

SOIL TEMPERATURES AND GROWTH OF ROOTED CUTTINGS OF RADIATA PINE

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ABSTRACT

Rooted cuttings with well-developed shoot buds, of two clones, were grown for 15 weeks at root temperatures of 3°, 6°, 10°, and 15°C in a controlled environment cabinet at day/night air temperatures of 15°/13°C. Whereas leaf growth was restricted at the cooler soil conditions, there was no reduction in shoot extension growth. Root growth at the cooler conditions was confined to a few thick roots, while at the warmer conditions the new roots were thin with numerous laterals. Limited measurements of foliage relative water content showed no differences in water stress. Plants grown at the cooler soil conditions had higher ethanol-soluble sugar levels. Rates of transpiration and total photosynthesis with soil at 15°C were 300 and 125% respectively of those at 3°C. The two clones differed in their rates of transpiration and in the relative quantities of ¹⁴C-photosynthate translocated to the roots.

Other work has shown that shoot growth of young seedlings is retarded at low soil temperatures, but this does not appear to be so where shoot growth is determined by extensions of a pre-formed bud.

INTRODUCTION

Cooper (1973), in a review of the influence of root temperature on plant growth, states that root temperatures can profoundly affect rates of growth and concomitant processes, and the distribution of growth within the plant. The optimum soil temperature, which depends on the other environmental conditions and on their duration, appears to vary from species to species (Cooper, 1973) and with age and size of plant (Hellmers, 1963).

There are two reports of the influence of root temperature on the growth of radiata pine. Babalola, Boersma, and Youngberg (1968) used a hydroponics system to follow the influence of root temperature on rates of carbon dioxide and water vapour exchange in 6-month-old seedlings. Bowen (1970) noted more and longer lateral roots at 27°C soil temperature than at 15°C. Babalola *et al.* (1968) maintained the seedlings for approximately 2 days at each of the soil temperatures, while Bowen (1970) harvested his seedlings when they were 3 weeks old. Both of these studies, therefore, were concerned with short-term changes in soil temperature of a few days' or weeks' duration, and used young seedling plant material.

To improve our understanding of the influence of soil temperature on the growth

of radiata pine, information is required from more adult trees, especially in soil temperatures maintained at a constant level for several months. Particular interest centres on the effect of soil temperature on the extension and development of the shoot from a well developed apical bud during its spring flush of growth.

MATERIAL AND METHODS

Rooted cuttings, approximately 30 cm tall, of two clones of radiata pine were potted in a 1 : 1 mixture of nursery loam soil and duff, 1 year after they were set as cuttings in the nursery and 4 months before the start of the experiment. The two clones selected (registered by the N.Z. Forest Service as No. 454 and 457) originated from 1-year-old seedlings which were repropagated periodically until 1968 when the material for this experiment was set. At the time of the experiment the plants were 6 years total-age from seed.

The rooted cuttings were taken from outdoors and placed in a CSIRO type-LBH controlled environment cabinet (Pescod, Read, and Cunliffe, 1962) in late winter (early August) before the terminal buds had started their period of rapid extension growth. The controlled-environment cabinet provided day/night air temperatures of 15°/13°C, with a 12-hour photosynthetic period coinciding with the day temperature period. A 2-hour period of low intensity incandescent light (8 Wm^{-2}) on each side of the photosynthetic period (80 Wm^{-2}) provided a photoperiod of 16 hours. Four soil temperatures, 3°, 6°, 10°, and 15°C \pm 1°C were provided by inserting the pots, in which the rooted cuttings were growing, in temperature-controlled water baths. The pots were sealed to prevent entry of water, but were left open at the top to allow air exchange. All the plants were watered as required. Half-strength Hoagland's nutrient solution (Went, 1957) was applied every 2 weeks. A total of 24 plants could be accommodated in the controlled-environment cabinet, and this allowed three replicates of each clone per soil-temperature treatment in a split-plot design. The plants were graded on size; the four largest plants of each clone were assigned to one block, and the four smallest to another block. One plant of each clone of each block was assigned at random to each soil-temperature treatment.

