INFLUENCE OF PHOTOPERIOD ON GROWTH AND WOOD FORMATION OF *PINUS RADIATA*

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ABSTRACT

Pinus radiata D. Don plants (seedlings; and rooted cuttings of two size-classes from semi-adult trees) were grown in the DSIR climate laboratory under different photoperiod treatments. The study was begun just prior to the summer solstice and ran for two consecutive 16-week treatment periods. The eight treatments included combinations of increasing, decreasing, constant long (16-h), and constant short (8-h) photoperiods.

Height increment showed marked differences between treatments. Although differing in pattern of height increment, the three classes of plant showed definite similarities in response to the various treatments. Short days and decreasing daylengths gave reduced height increment compared with long days. Maximum height increment and branch elongation were observed with increasing daylength followed by sustained long days. The responses to photoperiod were evidently superimposed upon an underlying tendency for elongation to occur in flushes interspersed with comparative rest periods.

Diameter growth showed less-pronounced differences between treatments and showed no clear parallel with height increment responses to photoperiod. There appeared to be some tendency for greater diameter increment to occur under decreasing photoperiod. The wood quality parameters associated with tracheid dimensions differed significantly between treatments. There was a tendency towards latewood characteristics in material with less active shoot elongation, i.e., short or decreasing photoperiod treatments, although not all treatment differences could be explained in terms of this effect.

Overall, there appeared to be a response to daylength shift over and above any response to absolute daylength.

INTRODUCTION

In many woody plants, photoperiod plays a prominent role in the rhythms of shoot growth (Downs, 1962; Romberger, 1963; Wareing, 1969). *Pinus radiata* D. Don,

however, has been rated as less photoperiodically responsive than many other trees (Vaartaja, 1959; Downs, 1962). Vaartaja (1959) found no increase in height growth under an artificial 16-h photoperiod compared with an 8-h photoperiod, and Downs (1962) observed only a 17% increase with 16-h days. Richardson (1964) however subsequently obtained evidence of a greater photoperiod response in height increment, while Sweet (1966) noted approximately double the shoot elongation under continuous light compared with 9-h days. Hellmers and Rook (unpubl. data), working with seedlings up to 6 months old, observed 88% greater height growth and 34% greater dry weight with an artificial 16-h photoperiod than with 8-h photoperiod. Florence and Malajczuk (1970) obtained a mean height for *P. radiata* seedlings grown under long photoperiod double that for seedlings grown under short photoperiod, and 63% greater mean total-plant dry-weight under the long photoperiod.

In the field *P. radiata* shows obvious seasonal growth rhythms in New Zealand, where the yearly range in photoperiod of approximately 8 to 16 h is wide enough to evoke many of the known photoperiodic controls.

Moreover, height increment (Doran, 1974) and diameter increment (Hedderwick; *see* Jackson *et al.,* 1976) of *P. radiata* have been observed to accelerate from minimal winter rates before there was any general rise in mean temperatures, thus suggesting an important influence of some other environmental factor, possibly photoperiod. A histological study (Barnett, 1971) has confirmed that cambial activity slows, but does not cease in young *P. radiata* trees at Rotorua in winter, and that both xylem cell expansion and cell division accelerate again shortly before the spring rise in mean temperatures. Similar observations of reactivation of cambium in late winter have been made for *P. radiata* in 1-year-old seedlings at Rotorua (Jenkins, 1975) and on trees in Canberra, Australia (K. R. Shepherd and H. Drielsma, unpubl. data), and in Victoria (Skene, 1969).

Wood properties, in particular the earlywood/latewood differentiation, have frequently been reported as being influenced by photoperiod treatment (e.g., Larson, 1962; Wodzicki, 1964; Denne and Smith, 1971; Heide, 1974). Typically, the production of earlywood has been associated with treatments which promote shoot elongation, raising the question of whether earlywood production is an immediate consequence of shoot extension rather than a direct effect of photoperiod.

Work on daylength has concentrated on studying the response of plants to constant photoperiods, or where daylength has been changed it has generally been changed abruptly. The few published studies using progressive increases and decreases in daylength (Robak, 1962; Magnesen, 1969; Leikola, 1970) did not include any comparison with constant long and short photoperiods.

