

TEMPERATURE AND GROWTH OF *Pinus Radiata*

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ABSTRACT

Radiata pine (*Pinus radiata* D. Don) has been planted extensively throughout New Zealand and differences in productivity in different areas have been attributed partly to growing temperatures.

The use of controlled-environment facilities has enabled a clearer understanding of the effects of temperature on many aspects of plant growth and development. This information has been used to improve predictions of survival, growth, and productivity of radiata pine in the nursery and the forest.

The productivity of radiata pine is comparable with the rates of dry matter production for many agricultural crops and its high growth rate is due to the temperatures of New Zealand allowing photosynthesis and growth throughout the year.

INTRODUCTION

Radiata pine (*Pinus radiata* D. Don) growing in New Zealand is widely acknowledged to be a species with a very high growth rate (Will, 1964, Madgwick *et al.*, 1977) and has been planted extensively throughout the country because of its vigour and good health and the use of its timber for a wide range of applications. In 1976, 82% of the 636 400 ha of exotic forest species in New Zealand were radiata pine, and during the last ten years the preference for it has strengthened. Differences in productivity in different parts of the country have been ascribed to differences in amount and distribution of rainfall, nutritional status of the soils, and growing temperatures (Jackson and Gifford, 1974). It is generally recognised that trees in the Southland Conservancy have a higher basal-area-to-height ratio than trees of the same age growing in the Rotorua Conservancy and it is likely that the difference of a few degrees in seasonal temperatures between these two areas is a contributing factor. In field studies, however, any measured growth response is a result of a combined influence of several environmental variables including temperature, solar radiation and humidity. Moreover, since the climate is continually changing it is difficult to relate the response in tree growth to a single environmental variable.

Over the last 14 years we at the Forest Research Institute (FRI) have used controlled-environment facilities, especially those at the FRI, Rotorua, and the DSIR Climate Laboratory, Palmerston North, to provide known, simplified, and reproducible environments to gain a better understanding of the effects of different climatic factors on the physiology and growth of radiata pine (Rook, 1966a). One of the climatic factors most studied has been temperature, but the effects are complex since the response of the plant depends on differences in diurnal and seasonal temperature ranges, periods of exposure, and stages of development of the plant. Several examples of this work are discussed briefly below.

Seed germination

Rook (1966b) germinated unstratified seed (previously in cold storage for several months) on wet filter paper in the dark at different temperatures and observed that the optimum temperature for fastest germination was about 25°C. The seeds required 21 days to germinate at 10°C, 14 days at 16°C, 7 days at 19°C and 28°C, and 5 days at 25°C. However, further work should be done using stratified seed and a wider range of temperatures.

Rooting of cuttings

As an alternative to growing radiata pine from seed it can be raised by vegetative propagation and considerable research has been carried out using controlled-environment facilities to define the optimum environmental conditions for rooting cuttings (Cameron and Rook, 1974). Cuttings set at day/night temperatures of 25°/15°C rooted after 10 weeks; rooting took 16 weeks at 20°/10°C, 22 weeks at 15°/5°C, and 24 weeks in undefined temperature conditions in the nursery at Rotorua. However, at 25°/15°C only 57% of the cuttings rooted compared with 70% at 20°/10°C and 36% at 15°/5°C. Further, the warmer growing conditions encouraged the development of fungal diseases while the coldest temperature regime generally appeared to cause lower metabolic rates. The optimum temperature regime of 20°/10°C appeared to be a balance between the reduction of the fungal disease problems and the maintenance of conditions warm enough to allow an adequate level of metabolic activity. The results from this study have been applied in the FRI nursery where large polythylene-covered frames have been set up to improve the speed of rooting of cuttings of radiata pine.

Day/night temperatures and growth of seedlings

Hellmers and Rook (1973) carried out a detailed and extensive study on the effects of different day/night air temperatures on the growth of radiata pine seedlings. Maximum height growth and needle length were measured in warm day (20° to 29°C) and

night (17° to 23°C) temperatures but increases in shoot diameter and root and total plant dry weights were significantly larger when the seedlings were grown under cool (approximately 5°C) night temperatures. The effect of day temperature, except at the extremes of the range, was small compared with the effect of the 5°C night temperature. For example, total plant dry weight of 6-month-old seedlings grown at day/night temperatures of $23^{\circ}/17^{\circ}\text{C}$ was only 72% of that of seedlings grown at $23^{\circ}/5^{\circ}\text{C}$, while total plant dry weight of seedlings grown at $17^{\circ}/5^{\circ}\text{C}$ was 97% of that of seedlings raised at $29^{\circ}/5^{\circ}\text{C}$ day/night temperatures. So the effect of cool night temperatures on growth and the distribution of growth within the seedlings was the most significant.