The experiment ran for 3½ months, during which extension of the initials present in the terminal bud occurred. Height and diameter growth were followed in 2-weekly measurements and, during the final week of the study, rates of transpiration, photosynthesis, and dark respiration were measured.

Relative water contents of 1-year-old foliage were recorded 8 weeks after the start of the experiment and during the last week. Rates of transpiration were determined gravimetrically on all plants, and during measurements the tops of the pots were sealed to prevent evaporation from the soil surface. Rates of carbon dioxide exchange were measured by infra-red gas analysis in an open system. On two plants of each clone in each soil temperature treatment, photosynthetic rates were measured at 15°C air temperature and approximately 70 Wm^{-2} light radiation level, and dark respiration was measured at 15°C. Plants were taken in random order for measurement during the day. Relative water contents were determined under low light levels for individual needles (Clausen and Kozlowski, 1965) on two fascicles of each plant. Ten days before the plants were harvested, the foliage of each was exposed to $50 \mu\text{C}$ of $^{14}\text{CO}_2$ and allowed to photo-

synthesise. At harvest all the plants were photographed, separated into foliage, stem, and root, and oven-dried at 80°C for at least 48 hours. Samples were then taken (i) to determine total ethanol-soluble sugar content using an anthrone reagent (Ebell, 1969), and (ii) to assay for radioactivity with a liquid scintillation spectrometer, the necessary corrections being made for background, counting efficiency, self-absorption, and quenching. The radioactivity per plant part was expressed as a percentage of the total radioactivity of the plant.

RESULTS

Shoot Growth

The lower soil temperatures gave slightly greater shoot extension (Fig. 1). However, the differences in amounts of extension were less than 4 cm between the coldest and warmest soil treatments and were not statistically significant at the 5% level (level of significance approximately 15%). Each of the plants had a large well-formed apical bud, and it has been assumed that essentially all of the shoot growth was by extension of preformed initials, and not via new initials laid down during the experiment. There were no differences in diameter growth of the new shoots between treatments.

