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AIR TEMPERATURE AND GROWTH OF RADIATA PINE SEEDLINGS

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ABSTRACT

Seeds of radiata pine (**Pinus radiata** D. Don), from a wind-pollinated Cambria (California) stand and control-pollinated trees in New Zealand, were germinated under uniform conditions. The seedlings were grown in the Duke University Phytotron under 30 combinations of day and night temperatures ranging from 5° to 32°C. The experiment covered 1080 seedlings, i.e., 36 seedlings, 18 from each source, in each of 30 treatments. Half the seedlings were harvested at the end of 3 months and the remainder at 6 months.

Although the tallest 3- and 6-month-old seedlings had grown under warm day (20° to 29°C) and night (17° to 23°C) temperatures, the relative growth rates between 3 and 6 months showed that the older seedlings at cold night temperatures (5°C) were growing the fastest.

Growth of shoot, root and total plant dry weight and diameter was significantly greater at a 5°C night temperature at both times and for both sources. The effect of day temperature, except at the extremes of the range, was minor compared to that of a 5°C night temperature. A trend, particularly apparent from the relative growth rate data from 3 to 6 months, showed increasing growth at the cool night (5° and 11°C) and cool day (17° to 23°C) temperatures. The

temperature regime affected also the distribution of growth within the seedling, with higher root/shoot ratios and lower height/diameter ratios being observed at the colder night temperatures. The Cambrian seedlings grew better than the New Zealand seedlings only at the high day temperatures of 32° and 29°C. The 6-month-old New Zealand seedlings were on average 12% larger than the Cambrian seedlings owing to differences in relative growth rates over the first 3 months, although the Cambrian seed was 13% heavier than that from New Zealand.

The temperature requirements for growth of radiata pine are compared with those of other species, and with the climate in its native habitat and in New Zealand.

INTRODUCTION

Although evolution can be expected to harmonise the growth mechanisms of a tree with the environment in which it grows (Callaham, 1962), the assumption should not be made that the native habitat of any species defines its potential environmental limits and the optimum conditions for growth. Jackson (1965) states, using radiata pine (*Pinus radiata* D. Don) as one of his examples, that a species may be more vigorous in countries where it has been introduced than in its native habitat and the range of tolerances of the introduced trees can be much wider than the natural range of the species would suggest. Thousands of hectares of radiata pine forests have been established in Australia, Chile, New Zealand, South and East Africa, and Spain (Scott, 1960) where this species has proved to be easily established, outstandingly vigorous, and highly profitable.

The purpose of this study was to determine more precisely the environmental requirements of radiata pine seedlings from two origins, in particular to examine the growth response to air temperature.

MATERIALS AND METHODS

This study was carried out in the Duke University Phytotron, a unit of the Southeastern Plant Environment Laboratories in North Carolina, United States (Kramer *et al.*, 1970). Seeds from two sources were used. One seed lot from wind-pollinated trees in a native stand was supplied by the California State Division of Forestry. These were collected in San Luis Obispo County from a stand which forms part of the Cambrian population of native radiata pine (Lindsay, 1937). The other seed lot was supplied by the New Zealand Forest Research Institute, Rotorua, and was from control-pollinated trees registered as "89 × 7" by the New Zealand Forest Service. The Cambrian (CA) seed were 13% heavier, on a fresh weight basis, than the New Zealand (NZ) seed.

All seed was stratified for 5 days at approximately 2°C, then sown in pots in a 50 : 50 mixture of vermiculite and gravel. Three seeds were sown in each pot (8 cm diameter and 0.36 litre capacity) and germinated in a temperature-controlled greenhouse at day/night temperatures of 23°/20°C. The pots were supplied with modified Hoagland's solution each morning and watered each afternoon.

Fourteen days after sowing, at which time the cotyledons were fully expanded, the seedlings were distributed at random to 30 combinations of day and night temperatures.

The day temperatures were 17°, 20°, 23°, 26°, 29°, and 32°C, in combination with night temperatures of 5°, 11°, 17°, 23°, and 29°C. The day and night temperatures were selected to cover the range of air temperatures for active growth of radiata pine and for comparison with temperature effects reported for other trees. One such response is to total daily heat, or heat sum in degree-hours, irrespective of time of application (Hellmers, 1962). The total daily degree-hours is the sum of the numerical value of the temperature above 0°C for each hour during a 24-hour day. For example, 8 hours at 20°C (= 160 degree-hours) and the remaining 16 hours at 5°C (= 80 degree-hours) give a total daily heat sum of 240 degree-hours for the 20°/5°C regime. The day and night temperatures selected allowed the same heat sum to be obtained by more than one day/night temperature combination. Because some trees respond to the difference between day and night temperatures (Kramer, 1957), regimes were selected with day/night temperature differentials of 3°, 6°, 9°, 12°, 15°, 18°, 21°, 24° or 27°C. Also, some of the regimes had nights warmer than days.

The seedlings were placed in temperature-controlled greenhouses for the 8 hour day temperature period and transferred to artificially-lit controlled environment chambers for the 16-hour night period. In the middle of the night period the plants were given 2 hours of 3000 lux incandescent light to provide a long day effect. At the time of transfer to their respective greenhouses the average oven-dry weights of 10 seedlings of each origin were 0.0370 g for the NZ seedlings and 0.0377 g for the CA seedlings.

Thirty days after the seedlings were transferred to their respective growing regimes, they were thinned to one/pot. This provided 36 seedlings/treatment, 18 seedlings of each origin, making a total of 1,080 seedlings in the study. Half were harvested after 3 months, the remainder at 6 months.

Plant heights were measured at 8-week intervals. Height, diameter at collar region, and oven-dried weights of roots and shoots were also measured on each seedling at harvest. Mean relative growth rates of the seedlings and different parts of the seedlings, such as roots and shoots, were calculated from the following formula (Kvet *et al.,* 1971):

$$\text{Mean relative growth rate} = \frac{\log_e W_2 - \log_e W_1}{t_2 - t_1}$$

where W = height, diameter, root, shoot or total plant dry weight

t = time

the suffixes 1 and 2 refer respectively to the first and second harvests.