Temperature and growth of older trees

Following the results of the previous study in controlled conditions, Jackson and Gifford (1974) successfully used the seasonal departure of ambient temperatures from the 'optimum' $20^{\circ}/5^{\circ}\text{C}$ day/night as a variable in a multiple regression model to relate the productivity of 10- to 20-year-old trees from sites all over New Zealand to environmental variables. Earlier attempts to relate productivity simply to ambient temperatures had failed.

In order to gain a clearer understanding of the effect of temperature on the growth of older radiata pine trees, Rook and Corson (1978) measured rates of carbon dioxide exchange in the crown of a 7-m tall tree in controlled conditions at a range of temperatures from 10° to 35°C and irradiance levels up to a maximum near full sunlight. The net balance of carbon from photosynthetic gains and respiratory losses over a 24-hour period was estimated at each of the temperatures. There was a significant net gain at day temperatures up to 25°C with a night temperature of 12°C but warmer growing temperatures resulted in a negative carbon balance. Maximum net gains in carbon were measured at the coolest temperature, 10° to 15°C , but it is also known that these conditions are sub-optimal for growth.

One of the obvious differences between trees and most agricultural crops is that trees are larger and consist of proportionately more structural material relative to meristematic tissue. Structural materials such as sapwood, however, include living cells which require carbohydrates in order to function. Respiration, which can be significantly decreased by a decrease in temperature of a few degrees (Q_{10} approximately 1.5), can be split into two components known as maintenance and constructive respiration. If carbohydrates are limiting for growth and the effect of temperature is only on the maintenance component, then cool night temperatures would lower the rates of maintenance respiration in the crown and stem (a major sink for carbohydrates) and so allow more carbohydrates to be available for growth *per se*.

Soil temperature effects

Another component of temperature generally is soil temperature but only a few short-term controlled-environment studies have been done with radiata pine to measure this effect. As well as influencing water and nutrient uptake by the roots,

soil temperature markedly affects the type of roots formed and shoot growth, especially leaf growth, suggesting that significant plant hormone concentration differences occur at different soil temperatures (Bowen, 1970; Rook and Hobbs, 1976). These responses appear to be similar to those reported for other plants (Cooper, 1973). Rook and Hobbs (1976) showed that roots of radiata pine grown at cool temperatures of about 3°C were few in number, thick, and unbranched compared with the many thin, intensively branched roots of plants grown at a soil temperature of 15°C . The cool soil temperatures also resulted in lower rates of leaf elongation and higher concentrations of soluble sugars than those in plants grown in the warmer soils.

Seasonal differences in temperature requirements

Jackson and Gifford (1974) pointed out the need to examine more closely the seasonal temperature optima for growth of radiata pine and it is obviously a gross oversimplification to expect one optimum day/night temperature regime for maximum tree growth throughout a year yet alone through the life of a tree. For example, the temperature optimum would be expected to be higher in summer than in spring. Rook (1969) showed that the optimum temperature for maximum photosynthesis in radiata pine varied with temperature at which the seedlings had been grown. The temperature optimum for seedlings grown at a day/night regime of $33^{\circ}/28^{\circ}\text{C}$ was 24°C , whereas it was 16°C for seedlings grown at temperatures of $24^{\circ}/19^{\circ}\text{C}$ and $15^{\circ}/10^{\circ}\text{C}$. Radiata pine seedlings can be acclimatised to different temperature regimes, and changes in rates of carbon dioxide exchange were measured within a few days of drastic changes in growing temperatures from $33^{\circ}/28^{\circ}$ to $15^{\circ}/10^{\circ}\text{C}$. Studies such as these improve our understanding of the response of radiata pine planting stock to being transferred from glasshouse to nursery or from nursery to planting site.

Radiata pine has no distinct dormant period in most parts of New Zealand and, although height and basal area growth slow down markedly during the winter months (Rook and Whyte, 1976; Jackson *et al.* 1976), appreciable growth still takes place. Barnett (1973) noted continuing cambial activity in winter and Bollmann and Sweet (1977) observed that although primordia initiation ceased during the winter months, extension of pre-formed initials could take place during winter. Plants are able to avoid damage from extreme environmental conditions in the winter by remaining dormant and any plant which continues to grow throughout the winter in New Zealand runs the risk of being injured by frost. Although the most severe frosts occur in winter, many forest areas experience damaging frosts during any season of the year. Trees grown in the nurseries at higher altitudes and colder temperatures are able to tolerate frosts about 3°C more severe throughout the year than stock from nurseries at lower altitudes and warmer temperatures (Menzies *et al.*, 1979). In summer, radiata pine will tolerate without damage minimum temperatures of about -6°C and gradually during the late summer, autumn, and winter it will harden off to tolerate temperatures of about -12°C by August; then, during spring it rapidly de-hardens again so that it will only tolerate temperatures of

-6°C. Tree species such as Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) show a much greater frost tolerance in winter but are more susceptible to spring, summer and autumn frosts, than radiata pine (Menzies, 1977). Radiata pine is therefore amazingly well suited to tolerate most frosts in this country and continue growth throughout the year.