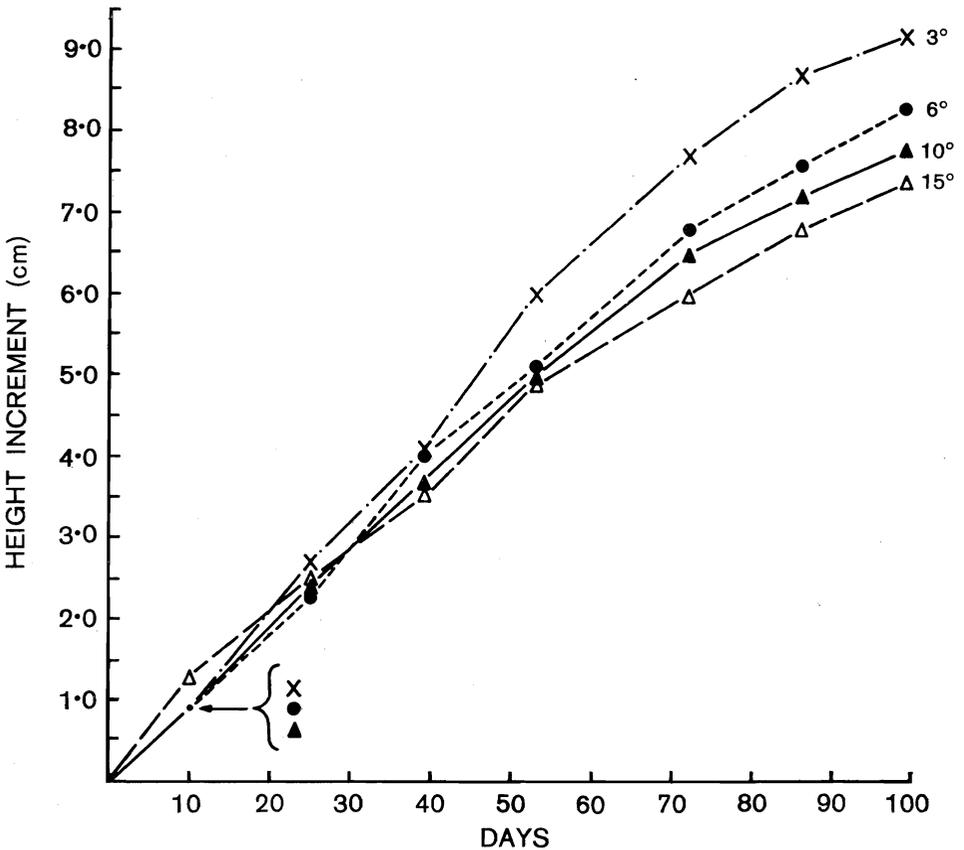


FIG. 1—The effect of soil temperature on height growth of rooted cuttings.

Leaf growth, in contrast to shoot extension, increased at higher soil temperatures. This is shown by the average ratios of foliage/stem dry weights; of 1.19, 1.33, 1.63 and 1.70 for soil temperatures of 3°, 6°, 10°, and 15° respectively; and is illustrated in Fig. 2. At the higher soil temperatures, mature expanded leaves were present over the entire length of the freshly elongated shoot, while at the lower soil temperatures leaf development was inhibited, with the terminal few centimetres of new shoot having leaves only partially expanded, or enclosed within the fascicle sheaths. In plants grown at cooler soil conditions, especially 3°C, the needles which had expanded were paler green in colour than those grown at the higher soil temperatures.



FIG. 2—Rooted cuttings of clone 454 grown at soil temperatures of, from left to right, 15°, 10°, 6°, and 3°C.

Root Growth

Striking differences in diameters and in frequency of branching of root growth between the soil-temperature treatments were obvious when the plants were harvested. At 3°C, root growth was confined to a few thick, fleshy roots while, in contrast, at 15°C growth was distributed over a larger number of thin, intensively branched roots. To convey these size differences, the thickest, white root-tip of each plant was measured. Average root diameters at 15°, 10°, 6°, and 3°C were 1.3, 2.2, 2.6, and 2.8 mm respectively. Both clones reacted similarly.

Relative Water Content

Values of relative water contents of all plants ranged from 75 to 89% with no suggestion of any differences in water stress between clones or between soil temperature treatments at either of the sampling times.

Rates of Transpiration

During the last week of the experiment, rates of transpiration were measured over a 4-day period. The rates of transpiration (Fig. 3) are expressed on a 24-hour basis and show significant differences (1% level) between soil-temperature treatments and between clones. The average rate of transpiration at 3°C was approximately one-third of that at 15°C, while raising soil temperature from 3° to 6°C almost doubled the rate of transpiration.

At each of the soil temperatures used, clone 457 had a rate of transpiration about 50% greater than that of clone 454.