This mean relative growth rate formula is derived from the equation

$$R^1 = \frac{1}{W} \cdot \frac{dW}{dt}$$

where R^1, the relative growth rate at any instant, is defined as the rate of increase in plant material/unit of plant material present (Kvet *et al.,* 1971).

Treatment differences were analysed at the 1% and 5% levels using Duncan's multiple range test (Duncan, 1955).

RESULTS

Mean values for shoot heights and diameters, and shoot, root, and total dry weights of 6-month-old seedlings are presented in the appendix with their significance rating, according to Duncan's multiple range test at the 1% probability level. In the appendix, treatments which are not significantly different from each other share a common number in the column marked MRT (multiple range test) and conversely those which are significantly different will not have a common number. For example, seedlings of NZ 20°/5°C do not have significantly greater total plant dry weights than seedlings of

NZ 23°/5°, NZ 26°/5°, NZ 29°/5° or NZ 17°/5°C but are significantly heavier than all the other seedlings from CA 23°/5° down the column. Full data have not been presented for the 3-month-old seedlings but these results can be supplied on request.

Height

Height growth of 3-month-old seedlings of both NZ and CA origin was favoured by warm day (23° to 29°C) and night (17° to 29°C) temperatures. Fig. 1 shows the height of CA seedlings.

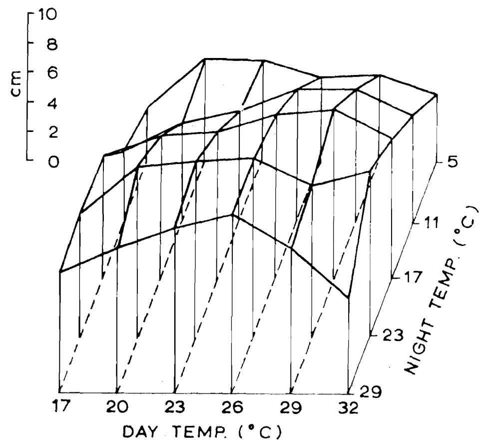

FIG. 1—Effect of day temperature (abscissa) and night temperature (third axis) on height growth (ordinate) of 3-month-old CA seedlings.

The tallest 6-month-old seedlings of NZ origin had grown at a day/night temperature of 26°/23°C. Generally, day temperatures between 20° and 29°C and night temperatures of 17° to 23°C appear to approach optimal for height growth of 3- and 6-month-old seedlings. The CA seedlings grew best in a day/night temperature regime of 23°/17°C, but seedlings grown under the full range of day temperatures tested (17° to 32°C), with night temperatures from 17° to 29°C, were not significantly smaller at the 1% level (Appendix).

Relative rates of height growth show a trend of increasing height growth with colder night temperatures, which is contradictory to the data for heights of 3- and 6-month-old seedlings. Although the 6-month-old seedlings were tallest at the warmer day and night temperature regimes, the seedlings growing at the colder night temperatures were growing at a faster rate at the end of 6 months. For example, the CA seedlings had relative growth rates of 0.117 mm/mm/wk at 17°/5°C compared to 0.091 at 23°/17°C and 0.059 at 26°/23°C.

The height growth of 6-month-old NZ and CA seedlings was compared at each of the temperature regimes and showed that growth of the NZ seedlings was significantly (at 0.1 % probability level) greater than that of the CA seedlings.

The CA seedlings were taller than the NZ seedlings at only two day/night temperatures, 32°/5° and 32°/11°C; at other temperatures they tended to be 25% shorter.

Height growth of the 6-month-old NZ seedlings plotted against daily heat sum is shown in Fig. 2. The data could not be accurately described by any single regression. Each set of night temperature regimes had a separate curvilinear relationship between daily heat sum and growth with day temperatures of 20° to 26°C generally being optimal for each night temperature. The seedlings did not respond to a given day and night temperature differential nor was there a close relationship between height growth and daily heat sum for the 3-month-old seedlings of both origins or for the 6-month-old CA seedlings.

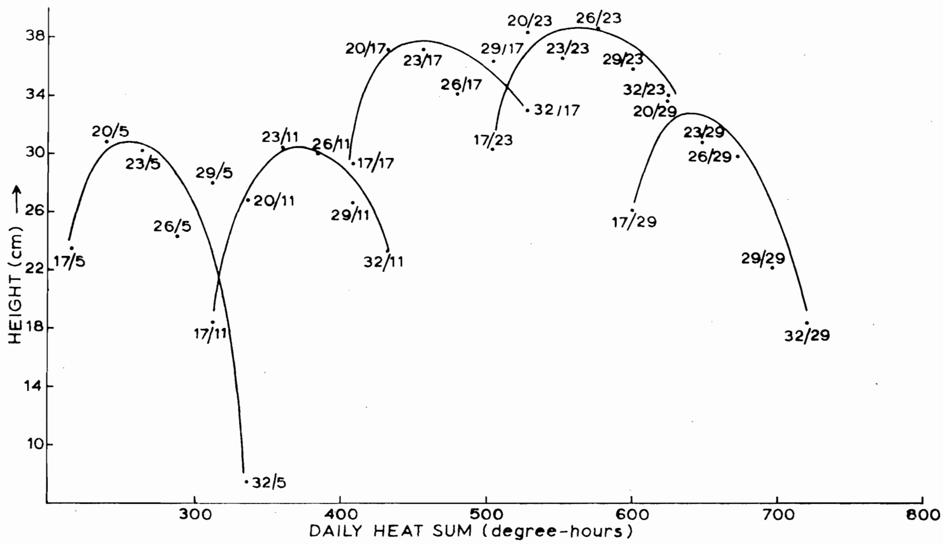

FIG. 2—Relationship between the height of 6-month-old NZ seedlings and daily heat sum.

