SEASONAL TRENDS IN TRANSLOCATION OF ^{14}C PHOTOSYNTHATE AND THEIR ASSOCIATION WITH WOOD FORMATION IN RADIATA PINE SEEDLINGS

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ABSTRACT

Seedlings of radiata pine (**Pinus radiata** D. Don), in their first year after transplanting from nursery beds, were labelled with $^{14}CO_2$ then harvested 3 weeks or, in one case, 6 weeks later. The proportion of current photosynthate retained by main stem needles fell from summer to low levels throughout winter then a rise occurred at the time of elongation growth in spring. The share of photosynthate to the lower stem wood rose from summer to a peak in autumn then dropped to low levels in midwinter and at time of flushing.

Cell measurements showed that maximum cross-sectional cell wall area coincided with the maximum relative labelling of the lower stem. When cell production is considered cell wall deposition was at a maximum slightly preceding this maximum relative labelling. The period of increase in relative labelling of the lower stem is prior to latewood formation and at a time of active cell division in the seedlings.

INTRODUCTION

Tree growth and wood development are interrelated and the translocation and utilisation of photosynthates could influence the type of wood produced by radiata pine (*Pinus radiata* D. Don). Gordon & Larson (1968) worked with red pine (*Pinus resinosa* Ait.) and proposed that the increase in secondary wall thickness with the transition to latewood type cells is due to the increased availability of photosynthate. This occurs when new needles cease to be a sink for photosynthates from older needles and export photosynthates along with those from older needles to increase the supply to developing tracheids.

In the present study, variation in translocation of current photosynthates of 1-year-old seedlings was followed from midsummer through to spring. Xylem cell dimensions and relative xylem cell production were studied to assess the relationship between patterns of translocation and cell production.

METHODS

One-year-old radiata pine seedlings were planted at 0.5×0.75 m spacing in a nursery plot in August 1971. Harvest dates for groups of six seedlings were at 3-week intervals from 12 January 1972 through to 11 October 1972 except for a 6-week interval between 28 June and 9 August.

Translocation of current photosynthates was studied in groups labelled 3 weeks before their collection except for those harvested on 9 August which were labelled 6 weeks previously on 28 June. The first two groups received 27 μC of $C^{14}O_2$ per plant and later groups 100 μC per plant.

On 12 January heights of all seedlings were recorded and subsequently height was measured when seedlings were labelled or harvested. At harvest each seedling was divided into six components:—root (cut at the cotyledonary node); branches including branch needles; stem needles; upper stem (above 50% height point as at 12 January); lower stem wood (bark removed); lower stem bark.

The seedling components were oven-dried, weighed, ground in a Wylie mill, and collected beneath a screen with holes 1 mm in diameter. From each component a sample (150 mg) of ground material was weighed into a scintillation vial. Samples were counted for radioactivity using a Packard liquid scintillation spectrometer with Packard premix "M" scintillant. Counts were corrected for counter efficiency, quenching, and self absorption to derive disintegrations per minute (DPM). The share of labelled photosynthates retained by components is expressed as the ratio of component DPM to seedling total DPM. A second ratio of DPM/g of component to seedling average DPM/g was also calculated but was similar to the first ratio in all but the branch components.

Stem sections were dissected at harvest time from the 50% height point as at 12 January, and these were fixed in glutaraldehyde (4%) and embedded in glycol methacrylate (Feder & O'Brien, 1968). Sections 3μm thick were stained with 0.05% toluidine blue. Cell diameter and cell wall thickness measurements were made using a filar micrometer eyepiece. Cell numbers per radial file were counted in a cambial region which, in the terminology of Wilson *et al.* (1966), includes the cambial zone plus the radially expanding xylem and phloem zones. Wolter's (1968) wound marking method was used to estimate relative activity of xylem cell production with cell counts, made from a wound mark, back to the cambial region. In other counts, made from a frost ring, the cell counts included the number of cells in the cambial region.

RESULTS
Translocation of Labelled Photosynthates

There were no marked changes in the share of labelled photosynthates to the roots during the period of the experiment (Fig. 1a).

For the bark components an initial period of relatively constant ratios occurred up to the collection labelled on 5 April (Fig. 1b), then there was a rise to peak ratios in seedlings labelled between 17 May and 9 August. A decline occurred in seedlings labelled on 30 August and 20 September.

