1600 to 2000 mm yr⁻¹ with a winter maximum of 200 mm month⁻¹ and a summer minimum of 100 mm month⁻¹ (Anon. 1992). Precipitation falls as snow from two prevailing weather systems; the west to northwest falls are heavier and more frequent and typically occur as blizzards and produce mostly drier snow. The south to southwest falls, on the other hand, are associated with lighter winds and snow which is typically wet and heavy.

The study site on Mt Stirling was located at 1545 m. The duration of continuous ground cover snow during the study (1992-1995) was always greater than one month per annum (Table 1) so this site was thus classified as subalpine (Costin et al. 1952). *E. pauciflora* ssp. *pauciflora* was the climatic climax species and existed as a pure stand at this site. The age of the trees as measured by increment core ranged from 99- to 182-years-old. The stand at the study site had a mean height of 9 m and a stand density of about 235 stems ha⁻¹. It would be classified as a low open forest by Specht

(1970). The understory was comprised of *Oxylobium alpestre* F. Muell., *Prostanthera cuneata* Benth, and a *Poa* sp. The soil was an alpine uniform humus (Northcote 1979) with a dark loamy, sandy A horizon, 350 mm deep having a bulk density (within the top 75 mm) of 0.67 g cm⁻³. There were no sharp boundaries between the successive horizons and one gradually merged with the next (cf. Costin et al. 1952). Numerous mountain earthworm (*Megascolex* sp.) cast filled tunnels were evident throughout the A horizon, and active *Megascolex* were observed during the winter. Floaters in the A horizon of undecomposed granitic rock accounted for a coarse fragment content of about 15% of soil volume. The pH of the soil (upper 100 mm) was 4.1 in water (mixture 4:1). The C horizon was noted by its lighter color and lack of earthworm activity. The parent material of Mt Stirling was of granitic origin. A thermohygrograph and a soil thermograph at 50 and 200 mm were kept on-site in a Stevenson's screen and maintained for the duration of the 31-month study. Environmental and physical constraints prevented continuous weather readings for July and August of each winter. The rainfall data were taken at an elevation of 1707 m from the Mt Buller weather station, which was about 6 km southwest of the Mt Stirling site.

Methods

A square plot (20 x 20 m) was delineated in November 1992. The plot had a slope of 20° with a southerly aspect. Seasonal root numbers from December 1992 to June 1995 of *E. pauciflora* were assessed from eight cores (70 mm diameter x 200 mm long) collected randomly each month at the site. There were abundant roots, with many root intercepts of *E. pauciflora* at all sampling points. Eucalypt long roots can be readily distinguished by their epidermis, root hairs, and shape of the root cap from the roots of understory species (cf. Chilvers 1972). Active root growth was determined under a stereo-microscope (x75) by examining carefully *E. pauciflora* root tips from each soil core. Root apices of 1st, 2nd, and 3rd orders were considered to be growing and only counted if they were white and abundantly supplied with root hairs (cf. Richardson 1958, Chilvers and Pryor 1965). Brown roots were assumed to be dormant and/or undergoing secondary development and were not counted. There was no evidence of root herbivory

TABLE 1. Duration of continuous snow cover at 1545 m on Mt Stirling, Victoria, Australia.

Year	Duration (weeks)
1992-93	18
1993-94	5
1994-95	14

during the study period. Ectomycorrhizal roots (as described by Chilvers and Pryor (1965)) were observed each month but not considered in this study. After each core was thoroughly examined the gravimetric soil water content was then determined. The only available access to the site during the winter snow-fall months was via cross-country skis and winter measurements included snow depths and snow densities as well as the monitoring of root numbers. In addition, one ski trip was made to the site on 1 August 1994 in between the regular sampling intervals. A hand held digital thermometer was used at 10 min intervals between 0500 and 0600 h and 1430 and 1530 h to obtain mean soil temperatures at 50 mm depth when the weather station was inoperable. These time periods were used because they represented the minimum and maximum occurrences of soil temperatures during September to June when the weather station was operational.

The live below-ground biomass of *E. pauciflora* separated from understory roots was quantified from 10 cores (70 mm diameter x 200 mm long) taken in the spring in October 1994 and again in 1995. *E. pauciflora* roots were divided into two diameter classes of <1 mm and 1-5 mm, and their masses were obtained after oven drying at 50°C for 72 h. The roots were then ignited in a muffle furnace at 550°C for 9 h to determine the mass of mineral matter (residual ash) in the sample. Results are presented as ash-free.