Diameter

Greatest diameter growth of 3-month-old seedlings occurred with night temperatures of 5° or 17°C. For some unknown cause a night temperature of 11°C inhibited growth even more than a 23°C night temperature. 29°C night temperature also gave less satisfactory growth (Fig. 3). Day temperatures over the whole range tested, i.e., 17° to 32°C, appeared to have only a small effect on diameter growth.

The 6-month-old seedlings grown under a 23°C day with a 5°C night developed the largest diameters. These older plants did not show as marked a suppression of diameter growth at 11°C night temperatures as did the younger plants.

The rate of diameter growth appeared to be decreasing at the higher temperatures and this trend was confirmed by calculating relative rates of growth for 3- to 6-month-old seedlings. The NZ seedlings in particular showed high relative growth rates at the colder day and night temperatures (Fig. 4), with a trend of reduced diameter growth at night temperatures above 17°C and day temperatures above 26°C. The CA seedlings showed higher relative growth rates at a night temperature of 11°C than at any other night temperature; the second best growth rate was at the night temperature of 5°C.

Although the NZ seedlings tended to have slightly larger diameters than the CA seedlings the differences were not significant at the 5% level.

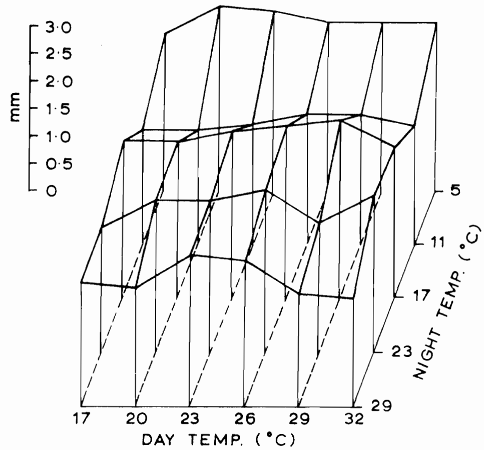

FIG. 3—Effect of day temperature (abscissa) and night temperature (third axis) on diameter growth (ordinate) of 3-month-old CA seedlings.

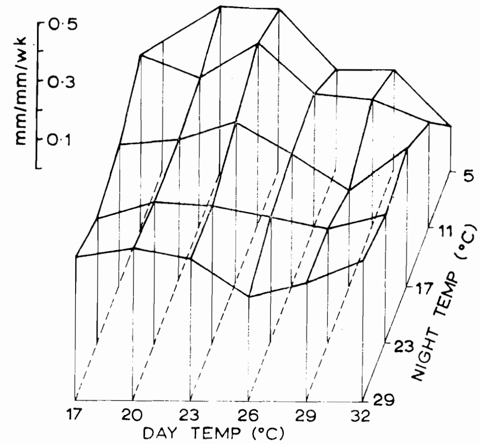

FIG. 4—Relative rates of diameter growth (ordinate) of 3 to 6-month-old NZ seedlings grown at different day temperatures (abscissa) and night temperatures (third axis).

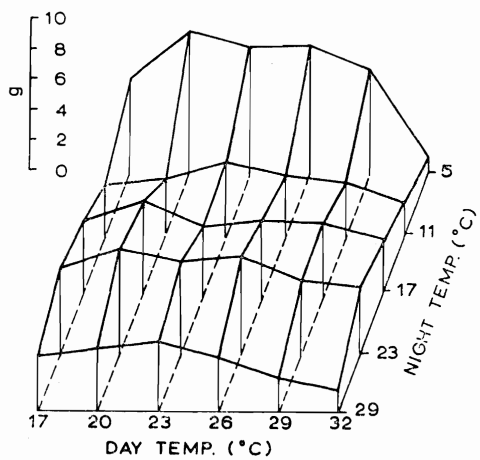

FIG. 5—Effect of day temperature (abscissa) and night temperature (third axis) on shoot dry weight (ordinate) of 6-month-old NZ seedlings.

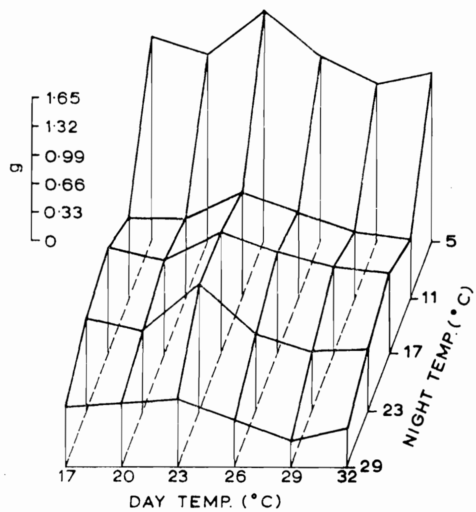

FIG. 6—Effect of day temperature (abscissa) and night temperature (third axis) on root dry weight (ordinate) of 6-month-old CA seedlings.

Shoot Dry Weight

The 3-month-old seedlings of both origins showed greatest shoot dry weight at a 5°C night temperature, with a secondary, although much lower, peak at 17°C. A day temperature of 23°C was generally the most favourable.

The shoot dry weights of 6-month-old seedlings of New Zealand origin are shown in Fig. 5, but the results are similar for seedlings of both origins (Appendix). A night temperature of 5°C combined with day temperatures of 20°C to 26°C gave greatest growth.

The highest relative growth rates of shoot dry weight for the 3- to 6-month-old NZ seedlings occurred at 17°/11°, 20°/5°, 23°/5° and 20°/11°C, and for the CA seedlings at 17°/11°, 17°/5°, 32°/29° and 20°/11°C. With one exception, all the above regimes have day and night temperatures in the cooler part of the range tested.

The differences in shoot dry weight between the 6-month-old seedlings of NZ and CA origins were highly significant (0.1% level) with the CA seedlings being heavier than the NZ seedlings under only four regimes: 32°/5°, 32°/11°, 32°/29° and 29°/17°C. Under all other regimes the NZ seedlings had greater shoot dry weights. The biggest differences were at day temperatures of 20° to 29°C with a 5°C night temperature; shoot dry weights of the NZ seedlings averaged 15% heavier than the CA seedlings (Appendix).