In the upper stem (Fig. 1c) there was a trend for increasing ratios from 12 January through to winter (7 June). From this point, there was a decline to the final collections. The maximum proportion of current photosynthates was translocated to the upper stem in the seedlings labelled just before bud burst.

Fig. 1d shows a steep trend to a greater share of current photosynthates for the branches throughout the study. This paralleled the increase with time in the dry weight ratio of the branches (unpub. data).

When DPM/g of branch component was expressed as a ratio of seedling average DPM/g, no trends were found. The trend in Fig. 1d, therefore, seems to reflect only the increase in dry weight of the branches relative to other components.

The ratios for radioactivity in the needles (Fig. 1e) showed a strong declining trend in the collections labelled from 12 January to 5 April. There was a period of uniformly low ratios in seedlings labelled from 26 April to 28 June, and then a rise in the ratios at the time of renewed stem elongation.

In the lower stem component (Fig. 1f) there was a trend towards rising ratios in the collections labelled from 12 January to 26 April. The share of photosynthates to the lower stem fell from high levels in autumn to low levels during winter (7 June and
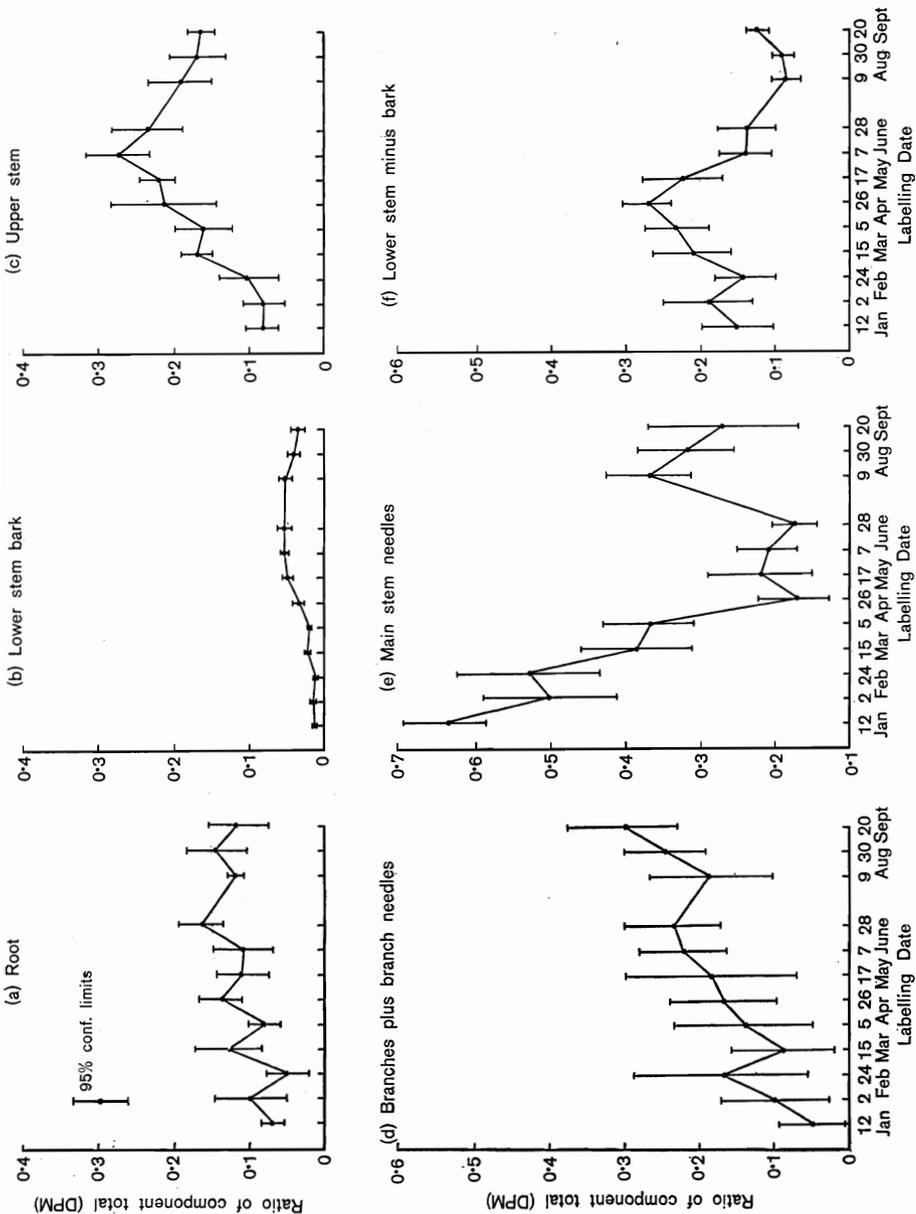