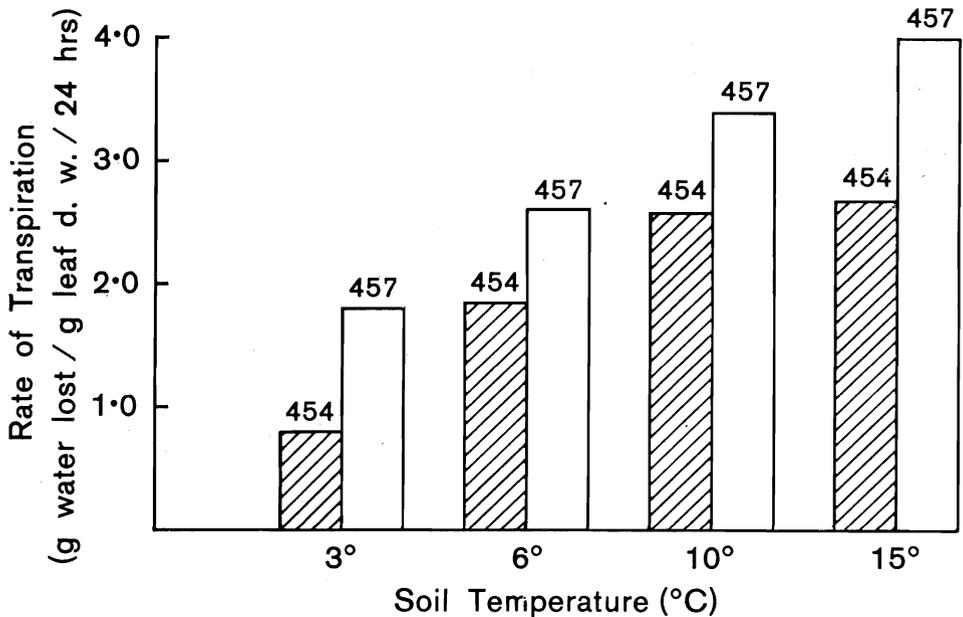


FIG. 3—Rates of transpiration of two clones of radiata pine growing at different soil temperatures.

Rates of Carbon Dioxide Exchange

Differences in rates of net photosynthesis and of dark respiration between soil-temperature treatments were not significant, although there was a trend of increasing photosynthesis and respiration with increase in soil temperature. In Fig. 4, rate of total photosynthesis (net photosynthesis plus dark respiration) has been plotted against soil temperature. The rate of total photosynthesis at a soil temperature of 15°C was 25% greater than that at 3°C.

Sugar Content

Ethanol-soluble sugar concentrations were considerably higher in all tissues (foliage, stem and roots) at the two lower temperatures. Average foliar values, in mg/g dry weight, were as follows:

Clone 457: 5.09 (3°), 5.24 (6°), 3.90 (10°), 3.95 (15°)

Clone 454: 5.74 (3°), 6.69 (6°), 4.46 (10°), 4.16 (15°) L.S.D. 5% ± 1.6

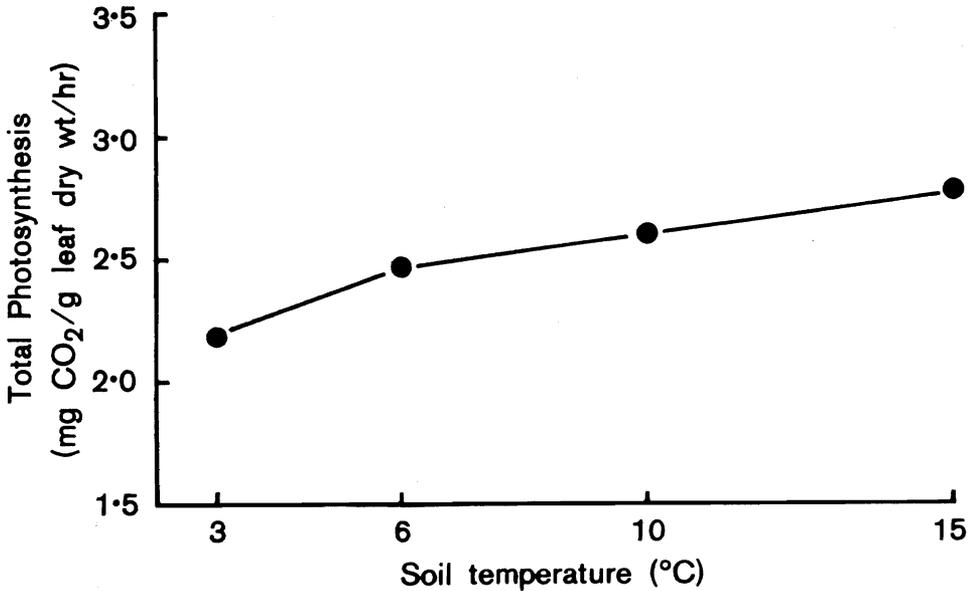


FIG. 4—Rates of total photosynthesis of radiata pine growing at different soil temperatures.

For the whole plant, average sugar concentrations in the 6°, 10°, and 15°C treatments were 104, 86, and 83% of the average at 3°C.