Root Dry Weight

A night temperature of 5°C was predominant in influencing root dry weight of the 3- and 6-month-old seedlings of both origins. Fig. 6 shows the effect of different day/night temperature regimes on the root dry weight of 6-month-old CA seedlings. The optimum day temperature was 23°C but the effect of this day temperature in promoting root growth was much less than that of a 5°C night temperature.

The data for root dry weight increment from 3 to 6 months showed considerable variation with no obvious trends apparent for either seed origin.

Differences in root dry weight between the two seedling origins were not significant. The root growth of the CA seedlings was greater than the NZ seedlings in four of the regimes with a day temperature of 32°C and in three of the five 29°C day temperature regimes. At day temperatures of 23° and less, the NZ seedlings had on average a 25% greater root dry weight than the CA seedlings.

Total Plant Dry Weight

A 5°C night temperature produced the heaviest 3-month-old CA seedlings. Night temperatures of 17° and 23°C and day temperatures of 20° and 23°C were also favourable to total dry matter production. In seedlings of NZ origin the two temperature regimes which produced the greatest dry matter in 3-month-old stock were 26°/5°C and 23°/23°C; the latter regime also gave the tallest seedlings. Seedlings from both sources showed poorest growth at 32°/11°, 20°/11°, 17°/11° and 32°/29°C.

At the start of the experiment the average dry weights of the NZ and CA seedlings were 0.0370 g and 0.0377 g respectively. Relative growth rates calculated for the first 3-month-period showed that the NZ seedlings were growing significantly faster than the CA seedlings—average relative growth rate for NZ seedlings was 0.265 g/g/wk compared with 0.251 for CA seedlings.

At only three temperature regimes were the CA seedlings growing appreciably faster than the NZ seedlings. These regimes were at 20°/5°, 23°/ 5°, and 32°/11°C.

For the 6-month-old seedlings, the pattern of total plant dry weight increases at various temperatures again showed the strong effect of night temperature, especially a 5°C night temperature. There was a slight dip in growth at a night temperature of 11°C. The trends shown in Fig. 7 for CA seedlings were similar for both seedling origins. Day temperature optima were 20° to 23°C; the effects of day temperature, with the exception of a 32°C regime, were minor compared to those of a night temperature of 5°C.

Relative growth rates for total plant dry weight of NZ seedlings from 3- to 6-month-old are presented in Fig. 8. The salient feature is the steep rise in relative growth rate at the cool day and night temperatures. The highest relative growth rate of 0.180 g/g/wk was found at 17°/11°C. The rates at 20°/5 °, 23°/5°, and 20 °/11°C were 0.157, 0.156, and 0.156 g/g/wk respectively. The CA seedlings likewise showed their highest relative growth rates at similar cool day and night temperatures, e.g., 0.187 g/g/wk at both 17°/11° and 17°/5°C.

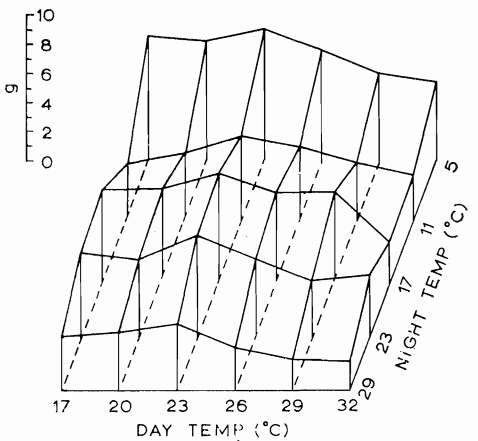

FIG. 7—Effect of day temperature (abscissa) and night temperature (third axis) on total plant dry weight (ordinate) for 6-month-old CA seedlings.

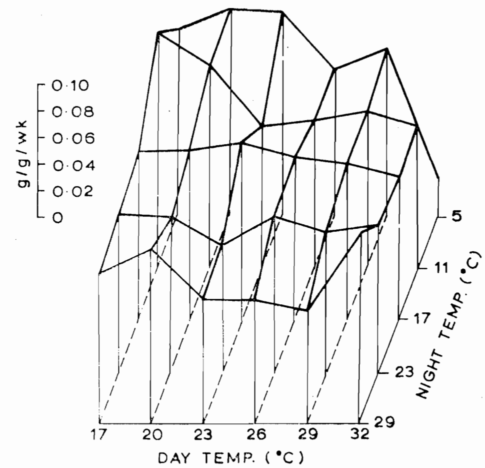

FIG. 8—Relative growth rate of total plant dry weight (ordinate) of 3 to 6-month-old NZ seedlings grown at different day temperatures (abscissa) and night temperatures (third axis).

Total plant dry weight for 6-month-old seedlings was plotted against daily heat sum for NZ seedlings (Fig. 9). This figure, apart from demonstrating the large effect of a 5°C night temperature, shows that a day temperature of 23°C is optimal for all night temperatures except 5°C and 23°C where a 20°C day temperature produced the greatest growth. These same patterns showed up for the CA seedlings except that the 23°C day temperature was also optimal with the 5°C night temperature.

No close relationship appeared between total plant dry weight and daily heat sum, average daily temperature, or difference between night and day temperatures. Thus, regimes of 29°/5° and 17°/11°C have the same daily heat sum (312 degree-hours), but dry matter production of the seedlings grown under the former regime is more than double that of the seedlings grown at 17°/11°C. A difference of 12°, 9°, 6° or 0°C between day and night temperatures, e.g., 23°/11°, 26°/17°, 29°/23° and 17°/17°C, produced seedlings with similar dry weights; approximately the same total dry weight was obtained even if the night temperature was 6°C warmer than the day temperature, e.g., 17°/23°C.