FIG. 1—Relative distribution of current labelled photosynthate. Ratios of component radioactivity/total radioactivity are shown for each of the six components. The labelling time for each collection is indicated. Each point is the mean for six seedlings.

28 June). In collections labelled on 9 August and 30 August the ratios were the lowest for the study at the time of renewed bud activity when there was an increased share of photosynthates to the foliage. Ratios in the lower stem component rose in seedlings labelled on 20 September.

Cambial Activity and Xylem Cell Measurements

For most of the study the cambial region contained about 11 cells per radial file. Numbers of cells decreased from 17 May to 28 June to an average of about eight (Fig. 2). Cambial region size increased again from 9 August to 11 October. Changes in size of the cambial region were mainly due to changes in the number of xylem cells undergoing enlargement.
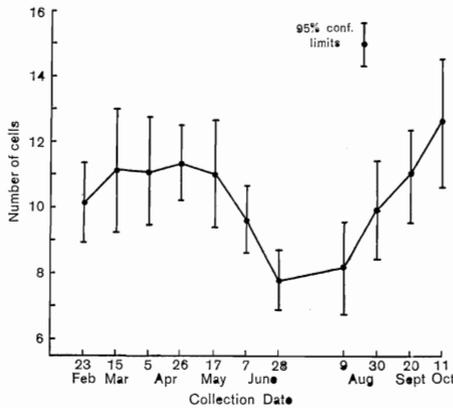
FIG. 2—Average number of cells in a radial row of the cambial region in the seedlings at the collection dates shown.

Active production of cells was in progress at the start of the study (Fig. 3) but peak production was detected in plants harvested on 5 April. Cell production then declined to 17 May. It was in seedlings collected on 17 May that a frost ring was first noticed. After this time wounds made for marking the xylem were obscured by frost damage so the frost damage itself was used as a marker. In Fig. 4 cell counts made from the frost ring show slow cell production from 17 May to 28 June and almost no production from 28 June to 9 August. Cell production was noticeable again from 9 August to 20 September and became active between 20 September and 11 October.