Translocation of ¹⁴C-photosynthate

Soil temperatures affected distribution of photosynthate within the plants (Fig. 5). With substantial plant-to-plant variation treatment differences overall were significant (at the 5% level) only for the stem ¹⁴C-contents. The pattern of ¹⁴C-labelling in the shoots accorded with the present observations on stem and leaf growth; more photosynthates being translocated away from the leaves under conditions for retarded leaf growth. As stem growth is virtually constant for all treatments, the curves in Fig. 5 indicate a very large difference in the movement of photosynthate from the leaves.

The greatest proportion (27%) of photosynthate accumulated by the roots was at 6°; at 3° and 15° it was only 17%. Although both clones showed similar response to soil temperature, they showed a clear-cut difference (significant at 1% level) in ¹⁴C-content of the roots. That of clone 457 averaged 26% of the total for the plant, while for clone 454 it averaged 16%.

DISCUSSION

The production of fewer and thicker roots at the cooler soil conditions is in agreement with other results (Hellmers, 1963; Cooper, 1973). Bowen (1970) noted greater lateral root production and growth in radiata pine seedlings at 25°C soil temperature than at 15°C. The marked differences in numbers and sizes of new roots produced at the various soil temperatures are likely to have resulted in different levels of metabolic

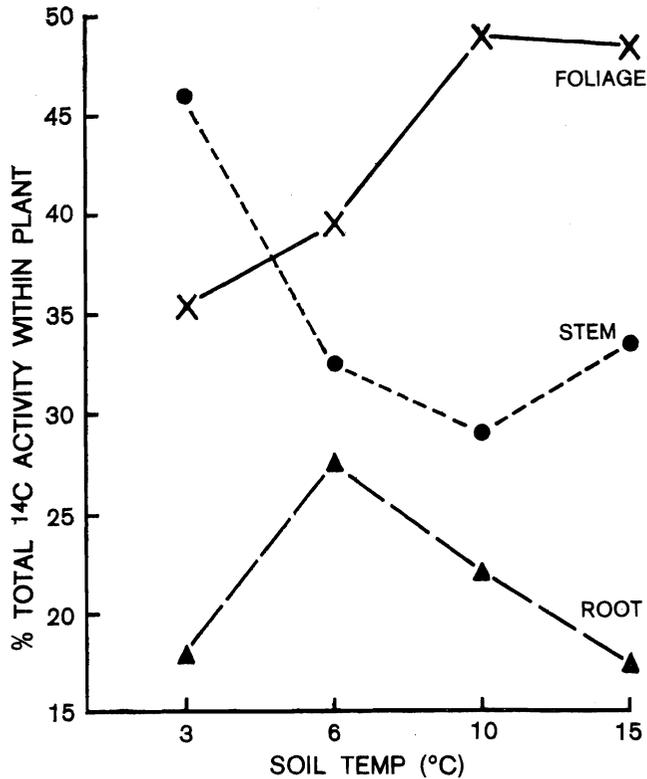


FIG. 5.—Translocation of ¹⁴C-labelled photosynthate to the stem, foliage, and roots of rooted cuttings growing at different soil temperatures.

activity and production of various growth factors; e.g., hormones, amino acids (Street, 1966).

The results from this study indicate that an increase in soil temperature from 3° to 15°C increased rates of transpiration and photosynthesis. This is in general agreement with other studies, including that of Babalola *et al.* (1968) on the effect of short-term changes in soil temperature on photosynthesis and transpiration of radiata pine seedlings. The biggest increase in rates of transpiration occurred between soil temperatures of 3° and 6°C. This type of response has been reported for various species (Cooper, 1973) and it has been suggested that it is due to the additive effects of temperature on viscosity of water and permeability of protoplasm (Kramer, 1956). The large differential effect of soil temperature on rates of photosynthesis and transpiration found in this study is surprising (cf. Havranek, 1972). Although it should be noted that the transpiration measurements were based on weight losses over 24 hours, the carbon dioxide exchange results were spot measurements of some 30 minutes duration and, therefore, relating one to the other should be treated with caution. However, Babalola *et al.* (1968) observed that in radiata pine seedlings transpiration rates increased twice as fast as photosynthetic rates when soil temperatures were raised from 10° to 15°C. Vogl, Polster, and Fuchs

(1972) also observed a more rapid increase in rates of transpiration than of photosynthesis in Scots pine when soil temperatures were increased from 6° to 30°C.