Other physiological processes affected by temperature

Temperature effects on rates of growth and on the distribution of assimilate within the tree are expressions of metabolic processes taking place within the plant. Few studies with radiata pine have been carried out where metabolic processes have been examined. However, in one experiment the carbohydrate composition and levels in seedlings grown at different night temperatures, but at the same day temperature (17°C) and light regime, were studied (A. M. Cranswick, unpublished results). It was found that starch levels in seedlings grown at warm nights (17°C) were 10-20% of the levels in seedlings grown at cool nights (5°C). The concentrations of the other carbohydrates, i.e., monosaccharides, cyclitols, and soluble sugar acids, were similar in both sets of seedlings.

It is known that growing temperatures affect cellular differentiation of the xylem and hence the structure of wood produced. Jenkins (1975) found that cool growing temperatures produced tracheids with larger diameters and thicker walls than those produced at warmer growing temperatures.

Bollmann and Sweet (1979) implicated temperature as one of the main causes for greater numbers of primordia in buds of radiata pine growing in four locations in the North Island. The buds of the trees at the warmest site had some 47% more primordia, five growth cycles instead of three, and longer shoots than trees of the same clone growing at the cooler sites. A larger number of growth cycles enables a greater number of long shoots and/or cones to be produced. The type of bud can also be modified by temperature. Lanner (1966) commented on the occurrence of 'foxtail' formation in radiata pine which was prominent in trees growing in the warm tropical climate of Hawaii. He observed trees in which the development of branches was inhibited and the needles were exceptionally long. One 6-year-old 6.7 m tall tree had no branches beyond 1.1 m above ground level. There appears to be a higher proportion of 'foxtailing' on radiata pine growing north of Auckland than in other parts of the country. It is worth noting that the effects of temperature on primordia initiation in the buds of trees are possibly long term since the initials in the buds may not elongate until almost 12 months after they are initiated, whereas in most agricultural crops primordia initiation and development occur over a few days or weeks.

GENERAL DISCUSSION

The examples above illustrate the state of our knowledge of the effects of temperature on the growth of radiata pine. Although fragmentary, it does provide a broad outline of the response of the species

to many aspects of temperature. Temperature requirements for survival are much easier to define, as attempted by Golfari (1963), than those needed to define productivity differences where a few degrees difference in temperature, together with interactions between other site factors, can produce large differences in productivity. The seed setting, germination, and early seedling growth stages of a tree crop are those most vulnerable to environmental extremes and the climatic range in which a species is successful is usually more restricted when the plant grows naturally than when it is raised in a sheltered nursery and planted out in a forest.

In forestry there is a very limited scope for the manipulation of the temperature environment of a crop. It is possible to do this in the nursery, and at the seedling stage the possibilities for optimising the temperature environment for vigorous early growth are the same as those for agricultural crops. When establishing a forest it is possible to select the best species, provenances, and perhaps individual genotypes to suit the temperature environment of the site. Genotypic differences in frost tolerance have been identified (M. Menzies, unpublished results), which indicates the feasibility of selecting clones of radiata pine with superior frost tolerance. Hellmers and Rook (1973) observed slightly higher growth rates at cold temperatures in seedlings raised from seed collected in New Zealand compared to seedlings originating from a native stand of radiata pine in Cambria, California, a warmer area than the New Zealand one. In recent years it has become standard forest establishment practice in many areas to cultivate the site completely prior to planting (Menzies, 1977; Washbourne, 1978). This process minimises weed competition and causes the exposure of the black soil surface which acts as a heat sink during the day and slowly releases the stored heat at night. This can reduce the frost level by 2° or 3°C (Gradwell, 1968). After planting, provided care is taken in the siting of new roads and in the felling of mature crop trees to avoid the development of frost pockets, little can be done to modify the temperature of the crop. Silvicultural operations such as thinning and pruning allow more air movement and presumably cause greater variations in the temperature distribution through the canopy, but these effects are small and are unlikely to cause a change in growth rate.

Although these studies have not produced any modifications to silvicultural treatments of radiata pine during the last decade, they have provided a sound basis for understanding growth responses to temperature. This is reflected in an increased confidence in our handling of the species and will help in the more accurate prediction of its survival, growth, and productivity. In New Zealand the productivity of radiata pine is greater than that for many agricultural crops. For example, Madgwick *et al.* (1977) recorded a gross production in radiata pine of 22-25 tonnes/ha/year during canopy closure with an average net dry matter production over 22 years of 14.4 tonnes/ha/year compared with rates of 7-14 tonnes/ha/year for lucerne (G. Horgan, pers. comm.), 18 tonnes/ha/year for oats (Eagles and Taylor, 1976), 25 tonnes/ha/year for maize as a fodder crop (Wallace and Davies, 1976), and even higher production has

been suggested for sugar beet. The high productivity of radiata pine seems to be due to its ability to photosynthesise and grow throughout the year, enabling photosynthate to be converted directly in growth and wood formation.

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