A transverse section of a seedling collected on 28 June (Fig. 5a) showed that secondary wall thickening was well advanced in cells very close to the inactive cambial region. In Fig. 5b the cambial region is shown 6 weeks later on 9 August. In some seedlings at this time renewed expansion of xylem cambial derivatives could be observed, indicating renewal of cambial activity. A transverse section (Fig. 5c) from a seedling harvested on 30 August showed that active expansion of xylem mother cells was in progress. Cell production was rapid between 20 September and 11 October. Fig. 5d shows an active cambial region of a seedling harvested on 11 October.
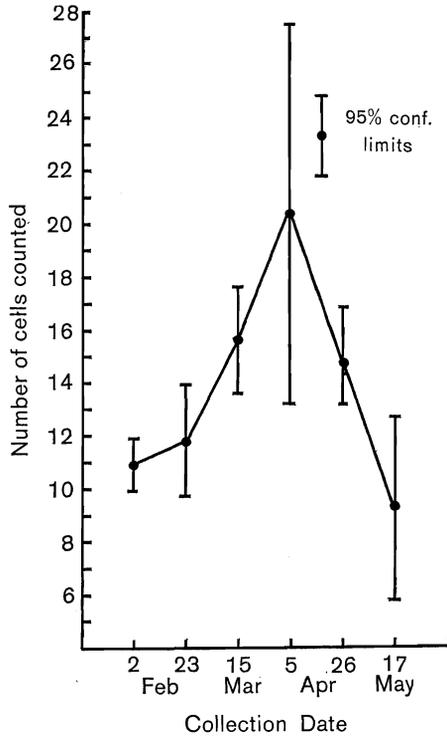
FIG. 3—Cell counts for seedlings collected
up to 17 May representing relative
cell production in the 3 weeks
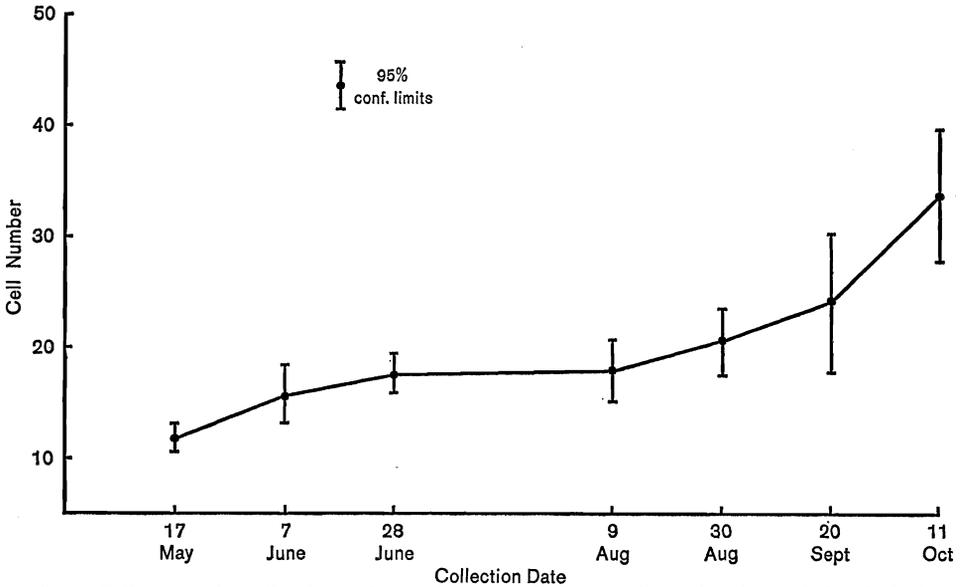immediately preceding the collec-
tion date.

FIG. 4—Cell counts in collections after 17 May, made from a frost ring formed shortly before
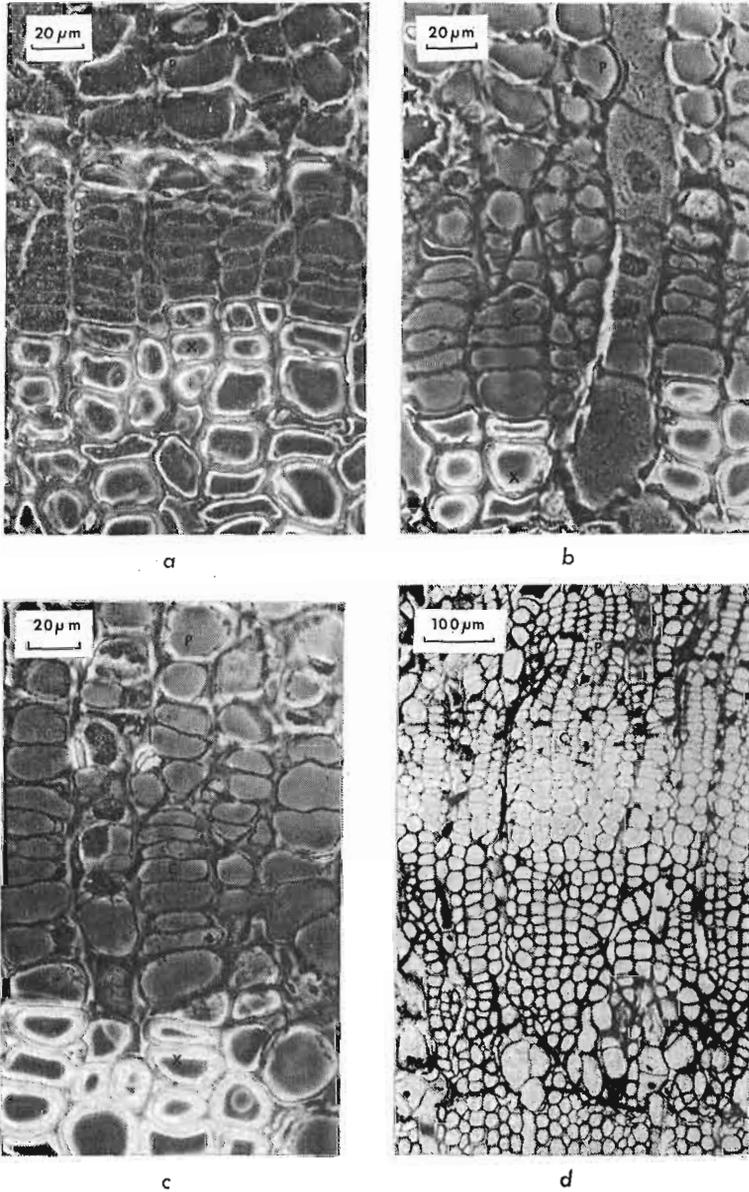17 May. Counts include cambial region cells.