Burdon (1974) has hypothesised that directional shift in daylength rather than any absolute daylength may be the critical factor in determining the photoperiod response of *P. radiata* in the field, but results of pilot trials were generally ambiguous.

The present study investigates further the reaction of seedlings and more adult material of *P. radiata* to photoperiod, including the reaction to slowly changing photoperiods compared with constant long or short photoperiods. The influence of treatments was assessed on growth and on the type of wood formed.

MATERIAL

Since seedlings with their indeterminate height-growth pattern might be expected to respond differently from older *P. radiata* which tend to grow in flushes (often not well-defined) from pre-formed buds, both seedlings and rooted cuttings were used in this study.

The seedlings, approximately 35 cm tall, had been raised as $1\frac{1}{2}/0$ stock in the Forest Research Institute nursery at Rotorua, and were transplanted into 3-litre pots with a 1 : 1 mixture of peat and topsoil approximately 2 months before the experiment. At the start of the experiment the seedlings had green tufts of primary needles at their apices, although the appearance of most of these tufts indicated a comparative lack of current extension growth.

One hundred and eight rooted cuttings, representing clonal material from twelve parent trees, were used in the study. Forty-eight of the cuttings ("small cuttings") were approximately 35 cm tall at the start of the study. These represented eight cuttings in each of six clones which were from 6-year-old parent trees, and had been grown for 2 years in the nursery before being transplanted into 9-litre pots of topsoil approximately 4 months before the start of the study. Three of these clones were from trees of high wood density, and the other three were from low-density parent trees. At the start of the experiment the small cuttings had very small, tightly sealed buds at the apices, and showed no signs of active shoot-extension.

The remaining cuttings ("large cuttings") were from 7-year-old ortets, representing a further six clones, and were approximately 100 cm tall. These cuttings were established and grown in the nursery for 2 years, then transplanted into 9-litre pots of topsoil 18 months before the start of the experiment. Thus, they were from trees 1 year older and they had been set as cuttings 1 year earlier than the small cuttings. One large cutting per clone was allocated to each treatment. In addition, three of these large clones had one extra ramet in each of the four initial photoperiod treatments; this was harvested at the mid-term of the experiment, 16 weeks after the start. The large cuttings, although they had sealed buds at their apices, showed active sub-apical shoot elongation at the start of the experiment.

EXPERIMENTAL

The controlled-environment facilities of the Climate Laboratory, Plant Physiology Division, DSIR, Palmerston North, were used. The experiment was started on 17 December, just before the summer solstice, when the natural daylength was slightly less than 16 h. The day before the start of the experiment the plants were transported approximately 350 km south from Rotorua to Palmerston North.

Four controlled-environment rooms were used to give four treatments initially and, by redistributing plants and changing photoperiod schedules at the mid-point of 16 weeks, eight photoperiod treatments were finally obtained (Table 1). Changes in photoperiod were made at weekly intervals. After the first 16 weeks all photoperiods were held for a week at either 8 h or 16 h before changes began again. At the end of the experiment, during weeks 33 and 34, final daylengths were maintained. For purposes of recording responses the following experiment periods were designated:

         Period 1:   0- 8 weeks   Period 3:   16-24 weeks
         Period 2:   8-16 weeks   Period 4:   24-34 weeks

TABLE 1—Photoperiod treatments

Treatment	Photoperiod during weeks 1-17	Photoperiod during weeks 18-34
DS	Decreasing from 16 to 8 h	Short constant 8 h
IL	Increasing from 8 to 16 h	Long constant 16 h
SI	Short constant 8 h	Increasing from 8 to 16 h
SS	Short constant 8 h	Short constant 8 h
LD	Long constant 16 h	Decreasing from 16 to 8 h
LL	Long constant 16 h	Long constant 16 h
DI	Decreasing from 16 to 8 h	Increasing from 8 to 16 h
ID	Increasing from 8 to 16 h	Decreasing from 16 to 8 h