Whereas shoot growth in the radiata pine trees used in this experiment depended on the extension of pre-formed cells in the buds, leaf growth depended both on expansion of cells of the leaf primordia, and on cell division localised at the base within the fascicle sheath (Kozlowski, 1971). Hence it is logical to suggest that the requirements for leaf growth, which entailed both cell initiation and expansion, would have been greater than those for stem extension, which required cell expansion only. The effect of low soil-temperatures in depressing rates of leaf growth observed in this experiment is in agreement with other studies on a variety of plant species (Cooper, 1973). Brouwer (1964), however, concluded that a persistent water stress reduced leaf growth, while Watts (1972) considered that water stress at low root-temperatures was not the main factor.

The leaf relative water contents noted in this study, although collected only twice during the 3½ months of the experiment, showed no indication of any differences in water stress between soil-temperature treatments. That there were no material differences in water stress between treatments is also supported by the fact that shoot extension was, if anything, favoured by lower soil temperatures. Severe and prolonged water stress in radiata pine trees typically causes a reduction in shoot extension, with the fascicles closely crowded together and the needles formed being short and thin. Higher soluble sugar levels at the lower soil temperatures suggest either that osmotic potentials increased to compensate for increased water potentials, or that there was less competition for available carbohydrates at lower soil temperatures and that reduced leaf growth was not caused by lack of carbohydrates. Other factors which should also be considered to affect leaf growth more than stem extension, are amino-acid and hormone supplies. Rates of amino-acid and hormone production, and supply from the roots to the shoots, have been shown to decrease with decrease in soil temperature (Street, 1966; Atkin, Barton, and Robinson, 1973; Lavender, Sweet, Zaerr, and Herman, 1973), and in this study the trees at the cooler soil conditions had slightly lighter green foliage. This aspect should be studied in more detail, but the present results showed no support for the contention that neither water stress nor an inadequate supply of carbohydrates was responsible for the reduced leaf growth.

Rooted cuttings of both clones of radiata pine used in this study reacted similarly to soil temperature. The only significant differences were in the rates of transpiration and in relative movement of ¹⁴C-photosynthate to the roots. Clone 457 showed a particularly high rate of transpiration, approximately 50% greater than that of clone 454 (cf. Jackson, Gifford, and Hobbs, 1973). However, those authors found the difference between the two clones fell to only about 5% under conditions of slight water stress in field conditions. It is interesting to note that the higher rate of transpiration of clone 457, as compared to clone 454, is associated with relatively greater movement of photosynthate to the roots. It is not known whether this greater photosynthetic supply to the roots of clone 457 promoted greater root growth or was stored in the root systems. The reasons for these clonal differences in rates of transpiration should be investigated further.

Shoot growth of seedlings of several coniferous species has been reported to be

retarded at cool soil conditions (e.g., Hellmers, 1963, for *Sequoia sempervirens*; Lavender and Overton, 1972, for Douglas fir). Rook (unpublished results) observed reduced height growth in small radiata pine seedlings at lower soil temperatures. Height growth of young seedlings is indeterminate, requiring both the initiation of new primordia and their expansion (Kozlowski, 1971). In this study leaf growth was inhibited at the lower soil temperatures, possibly because of reduced rates of cell division, and the reduced height growth of seedlings in earlier studies may be accounted for by a similar lowered rate of cell division. Although the first flush of growth resulting from the expansion of pre-formed cells of the buds of older trees was not reduced, it is likely that, because of lower rates of leaf growth and possibly root metabolism, future flushes of shoot growth would be reduced. This should be investigated further, and particular attention paid to the influence of soil temperature on the number of primordia laid down in the bud.