FIG. 5—Micrographs of stem transverse sections. a, b, and c viewed with
phase contrast (x = xylem, c = cambial region, p = phloem).
(a) collected 28 June—secondary wall thickening was well ad-
vanced in cells very close to the less active cambial region. (b)
collected 9 August—cambial derivatives are expanding adjacent to
thick-walled xylem cells and cell division is in progress in a ray
initial. (c) collected 30 August—active division and expansion of
xylem derivatives from the cambium is in progress exterior to
radially narrow cells arrowed. (d) collected 11 October—with very
active cambial region. Effects of frost damage mainly before 17
May can be seen and it is evident how thin-walled cells, many
originating from the rays, expanded into radial cracks created by
the frost damage.

A number of collections were intensively measured up to the time that frost damage (see Fig. 5d) affected normal cell production (shortly before 17 May). Cell diameters (Fig. 6a) were variable but cell wall thickness (Fig. 6b) showed a tendency to rise from 15 March to a maximum on 26 April. Cross-sectional cell wall area per cell showed a very similar rise to a maximum on 26 April (Fig. 7). This maximum coincided with the maximum relative labelling of the lower stem. Production of thickest cell walls was at a time when cell production was high but not at the maximum. Peak cell production, as indicated by the cell counts (Fig. 3), was from 15 March to 5 April.

An index of cross-sectional cell wall area (CWI) laid down by the tissue was obtained from the product of cell wall area and the cell count. Average CWI (Fig. 8) was at a maximum on 5 April.

DISCUSSION

Sustained translocation of current photosynthates to the roots was probably due to the importance of root growth in the seedlings in their first year of growth after transplanting and such a trend may not be sustained in larger trees. In other *Pinus* species peaks in translocation of labelled photosynthate to the roots have been found in the late summer to autumn (Shiroya *et al.*, 1966; Ursino *et al.*, 1968; Schier, 1970) and other peaks occur prior to bud break (Shiroya *et al.*, 1966; Gordon & Larson, 1968; Zeimer, 1971).

In autumn and winter, the increased proportion of photosynthates translocated to the bark could be stored for subsequent growth but could also be used for continued phloem development (Barnett, 1971) and for some cortical and phellogen activity.

Cell production to the xylem was virtually nil during the period 28 June to 9 August (Fig. 4). Renewed activity in cell division and cell expansion in the cambial zone and differentiating zones of the xylem was in evidence in some seedlings harvested on 9 August. This is in agreement with the time of reactivation found by Barnett (1971). It also closely follows times for reactivation of growth in radiata pine growing in Victoria (Skene, 1969) and in Canberra (Shepherd & Drielsma, unpub. data). Jenkins & Shepherd (1974) showed that a rise in indole-acetic acid (IAA) level in young tree stems of radiata pine at the time of activation of cambial activity preceded any noticeable rise from winter temperatures. Fig. 9 shows that for the year of the present study mean maximum temperature did not rise above winter levels until early September. Mean minimum temperatures were variable through the winter to spring period but were at low levels in early August when initiation of cambial activity was observed. This suggests that a rise in current temperature is not a major factor in the renewal of cambial activity in spring.

When xylem cell production was negligible in winter a low proportion of available photosynthate was translocated to the lower stem. This proportion was lowest in seedlings labelled on 9 August and 30 August (the time of resumption of active growth by the terminal buds and the cambial zone) while the share of photosynthates in the needles shows a dramatic rise from low winter levels. This is indicative of the increased demand by buds and new needles for products of photosynthesis at this time of the year and is associated with little secondary wall thickening of the newly produced cells in the cambial region (Fig. 5c).