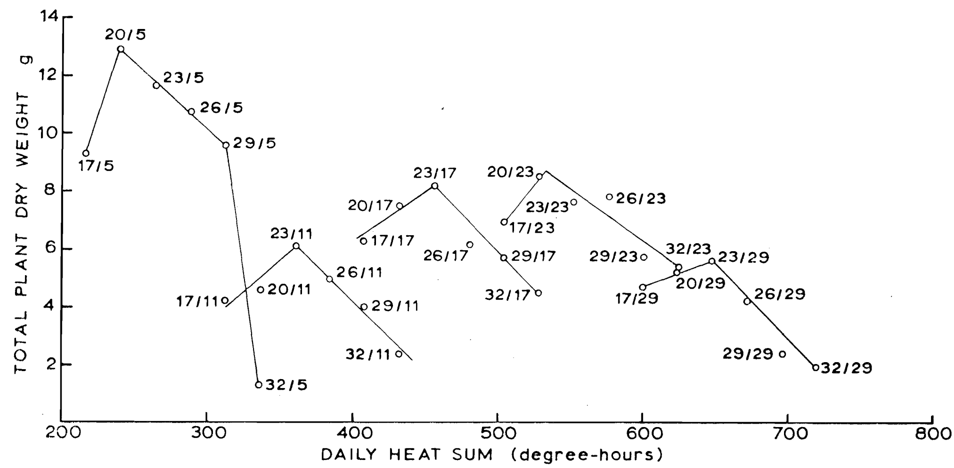

FIG. 9—Relationship between total plant dry weight of 6-month-old NZ seedlings and daily heat sum.

Root/Shoot/Ratio

The results presented separately for root and shoot dry weights suggested differences in root/shoot ratios with temperature. The seedlings grown at a 5°C night temperature had the highest root/shoot ratio, and the value of this ratio decreased with increasing night temperature. The 6-month-old NZ seedlings had ratios of 0.49, 0.31, and 0.27 at 17°/5°, 17°/17°, and 17°/29°C respectively; the CA seedlings had root/shoot values of 0.39, 0.30, and 0.24 in the corresponding regimes. Similar trends were found for the 3-month-old seedlings of both origins.

Numbers of Surviving Seedlings

Thirty-four and 28 seedlings of the CA and NZ origins respectively died during the course of the experiment. Single deaths per temperature regime were associated with the higher day and night temperatures, and multiple deaths per treatment (five or six deaths) occurred at 26°/5°, 29°/5°, and 32°/5°C. No deaths occurred at the other 5°C night temperature regimes.

Twisted Stems

Warm conditions of 32° and 29°C days with nights warmer than 5°C caused the 6-month-old seedlings to develop a kink in the stem. Even though the plants were watered twice daily it could possibly have been due to water stress under these high temperatures.

DISCUSSION

Night temperature was found to be the most important daily temperature parameter affecting growth in radiata pine seedlings. Previous work with this species (Cremer, 1968; Rook, 1969; Wood, 1969; and Florence and Malajczuk, 1970) indicated optimum temperatures for growth of 21° to 24°C day temperature with a 5°C drop in night temperature. All four of these studies, however, used a restricted range of growing temperatures with a constant day/night temperature differential of 5°C and completely missed the large effect of the increased growth under the cool nights. This example, in fact, shows one of the dangers of interpreting controlled environment studies. The present conclusion that the 5°C night temperature produces greatest growth is limited to the range of temperatures tested. Thus a 3° or 7°C night temperature might be better than 5°C and perhaps a day period of 12 or 16 hours at 20°C would be better than the 8 hour day period used in this experiment.

The only apparent exceptions to the conclusion that a 5°C night temperature was most beneficial for growth of radiata pine seedlings were the data for height growth of 3- and 6-month-old seedlings. The tallest seedlings were observed growing under the warmer day and night regimes (Figs. 1 and 2, and Appendix). However, the relative height growth data for the 3- to 6-month-old seedlings indicated that the seedlings growing at the cooler day and night temperatures were starting to grow more rapidly than the seedlings at the warm temperature regimes. Larger trees of this species might be expected to have temperature optima for height growth similar to those for diameter, shoot, root, and total plant dry weight, namely day temperature less than 23°C and above 17°C with night temperatures of less than 11°C. The larger NZ seedlings showed these trends more strongly than the CA seedlings and it is tempting to speculate that the cool night temperatures allow the seedlings to conserve carbohydrates, and that this more economical use of carbohydrates becomes more important as the seedling grows larger. Rook (1969) observed that the optimum temperature for net photosynthesis of radiata pine seedlings growing at day temperatures of 15° and 24°C, with a 5°C drop in night temperature, was about 16°C. A combination of cool day and night temperatures might provide radiata pine seedlings with maximal amounts of photosynthate for growth. Cool days could bring about maximum net photosynthetic output by the seedling and there is some justification (Proc. IBP/PP Technical Meeting, Trebon, 1969) for considering that respiration may be subdivided into metabolic respiration and maintenance respiration. Cool night temperatures could possibly boost growth by reducing the rate of maintenance respiration or reducing the wastage of photosynthate by some other means, such as inhibiting the production of secondary products.

The temperature regime at which the seedlings were grown altered the distribution of growth within the plant. Different optimum temperatures for height and diameter growth have already been noted. Root growth was encouraged compared to shoot growth at the cooler night temperatures. The increased growth of roots and stem diameter at the cooler night temperatures again could be a reflection of the greater amount of photosynthate present for growth. It is generally recognised that the apical meristem is at an advantage compared to the cambium and roots under conditions of limiting photosynthate availability.