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REFERENCES

- ATKIN, R. K., BARTON, G. E. and ROBINSON, D. K. 1973: Effect of root-growing temperature on growth substances in xylem exudate of *Zea mays*. **J. exp. Bot.** **24**: 475-87.
- BABALOLA, O., BOERSMA L. and YOUNGBERG, C. T. 1968: Photosynthesis and transpiration of Monterey pine seedlings as a function of soil water suction and soil temperature. **Plant Physiol.** **43**: 515-21.
- BOWEN, G. D. 1970: Effects of soil temperature on root growth and on phosphate uptake along *Pinus radiata* roots. **Aust. J. Soil Res.** **8**: 31-42.
- BROUWER, R. 1964: "Responses of Bean Plants to Root Temperatures. I: Root Temperature and Growth in the Vegetation Stage". Jaarb. Inst. Biol. Scheik, Onderz, Landgewass. pp 11-23.
- CLAUSEN, J. J. and KOZLOWSKI, T. T. 1965: Use of the relative turgidity technique for measurement of water stresses in gymnosperm leaves. **Canad. J. Bot.** **43**: 305-16.
- COOPER, A. J. 1973: "Root Temperature and Plant Growth—A Review" Commonwealth Bureau of Horticulture and Plantation Crops, East Malling, Maidstone, Kent, U.K.: 73 pp.
- EBELL, L. F. 1969: Variation of total soluble sugars of conifer tissues with method of analysis. **Phytochemistry** **8**: 227-33.
- HAVRANEK, W. 1972: Über die Bedeutung der Bodentemperatur für die Photosynthese und Transpiration junger Forstpflanzen und für die Stoffproduktion an der Waldgrenze. **Agnew. Bot.** **46**: 101-16.
- HELLMERS, H. 1963: Effects of soil and air temperatures on growth of redwood seedlings. **Bot. Gaz.** **124**: 172-7.
- JACKSON, D. S., GIFFORD, H. H. and HOBBS, I. W. 1973: Daily transpiration rates of radiata pine. **N.Z. J. For. Sci.** **3**: 70-81.
- KOZLOWSKI, T. T. 1971: "Growth and Development of Trees. Vol. I: Seed Germination, Ontogeny and Shoot Growth". Academic Press, N.Y. 207-386.
- KRAMER, P. J. 1956: Physical and physiological aspects of water absorption. In "Encyclopaedia of Plant Physiology, Vol. 3", Ed. W. Ruhland. Springer-Verlag, Berlin. 124-59.
- LAVENDER, D. P. and OVERTON, W. S. 1972: Thermoperiods and soil temperatures as they affect growth and dormancy of Douglas fir seedlings of different geographic origins. **Ore. For. Res. Lab., Res. Pap.** **13** 26 pp.
- LAVENDER, D. P., SWEET, G. B., ZAERR, J. B. and HERMANN, R. K. 1973: Spring shoot growth in Douglas-fir may be initiated by gibberellins exported from the roots. **Science** **182**: 838-9.

- PESCOD, D., READ, W. R. and CUNLIFFE, D. W. 1962: Artificially Lit Plant Growth Cabinets. In "Proceedings of a Symposium on Engineering Aspects of Environment Control for Plant Growth". CSIRO, Melbourne, Australia, p. 175-89.
- STREET, H. E. 1966: The Physiology of root growth. **Annual Review of Plant Physiology** 17: 315-44.
- VOGL, M. POLSTER, H. and FUCHS, S. 1972: Über den einfluss der Bodentemperatur auf den Gaswechsel der Nadeln Koniferenjüngpflanzen. **Biol. Zbl.** 91: 757-62.
- WATTS, W. R. 1972: Leaf extension in **Zea mays**: I: Leaf extension and water potential in relation to root-zone and air temperatures. **J. exp. Bot.** 23: 704-12.
- WENT, F. W. 1957: The Experimental Control of Plant Growth. **Chronica Botanica** 17: 343.