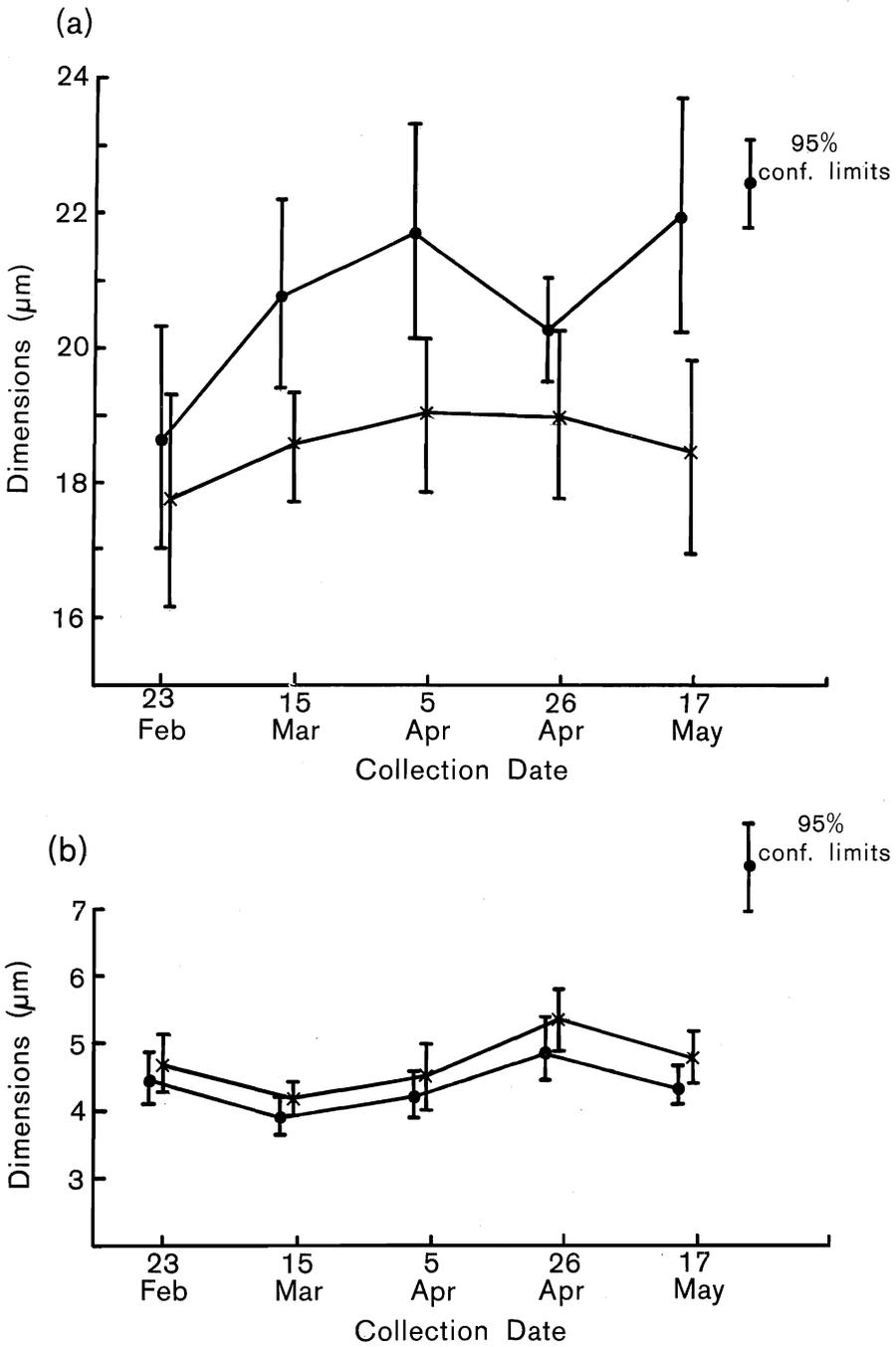More labelled photosynthates are translocated to the lower stem in autumn. The