Growth of 3-month-old seedlings (Fig. 3) and, to a lesser extent, growth of 6-month-old seedlings (Fig. 7) appeared to be inhibited at 11°C night temperature compared with growth at 5° or 17°C night temperatures. This had the effect of producing a double peak in dry matter growth, with the major one at 5°C and the minor at 17°C, and a depression in growth between these two night temperatures. The relative growth rate data showed that growth at 11°C night temperature was accelerating as the seedlings became larger and, therefore, the apparent inhibition of growth at 11°C night temperature may be only a transitory effect in young seedlings. One explanation for this double peak in the growth data could be that the optimum night temperature for cell production by the apical meristem was higher (e.g., night temperature of about 17°C) than the optimum temperature for cambial growth, which could be around 5°C. Hellmers (1966) observed that the optimum temperatures for height growth in red fir (*Abies magnifica* A. Murr.) seedlings were warmer than those for diameter growth or dry matter production. Height growth in the radiata pine seedlings younger than 3 months old was most rapid at the day temperatures of 20° to 29°C and night temperatures of 17° to 23°C, while the most rapid diameter growth occurred at this age of seedling at 5° or 17°C night temperature. The apparently rapid diameter growth at the 17°C night temperature could have been a carry-over effect of the influence of the higher temperatures on height growth.

The daily heat requirement for optimum growth of seedlings has now been studied for several forest species (Hellmers, 1962, 1964; Brix, 1971) but there appears to be no common response to temperature. Kramer (1957) and Hellmers (1962) claim that loblolly pine (*P. taeda* L.) made more shoot growth when the day temperature was 12° to 16°C higher than the night temperature, and growth was reduced as day and night temperatures approached equality. Although both authors suggested that the differential between day and night temperatures was the critical daily temperature parameter, the temperature regimes which actually produced the greatest growth had night temperatures of 7° and 11°C; cool night temperatures rather than day/night temperature differentials might, in fact, have been the critical temperature parameter. Digger pine (*P. sabiniana* Dougl.), which like radiata pine is indigenous to California, did respond strongly to night temperature (Hellmers, 1962). A night temperature of 17°C was significantly more effective at promoting growth than a 7° or 26°C night temperature for 8-month-old seedlings. Day/night temperature differential had no observable effect on growth rate; a constant day/night temperature of 17°C produced the best seedlings. Callaham (1962) noted that height growth in *P. ponderosa* Laws. is greatest under warm (22°C or higher) night temperatures. In contrast, growth of Jeffrey pine (*P. jeffreyi* Grev. and Balf.) and erectcone pine (*P. brutia* Ten.) was strongly correlated with the number of degree-hours the plants received (Hellmers, 1962), irrespective of whether the nights were warmer than the days or vice versa. The response of radiata pine seedlings to temperature fits most closely to the response of loblolly pine, if it is accepted that it is the cool night temperatures which determine growth, not the differential between day and night temperatures. Scott (1960) observed that radiata pine "appears to be able to grow at lower temperatures than most other conifers" and the results from this study suggest that seedlings of this species prefer cool day and night temperatures.

Radiata pine in its native habitat in San Luis Obispo, California grows in a wet winter/dry summer climate with a mean monthly temperature of 12°C in the colder months and about 17.5°C in the warmer months; the mean monthly maximum and minimum temperatures for the colder months are approximately 16° and 5°C respectively and during the warmer months 25° and 11°C respectively (Lindsay, 1937). Temperatures between the monthly mean and the monthly minima may be taken to indicate the night temperatures, and the temperatures between the mean and the maxima the day temperatures. The importance of cool night temperatures to the growth of radiata pine might well be a result of the adaptation of this species to the climate of that part of California. New Zealand generally has summer day temperatures 2° or 3°C cooler, and mean daily minimum temperatures from near freezing to about 12°C. Although the data from this study suggest that these temperatures are near optimal for seedling growth, more information should be obtained about the effect on growth of night temperatures from 0° to 10°C.

Shepherd, according to Cremer (1968), found that best diameter growth of radiata pine occurs in Victoria, Australia, when daily minima and maxima average 10° and 24°C respectively. For 1-year-old radiata pine growing in a nursery at Rotorua, New Zealand, Rook (1971) observed relative growth rates, for dry matter production, of 0.168 g/g/wk when the mean, mean daily maximum and mean daily minimum temperatures were 15.5°, 21°, and 11°C respectively, and when these remained fairly constant over the 3 month period of the experiment. Seedlings in a regime of 23°/11°C in the Duke Phytotron had a mean relative growth rate of 0.114 g/g/wk but the difference in the two rates could be due to several factors, including higher light intensities in Rotorua and different photoperiod treatments.

In interpreting differences between the NZ and CA seedlings it should be remembered that the NZ seed were from one controlled pollination only and are not necessarily indicative of the NZ population as a whole. Similarly, the CA seed were collected from only a few trees and cannot be considered as representative of the Cambrian population. The main difference in response to temperature of the two seed origins was that the NZ seedlings generally grew better than the CA seedlings under the colder day temperatures. At day temperatures of 32°C, and in some instances at 29°C, the CA seedlings grew faster than the NZ seedlings. It is interesting to note that the CA seedlings had higher root/shoot ratios than the NZ seedlings at all the 29° and 32°C day temperature regimes. At day temperatures lower than 29°C, seedlings from both origins had similar root/shoot ratios. Florence and Malajczuk (1970) found that NZ progenies of radiata pine showed slower height growth than any of four Australian progenies at low temperatures (19°/15°C). In fact, these authors claim that the NZ progenies, relative to their growth at high temperatures, grew less vigorously at low temperatures than progenies of other regions.

The 6-month-old NZ seedlings were on average 12% bigger than the CA seedlings, although the CA seed were 13% heavier than the NZ. Fourteen days after sowing, when the seedlings were transferred to their respective day/night temperature regimes, the CA seedlings were 2% heavier than the NZ seedlings. The relative growth rate data showed that the NZ seedlings were growing considerably (5.6%) faster than the CA seedlings over the first 3 months, but from 3 to 6 months there were no significant differences in relative growth rates between the two seedling origins. The initial difference in growth rate may be partly ascribable to germination energy, but other differences, e.g., food reserves, rate of leaf production, photosynthetic efficiency of the cotyledons or primary needles, could be involved.

It is generally accepted that seedlings from a controlled pollination are less variable than seed from an open-pollinated stand. There were no significant differences in the coefficients of variation between the NZ seed from a controlled pollination and the CA seed from an open-pollinated stand. The coefficients of variation obtained were undoubtedly reduced by grading the seed before sowing, when the abnormally large and small seed were removed, and again when the two smaller seedlings were culled to leave one seedling/pot. There were no significant trends of increasing variation in growth at the more extreme environments, but there was an increasing number of seedling deaths in those regimes combining high day and low night temperatures.