Twelve *E. pauciflora* saplings or trees ranging in height from 1 to 7 m were selected from the site in March 1994 and shoot growth was measured until June of 1995. Shoot growth (length and width of buds and leaves and stem girth at dbh) was measured similarly to that described by Ashton (1975) with vernier calipers (accurate to 0.1 mm). At least three shoots were measured per sapling or tree and active growth was considered to commence when the first leaf emerged from the terminal bud. Throughout the shoot measurement period only 2 of the 36 buds measured experienced some herbivory. In those cases measurements were taken from the primary axillary bud (see Cremer 1972 for terminology).

A step-wise multiple regression was used to examine empirical relationships between growth and some environmental factors for *E. pauciflora* (see Costin 1965, Slatyer and Morrow 1977). The same method was employed in this study us-

ing the software of StatView V4.0 to examine relations between and among root growth and environmental factors. Root numbers were considered as the dependent variable and soil temperature and soil water content as independent variables. The equation was of the form:

$$R_p = b_1(T_s) + b_2(\theta_g) + b_0$$

Where:

- R_p = the number of uninfected white roots
- T_s = the soil temperature at 50 mm in °C
- θ_g = gravimetric water content (wt/wt)

The statistical significance was determined at $P \leq 0.05$.

Results

The monthly root numbers, maximum and minimum soil temperatures at a depth of 50 mm depth, and the gravimetric water content over a 31-month period are presented in Figure 1. In general, root growth of *E. pauciflora* followed the seasonal pattern of soil temperature, increasing into summer and decreasing into winter (Figure 1B). When all of the months of the years were considered, stepwise regression showed that temperature contributed largely but soil water content relatively little to the variation in root numbers (Table 2). However, during the months of low soil water (December through March) soil water content did contribute significantly and more so than soil temperature (Table 2). Temperatures did not decline below 0.5°C at 50 mm depth during any sampling occasions (Figure 1B). Some root growth of *E. pauciflora* occurred at soil temperatures < 3°C under snow cover (Table 3) in early winter in three consecutive years (Figure 1A). A period of root dormancy of about 1 month was observed during the winter (August) of 1994 (Figure 1A and data not shown for 1 August). In September 1993 spring root growth commenced when soil temperature at 50 mm depth reached 3.5°C whereas in September 1994 it occurred when the soil temperature was 1.5°C under 550 mm of snow (Figure 1B).

There was a considerable drop in root numbers during three consecutive January's (mid-summer) followed by a rapid increase in February root growth (except in 1995) (Figure 1). Soil temperature and water content in January 1993 and 1994 did not appear to be limiting for root growth