FIG. 6—Measurements of the most recently matured xylem cells in the seedlings at the collection times indicated.
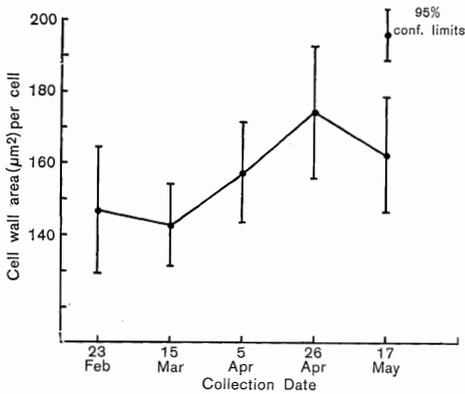
(a) Cell diameters

(b) Cell wall thickness

FIG. 7—Cross-sectional cell wall area per xylem cell, derived from radial and tangential measurements of cell diameter and lumen dimensions of the most recently matured xylem cells at the collection times indicated.
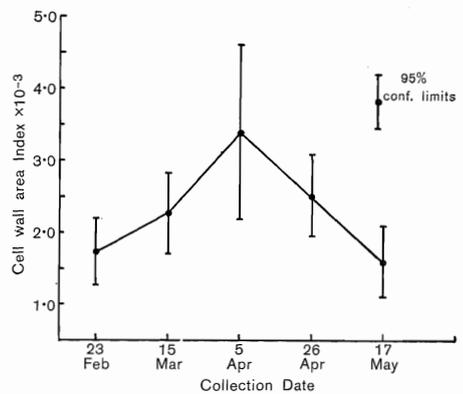
FIG. 8—Indices of cell wall area laid down per radial file in the 3-week period up to the collection times indicated. The indices are the products of seedling cell production indices and calculated cell wall areas.
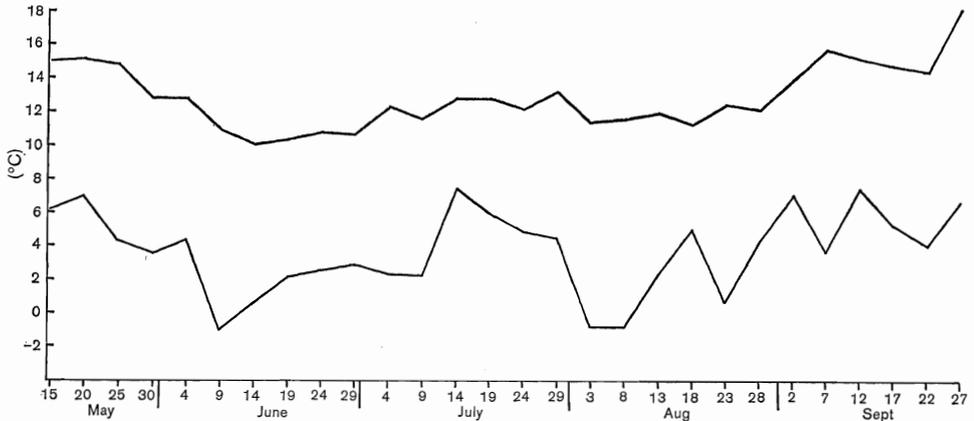

FIG. 9—5-day averages of daily maxima and minima temperatures from May to September 1972 recorded at the Forest Research Institute, Rotorua, approximately 1 km from the study area.

pattern is similar to that described for young *P. resinosa* trees where, at the time of cessation of elongation in current year needles, there is a great increase in the amount of ^{14}C translocated to the stem (Gordon & Larson, 1968). Radiata pine can have several flushes of height growth; red pine has height growth and needle elongation confined mainly to a single flush of growth. In the radiata seedlings height increment was greatest in the period 23 February to 15 March (Table 1). From this time height increment declined and was negligible from 17 May to 9 August. When relative

TABLE 1—Height increments for 3-week periods preceding the harvest
dates indicated