The photoperiod consisted of an 8-h photosynthetic period with irradiance (P.A.R. 400-750 nm) levels of 171 to 185 W/m^2 (approx. 700 $\mu E/m^2/s$) throughout the experiment, for a total light-energy input over the 8 h of *ca.* 20 000 000 $\mu E/m^2$. The photoperiod extensions were provided by tungsten iodide lamps giving 7.0 $\pm$ 0.5 W/m^2 (approx. 28 $\mu E/m^2/s$) at the tops of the plants, and entailed an equal extension period on either side of the photosynthetic period. Therefore, even for the longest photoperiod extension the additional energy-input from the incandescent lamps was very little, being not more than about 800 000 $\mu E/m^2$ or 4% of the total, when the day was extended to 16 h. For the shortest photoperiod the incandescent lamps were switched on and off 5 min before and after the high-irradiance lamps. The increasing and decreasing photoperiods were provided by increasing or decreasing the duration of the photoperiod by 30-min steps at the start of each week throughout the 16-week period.

Day/night temperatures of 20°/5°C $\pm$ 0.5°C were based on the results of a temperature study for this species by Hellmers and Rook (1973). In the present study the day-to-night and night-to-day temperature changeovers were gradual over 2.5 h. The day temperature coincided with the full 8 h of high irradiance. Relative humidities during the day and night periods were 78 $\pm$ 5% (5 mb VPD) and 65 $\pm$ 5% (3 mb VPD), respectively.

The plants were watered as dictated by the drying of the soil surface, and they were saturated every 2 weeks immediately after the height and diameter measurements were completed. During the study the trees were supplied with quarter-strength modified Hoagland nutrient solution in the first week of each month. To reduce positional effects the trolleys holding the plants were rotated weekly within the controlled-environment rooms.

MEASUREMENTS

Measurements of height and stem diameter (5 cm above soil surface) were made every 2 weeks. Twelve seedlings were harvested from each of the four initial photoperiod treatments at the half-way point of the experiment, and from each of the eight treatments at the end of the study. The plants were separated into foliage, stemwood, bark, roots, and, in the final harvest only, branches (wood plus bark). Components were oven-dried

at 80°C for more than 48 h and weighed. The lengths of the three longest branches on each seedling were measured also at the end of the study.

For each cutting the length of the last fully elongated shoot cycle* of the leader was measured and the numbers of needles on that length of stem were counted, at the final harvest. Needle densities were calculated. Needle lengths were recorded, on the small cuttings only, for the previous shoot cycle.

The number of white root tips and their length were recorded for all cuttings at the final harvest. Since the amount of new root growth was very much greater in the seedlings than in the cuttings, a visual grading of root growth was made for seedlings. A three-point scale of root abundance was based on the numbers and lengths of white tips at the soil/pot interface; counts were made on 24 seedlings to provide a quantitative base for the scale.

Xylem samples of the newly-formed wood from the stem 5 cm above the soil surface were taken from six seedlings per treatment and from all cuttings at the final harvest. Samples were fixed in glutaraldehyde, embedded in glycol methacrylate (Feder and O'Brien, 1968), and sectioned. A filar micrometer eyepiece was used to measure radial diameter and tangential double wall thickness of the outermost fully differentiated xylem cells from each of 25 separate radial files. A wound mark placed in the wood 3 weeks before the plants were harvested (Wolter, 1968) was used as a marker for cell counts from 10 radial files to assess relative cell production. Counts were also made of cells from 10 radial files of the cambial region which included the cambial zone and the zone of radially-expanded xylem and phloem cells (Wilson et al., 1966).

Analyses of variance were used to test for significant treatment differences. Tukey test (5% probability level) was used for single comparisons of balanced sets of data, and Scheffé's test (5%) was used for unbalanced analyses and for multiple comparisons. Where appropriate, the square root transformation was used for analysis, although values presented in figures and tables are arithmetic means. With the wood properties, analysis of covariance was used in addition to test for residual treatment differences after adjusting for individual covariance on preceding height increment.