The crookedness associated with some but not all of the seedlings was apparently a result of the environmental conditions. Either high temperatures or water stress at critical times during growth, or both, could be the cause.

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APPENDIX

Summary of Experimental data for the New Zealand (NZ) and Californian (CA) seedlings grown for 6 months at different day/night temperature (°C) regimes

Height (cm)			Diameter (mm)			Shoot Dry Weight (g)			Root Dry Weight (g)			Total Plant Dry Weight (g)		
Treatment	Mean	MRT*	Treatment	Mean	MRT*	Treatment	Mean	MRT*	Treatment	Mean	MRT*	Treatment	Mean	MRT*
NZ 26/23	38.6	1- 8	NZ 23/5	6.6	1-10	NZ 20/5	9.53	1- 3	NZ 20/5	3.34	1- 4	NZ 20/5	12.87	1- 4
NZ 20/23	38.4	"	CA 23/17	6.6	"	NZ 26/5	8.57	2- 4	NZ 17/5	3.06	2- 7	NZ 23/5	11.41	2- 5
NZ 23/17	37.1	2-10	CA 23/23	6.3	2-12	NZ 23/5	8.38	"	NZ 23/5	3.03	"	NZ 26/5	10.71	3-12
NZ 20/17	37.1	"	NZ 23/17	6.1	3-13	NZ 29/5	7.09	3-10	CA 23/5	2.74	3-10	NZ 29/5	9.60	4-15
NZ 23/23	36.6	3-12	NZ 20/5	6.1	"	NZ 20/23	6.81	"	NZ 29/5	2.51	4-11	NZ 17/5	9.33	"
NZ 29/17	36.3	"	CA 23/5	6.1	"	NZ 26/23	6.39	4-10	CA 17/5	2.42	"	CA 23/5	9.10	6-17
NZ 29/23	35.8	"	NZ 23/11	6.0	4-13	CA 23/5	6.36	"	CA 20/5	2.22	5-13	CA 17/5	8.65	7-17
NZ 26/17	34.1	4-14	NZ 29/5	6.0	5-14	NZ 23/17	6.30	"	CA 26/5	2.20	6-15	NZ 20/23	8.52	8-17
NZ 32/23	34.0	5-15	NZ 26/5	5.8	6-15	NZ 17/5	6.26	"	NZ 26/5	2.14	6-17	CA 20/5	8.26	9-17
CA 23/17	33.0	6-16	NZ 32/17	5.8	7-16	CA 17/5	6.23	"	CA 32/5	2.02	8-20	NZ 23/17	8.22	10-18
NZ 32/17	32.9	7-18	NZ 20/17	5.8	"	NZ 20/17	6.05	5-11	NZ 23/17	1.92	"	NZ 26/23	7.83	11-19
CA 29/17	32.9	"	NZ 26/17	5.8	"	CA 20/5	6.04	"	CA 29/5	1.87	9-21	CA 26/5	7.72	11-22
NZ 20/29	31.6	7-20	CA 32/5	5.8	"	NZ 23/23	6.01	"	NZ 20/23	1.72	"	NZ 23/23	7.59	11-23
NZ 23/29	30.8	8-21	NZ 20/23	5.7	8-17	CA 23/17	5.70	6-13	NZ 23/23	1.58	9-22	NZ 20/17	7.46	"
NZ 20/5	30.8	"	CA 23/11	5.7	"	NZ 17/23	5.62	"	CA 23/23	1.51	12-23	CA 23/17	7.16	11-24
CA 23/23	30.4	9-22	CA 26/17	5.7	"	CA 26/5	5.52	7-14	NZ 17/17	1.49	"	NZ 17/23	6.94	"
NZ 23/11	30.4	"	CA 26/5	5.7	"	CA 23/23	5.31	"	CA 23/17	1.46	13-24	CA 23/23	6.82	"
NZ 17/23	30.3	"	NZ 23/23	5.6	9-18	CA 20/17	4.96	"	NZ 26/23	1.44	"	NZ 17/17	6.30	13-25
NZ 23/5	30.2	"	CA 26/11	5.6	"	NZ 17/17	4.81	7-15	NZ 20/17	1.42	"	NZ 26/17	6.15	"
NZ 26/11	29.9	"	NZ 26/23	5.5	"	NZ 29/23	4.81	"	NZ 23/11	1.42	"	CA 29/5	6.12	14-26
NZ 26/29	29.8	"	CA 29/17	5.5	"	NZ 26/17	4.76	"	NZ 26/17	1.40	"	CA 20/17	6.09	"
CA 26/17	29.7	"	NZ 17/5	5.4	"	CA 29/17	4.73	7-16	CA 17/17	1.37	14-25	NZ 23/11	6.09	"
NZ 17/17	29.3	10-23	CA 17/5	5.4	"	NZ 29/17	4.70	"	NZ 17/23	1.32	"	CA 17/17	5.96	"
CA 20/17	29.2	"	CA 20/17	5.3	"	NZ 23/11	4.67	"	CA 23/11	1.28	15-26	CA 26/17	5.82	"
NZ 29/5	27.9	11-24	CA 17/17	5.3	"	NZ 23/29	4.65	"	CA 26/17	1.23	16-27	CA 29/17	5.78	"
CA 23/29	27.3	"	CA 29/5	5.3	"	CA 26/17	4.59	"	CA 20/17	1.13	17-28	NZ 29/23	5.75	"
CA 17/17	27.1	"	CA 32/23	5.3	"	CA 17/17	4.59	"	CA 17/23	1.10	"	CA 23/11	5.73	"
CA 26/11	27.1	"	CA 32/11	5.2	11-19	CA 17/23	4.56	"	NZ 26/11	1.09	"	NZ 29/17	5.71	"
CA 32/17	26.9	"	CA 20/5	5.2	"	CA 23/11	4.44	"	NZ 17/11	1.06	19-28	CA 17/23	5.66	"
NZ 20/11	26.8	"	NZ 29/11	5.2	"	NZ 32/23	4.43	"	CA 29/17	1.06	"	NZ 23/29	5.65	"