Harvest date	Average height increment (cm)
2 February	2.6
23 February	4.3
15 March	4.8
5 April	2.3
26 April	2.6
17 May	2.1
7 June	0
27 June	0
9 August	0
30 August	0.8
20 September	0.9
11 October	1.8

labelling of the lower stem was maximum (26 April) the rate of height increment had fallen. Production of new needles and the ratio of number of needles elongating to number of mature needles would also decrease with the reduction in height increment. In red pine, as the new needles matured and became net exporters of photosynthates, food supply for developing xylem tracheids increased and production of thick-walled latewood type cells commenced (Gordon & Larson, 1968). The present study indicates that a similar relationship occurs in radiata pine but prior to latewood formation. The thickest cell walls were produced at the time of maximum relative labelling of the lower stem but before reduction in cell radial diameter resulted in latewood type cells. When rate of cell production is considered total production of xylem cell wall material was at a maximum slightly before the peak translocation of radioactive photosynthates to the lower stem.

Jackson (1969) studied growth of 5-year-old naturally regenerated radiata pine in Kaingaroa Forest (56 km from Rotorua) and showed maximum rates of tree stem increment in January, February, and March following an October to December peak in height growth. The present study also shows a pattern of greatest cell production in the seedlings following the peak in height increment. This time of maximum activity in cell production also corresponds to maximum cell wall thickening activity in the tissue. Cell walls tend to be thicker at this time than earlier in the season and a greater proportion of available photosynthate is translocated to the cambial region. Autumn is, therefore, a very important period of the year, when a large number of thick-walled cells are formed before true latewood formation.

During this period any environmental conditions influencing rates of photosynthesis would be expected to have a marked influence on productivity of the cambiums and the thickening of xylem cells. Differences in environmental conditions may explain differences between the conclusions of the present study and those of Skene (1969)

for radiata pine trees growing in Victoria, Australia. Skene (1969) found a reduced rate of cell wall deposition by the cambial tissue as a whole during the February to May period. The marked difference between January to May rainfall during Skene's study and the rainfall during the present study can be seen from Fig. 10. Tree moisture stress is known to reduce photosynthesis (Brix, 1972), and the reduced cell wall deposition found by Skene (1969) may have resulted from a lower photosynthesis rate caused by the low summer rainfall.
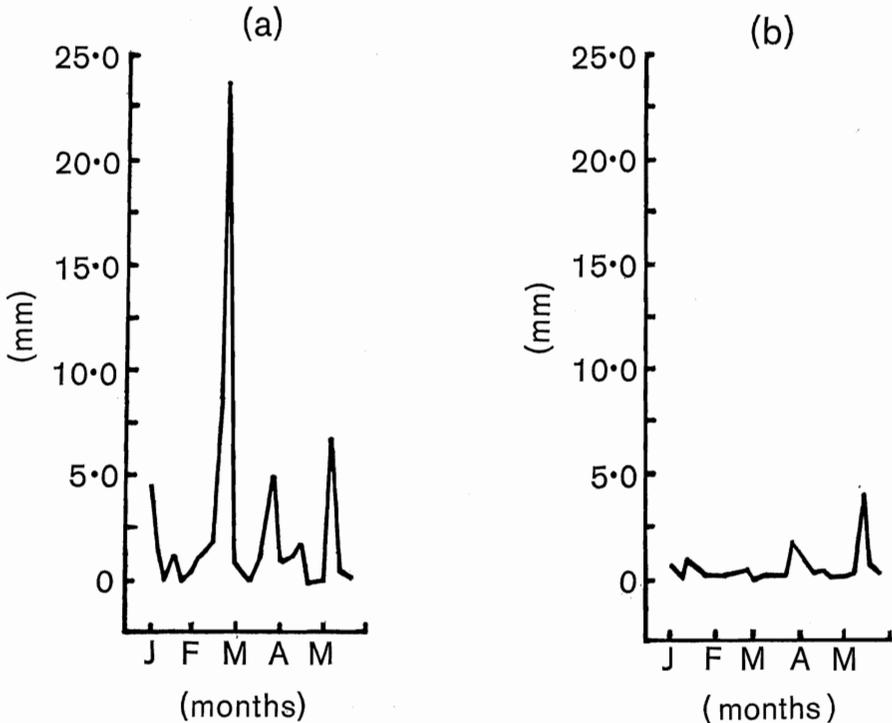
FIG. 10—Weekly rainfall in two studies (a) records of Forest Research Institute, Rotorua, for first five months of 1972, (b) redrawn from Fig. 1 of Skene (1969).

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