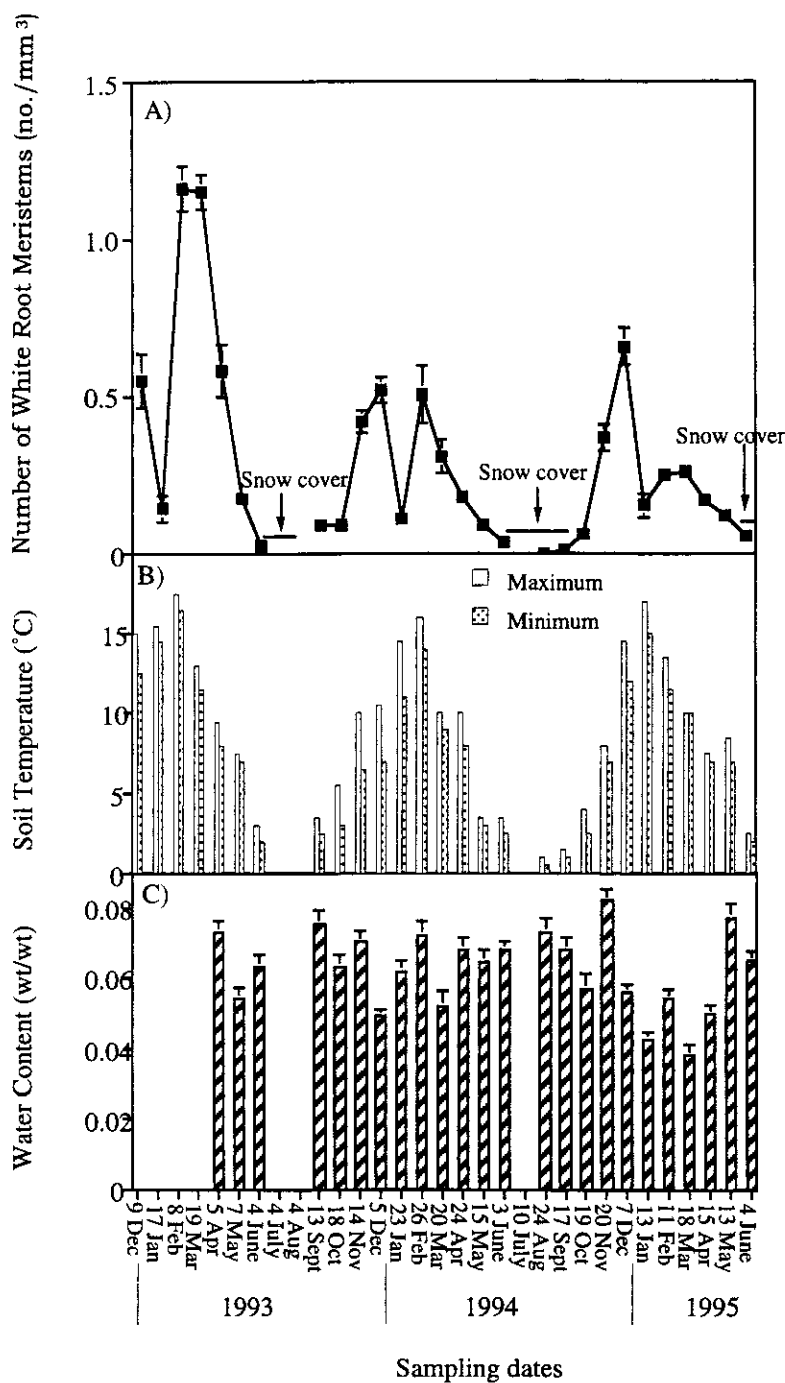


Figure 1. Monthly root numbers of *E. pauciflora* in the surface 200 mm of the mineral soil (A), maximum and minimum soil temperatures at 50 mm soil depth (B), and gravimetric water content of the surface 200 mm soil layer (C) on Mt Stirling, Victoria, Australia. Vertical bars indicate \pm SE of each mean, $n=8$. Error bars are not shown when smaller than the symbols.

TABLE 2. Results of multiple regression analyses of root numbers as a function of soil temperature and gravimetric soil moisture content for 3 time periods—summer (Dec-Mar), other months, and all months. T_s = Soil Temperature ($^{\circ}\text{C}$) at 50mm; θ_r = Gravimetric soil moisture content (wt/wt).

Occasion		Variable		Intercept	r^2	P value
		T_s	θ_r			
Dec-Mar	F value	24	36			
	Coeff.	1.36	438.82	-13.50	0.41	0.05
Other Months	F value	233	5			
	Coeff.	3.21	300.40	-26.11	0.43	0.01
All Months	F value	109	7			
	Coeff.	2.88	235.24	-18.86	0.46	0.01

TABLE 3. The range of snow depths and snow density at 1545 m on Mt Stirling, Victoria, Australia from 1992 to 1995. Values in parentheses are \pm SE, $n=8$.

Sampling Date (days)	Snow Depth (m)	Snow Density (g cm^{-3})
1 Sept 1992	2.0-2.10	0.44(0.01)
13 June 1993	0.30-0.35	0.20(0.01)
23 Aug 1994	0.45-0.55	0.41(0.02)
17 Sept 1994	0.40-0.70	0.45(0.03)
4 June 1995	0.08-0.10	0.18(0.01)

(Figures 1B & C). An examination of the duration of shoot and root growth of *E. pauciflora* revealed several salient features (Figure 2). Root growth of *E. pauciflora* on Mt Stirling continued for at least 1 month after shoot growth had stopped in April 1994 and resumed at least 1 month before shoot elongation in November 1994. The root growing season extended 1 month beyond that of shoot growth in 1995. In addition, as shoot growth peaked in January of 1995 root numbers were markedly depressed, and a second maximum in root growth coincided with slowing autumn shoot growth (Figure 2).

The mean below-ground biomass of *E. pauciflora* fine roots (<5 mm diameter) in the top 200 mm of the soil in October, 1994, was 8.3 t ha^{-1} ($\pm 1.3 \text{ SE}$). In October, 1995, it was slightly higher at 8.9 t ha^{-1} ($\pm 1.1 \text{ SE}$) but not significantly so. The mineral contamination of roots on each occasion was < 5%.