NZ 29/11	26.6	13-25	CA 32/17	5.1	"	CA 26/23	4.40	8-17	CA 26/11	1.02	"	CA 32/5	5.55	16-27
CA 26/23	26.2	13-27	NZ 20/11	5.1	"	NZ 20/29	4.26	"	NZ 29/17	1.01	"	NZ 32/23	5.34	"
NZ 17/29	26.1	"	NZ 17/17	5.1	"	CA 29/5	4.25	9-18	NZ 17/29	1.00	"	CA 26/23	5.32	"
CA 32/11	25.2	16-28	NZ 29/23	5.1	"	CA 20/23	4.25	"	NZ 23/29	0.99	"	NZ 20/29	5.19	16-28
CA 17/23	25.2	"	NZ 29/17	5.1	"	NZ 26/11	3.91	9-19	NZ 20/11	0.97	"	CA 20/23	5.19	"
CA 20/23	25.0	"	CA 20/23	5.1	"	CA 26/11	3.89	"	CA 32/17	0.97	"	NZ 26/11	5.00	"
CA 17/29	24.6	"	NZ 26/11	5.0	"	CA 23/29	3.85	"	CA 17/11	0.95	"	CA 26/11	4.91	"
CA 20/29	24.4	17-28	NZ 32/23	5.0	"	NZ 17/29	3.69	"	NZ 29/23	0.94	"	NZ 17/29	4.69	20-29
NZ 26/5	24.3	"	CA 20/11	5.0	"	NZ 20/11	3.69	"	CA 20/11	0.94	"	CA 23/29	4.66	"
CA 23/11	24.1	"	CA 26/23	5.0	"	NZ 32/17	3.60	12-20	CA 20/23	0.94	"	NZ 20/11	4.64	"
CA 32/23	23.6	"	CA 29/11	5.0	"	CA 20/11	3.55	"	NZ 20/29	0.94	"	CA 20/11	4.49	21-30
NZ 17/5	23.5	"	NZ 23/29	4.9	"	NZ 26/29	3.54	"	CA 26/23	0.92	"	CA 32/17	4.48	"
NZ 32/11	23.3	19-28	NZ 17/23	4.9	"	CA 32/5	3.53	"	NZ 32/23	0.91	"	NZ 32/17	4.46	"
CA 29/11	23.1	"	CA 23/29	4.9	"	CA 32/17	3.52	"	NZ 32/17	0.86	"	NZ 17/11	4.23	"
CA 20/11	22.9	"	CA 29/23	4.8	"	NZ 29/11	3.29	"	CA 23/29	0.81	"	NZ 26/29	4.22	"
NZ 29/29	22.1	"	CA 17/23	4.8	"	CA 20/29	3.27	"	CA 29/11	0.79	"	CA 20/29	4.03	"
CA 26/29	21.8	"	NZ 32/5	4.8	"	CA 32/23	3.27	"	CA 20/29	0.76	"	NZ 29/11	4.02	"
CA 23/5	21.0	"	NZ 32/11	4.7	13-20	NZ 17/11	3.17	"	CA 32/23	0.74	"	CA 32/23	4.01	"
CA 29/29	20.5	"	CA 20/29	4.6	13-21	CA 29/11	3.06	"	NZ 29/11	0.73	"	CA 29/11	3.85	"
CA 29/23	20.2	"	NZ 17/11	4.6	"	CA 17/29	3.02	"	CA 17/29	0.72	"	CA 17/11	3.76	"
CA 20/5	18.9	"	NZ 17/29	4.6	"	CA 29/23	2.97	"	CA 29/23	0.72	"	CA 17/29	3.74	"
CA 26/5	18.5	"	NZ 26/29	4.6	"	CA 17/11	2.81	"	CA 32/11	0.71	"	CA 29/23	3.68	"
NZ 17/11	18.4	"	CA 26/29	4.5	"	CA 26/29	2.42	"	NZ 26/29	0.68	"	CA 32/11	2.98	"
NZ 32/29	18.4	"	NZ 20/29	4.4	"	CA 32/11	2.27	"	CA 26/29	0.56	"	CA 26/29	2.97	"
CA 17/5	17.0	"	CA 17/11	4.3	"	NZ 29/29	2.16	"	CA 32/29	0.48	"	NZ 29/29	2.42	"
CA 32/29	16.9	"	CA 17/29	4.1	"	NZ 32/11	1.95	"	NZ 32/29	0.41	"	NZ 32/11	2.34	"
CA 32/5	16.1	26-29	CA 29/29	3.9	"	CA 29/29	1.94	"	NZ 32/11	0.39	"	CA 29/29	2.26	"
CA 17/11	15.2	"	CA 32/29	3.5	"	CA 32/29	1.66	"	CA 29/29	0.32	"	CA 32/29	2.14	"
CA 29/5	14.8	"	NZ 29/29	3.4	"	NZ 32/29	1.50	"	NZ 29/29	0.27	"	NZ 32/29	1.91	"
NZ 32/5	7.4	"	NZ 32/29	3.4	"	NZ 32/5	1.16	"	NZ 32/5	0.17	"	NZ 32/5	1.33	"

* Mean values having a common number do not differ significantly at the 1% level using Duncan's multiple range test (Duncan, 1955). For example the height of the CA $23^{\circ}/23^{\circ}$ seedlings differs significantly from the NZ $26^{\circ}/23^{\circ}$ seedlings but not from the NZ $23^{\circ}/17^{\circ}$ because the numbers 9 and 10 are common to CA $23^{\circ}/23^{\circ}$ and NZ $23^{\circ}/17^{\circ}$, but CA $23^{\circ}/23^{\circ}$ and NZ $26^{\circ}/23^{\circ}$ have no common numbers.