Discussion

The seasonal variability in root numbers of *E. pauciflora* was related primarily to soil temperature and secondarily to soil water content. New

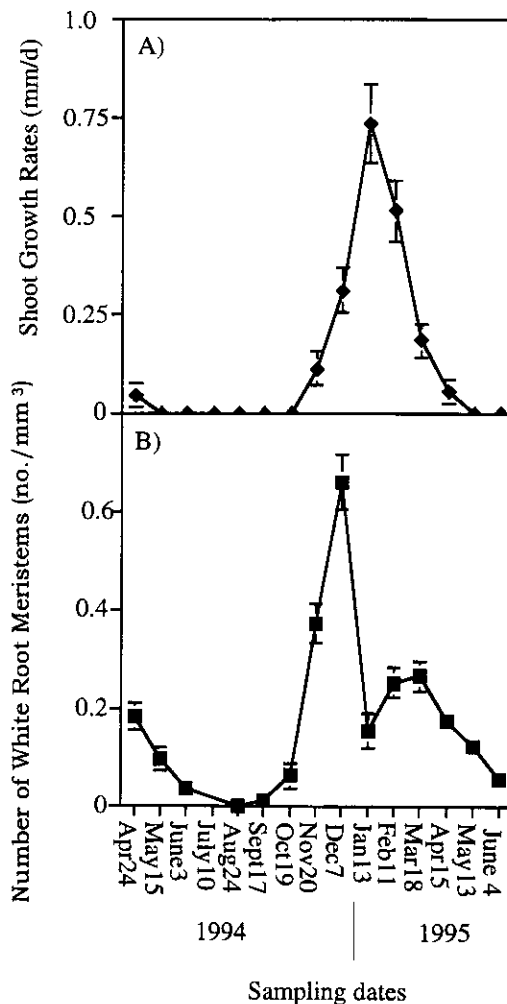


Figure 2. Shoot growth (A) and root numbers (B) of *E. pauciflora* on Mt Stirling, Victoria, Australia. Vertical bars indicate \pm SE of each mean: $n=8$ for roots and $n=36$ for shoots. Error bars are not shown when smaller than the symbols.

root numbers (at both 50 and 200 mm depths) were low at low soil temperatures at the beginning and end of winter and increased with soil temperature. The occasional reduction in root numbers during summer when soil temperatures were still high may have been related to low soil water contents in some but not all instances (Figure 1, Table 2). For example, the reduction of root growth in January 1995 could have been caused by low soil moisture content from December 1994 to January 1995 experienced at the site (Figure 1C). However, the second peak in root growth in March 1995 took place at a lower soil water content and a lower soil temperature than in January 1995 (Figure 1C). Seasonal root production of *E. marginata* Donn ex Sm. within the top 50 mm was characterized by flushes of long- and short-roots in early summer (December) and later autumn (May/June) and after light summer rains (<5 mm). It was concluded that both root initiation and elongation were markedly periodic (Dell and Wallace 1983). Dell and Wallace (1983) postulated that periods of root inactivity were a result of seasonal drought conditions in the Western Australian summer, and low soil temperatures and/or hormonal levels during late winter (August). The seasonal pattern of root numbers of *E. pauciflora* was similar to that of *E. marginata* although the mid-summer drop in *E. pauciflora* root numbers was shorter and not always associated with low soil moisture. *E. pauciflora* ssp. *pauciflora* and *E. marginata* are geographically and altitudinally dissimilar yet it is interesting that both species displayed similar seasonal patterns of root growth.

At high-elevations in the Southern New Zealand Alps *Nothofagus solandri* var. *cliffortioides* (Hook. f.) Poole and *P. contorta* Dougl. also showed a similar bimodal seasonal pattern of root growth (Benecke et al. 1978). Spring root growth commenced as the soil temperature approached the 10°C soil isotherm, and autumn root growth rates declined when the soil temperature dropped below 10°C (Benecke et al. 1978). In addition, Benecke et al. (1978) recorded a drop in root production due to a mid-summer moisture stress. By contrast, *Abies amabilis* in the Cascade Mountains of Washington State, exhibited several peaks in root growth that were non-synchronous with soil temperature during the year. Root production increased sharply 2 weeks before the soil temperature warmed in the spring and declined

much slower than the soil temperatures through the autumn and the winter (Keyes 1982). In the present study there was a reduction in root numbers in January 1995 without any corresponding reduction in shoot growth rates. If there was significant water stress at this time, then a reduction in shoot growth would have been expected as well. The fact that no shoot growth reduction was observed is consistent with the view that there is some internal periodicity in root growth which is independent of the external environment (cf. Teskey and Hinckley 1981), but this assumes that root herbivory can be excluded.

The duration of shoot growth of *E. pauciflora* on Mt Stirling lasted approximately 7 months which is consistent with other subalpine studies of this species (Slatyer and Morrow 1977) and less than the 7 to 9.5 months of shoot growth reported for lower elevation montane *E. regnans* F. Muell. (Ashton 1956, 1975). Growth of roots in the spring prior to shoot elongation is well documented for many Northern Hemisphere trees (Lyr and Hoffmann 1967) and was found in this study for *E. pauciflora*, with *E. regnans* (Ashton 1956), and for *E. marginata* by Dell and Wallace (1983), who, however, found root production in spring preceded shoot production by several months and that root production is summer was greatly reduced by water stress. Assimilate partitioning, as suggested for other species by Keyes (1982), may account for the increase in shoot growth and the decrease in mid-summer root numbers of *E. pauciflora*. However, other complex interactions between hormones, soil moisture and competing vegetation may also have caused this reduction. Winter root growth under a snow cover was observed on Mt Stirling and has also been recorded in North America for *A. saccharum* (Morrow 1949), *Prunus salicina* Lindl. budded on *P. cerasifera* Ehrh. (Bhar et al. 1970), and *A. amabilis* (Keyes 1982). Perhaps one outcome of continued (slow) root growth into unexploited soils in the winter is the establishment of a root-framework with a potential to produce new meristems upon renewed spring root growth. Moreover, the early spring resumption of tree root growth at low soil temperatures, in some cases under a snow cover, could provide a competitive advantage over understory root growth, and may also compensate for a mid-summer reduction in root production.

The ability to renew spring root growth under a snow cover does not appear to have been

conferred to roots of *N. solandri* var. *cliffortioides*. In this species the initiation of root growth was delayed by 2 to 3 weeks in September 1965 because of a remaining snow cover which maintained the soil temperature near 0°C (Benecke et al. 1978). Nevertheless, some root growth of *N. solandri* var. *cliffortioides* was recorded by these workers in June and mid-July 1964 (presumably not under snow cover but not stated) and they concluded that these root systems were capable of physiological activity for 9 months or more of the year. This was also found with roots of *E. pauciflora* on Mt Stirling.

Keyes (1982) found that root initiation of understory vegetation occurred 2 to 3 weeks earlier in the spring-time than that of *A. amabilis*. No white roots of understory species on Mt Stirling were observed in September 1994 under a snow cover with soil temperatures of 1.5°C (data not shown).

The causes of periodicity in root growth and the correlated growth of roots and shoots are linked to carbohydrates and source-sink relationships, water relations, and hormonal factors (Borchert 1991). Current photosynthate is required for root elongation [starch mobilization may explain root growth, which is required for bud expansion in the early spring, but current carbohydrates are required for root elongation (Wilson and Bachelard 1975, Webb 1976, van den Driessche 1987, Vapaavuori et al. 1992)]. Since root growth is associated with that of the shoot, there is a correlating influence of one on the other (Kramer and Kozlowski 1979). Water stress may provide the best explanation of correlated growth (Kramer 1983). Shoot growth may be regulated by root-

limiting supply of water (Sands and Mulligan 1990). Likewise, shoot growth influences root growth by providing a source of carbon and energy (Sands and Mulligan 1990). Root growth precedes shoot growth in the spring, and the hormonal influences from the shoot (auxin) are required for shoot growth and root influences (cytokinins) also play a role (Pilet 1991). Furthermore, hydraulic conductivity also increases in the spring and improved water relations may assist spring growth (Teskey et al. 1984).

In conclusion, the seasonal variability in root numbers of mature subalpine *E. pauciflora* saplings and trees appeared to be related more to soil temperature and less to soil water content. Furthermore, evidence is presented which suggested that root periodicity in *E. pauciflora* may also be endogenous and can occur independently of the external environment.

Acknowledgements

Dr Reese Halter was the recipient of a postgraduate scholarship from Global Forest and acknowledges research grants from The University of Melbourne and the Commonwealth Scientific and Industrial Research Organisation (CSIRO), Division of Forestry, Cooperative Research Agreements. It is a pleasure to acknowledge the many stimulating discussions and contributions of Professor Roger Sands, School of Forestry, University of Canterbury, New Zealand, formerly at the School of Forestry, The University of Melbourne, Australia, and Dr David H Ashton, School of Botany, La Trobe University, Australia, formerly at the School of Botany, The University of Melbourne, Australia, throughout my doctoral studies.

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Received 7 March 1998

Accepted for publication 20 October 1998