Additional measurements were made of bud lengths, chlorophyll contents, and patterns of ^{14}C-photosynthate distribution within the plants, but limitation of space prevents presentation of these results here. This information is available on request from the editor in an unpublished report by the authors (1976).

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* Shoot cycle (cf. "Internode", as defined by Shaw — 1914) refers to the interval along the stem which is normally demarcated by the points of emergence of consecutive branch clusters. Sometimes, however, branches may not be present, and the limit of a cycle is recognisable as the base of a zone of bare cataphylls which do not subtend fascicles. A slowing or cessation of elongation of the shoot axis (ignoring short-term effects of temperature) between elongation maxima of successive shoot cycles is termed a **resting phase**. The occurrence of a maximum in shoot elongation before or after a resting phase is for present purposes termed a **flush**, which may embrace the elongation of more than one shoot cycle. It must be emphasised that the distinction drawn here between flushes and rest periods as they occur in **P. radiata** is typically quantitative rather than qualitative. The definition of a resting period does not imply anything about the rate of primordial initiation.

RESULTS

Height Increment

Large cuttings

Height growth generally remained fairly rapid over the first 8 weeks as the already elongating shoot cycle continued to elongate. The increment rate then declined before increasing again over the second half of the study (Fig. 1). This pattern was related to some plants showing a resting phase. In three treatments, DS, SS, and LD, however, no clear resurgence of growth occurred. Only after period 2 did the responses to initial photoperiod treatment become statistically evident; significantly greater increment was associated with initial increasing photoperiod rather than with initial decreasing photo-period. In period 4, plants in increasing and long-day photoperiods showed greatest height growth.
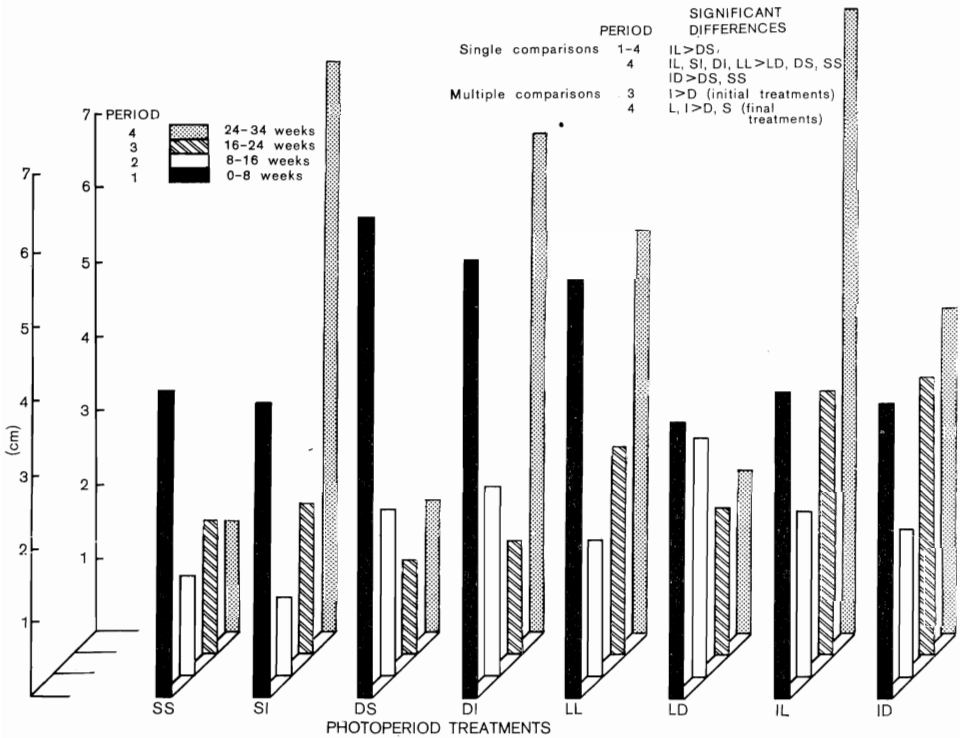

FIG. 1—Height increments — large cuttings.

Small cuttings

Height growth was slow during periods 1 and 2 (Fig. 2), amounting only to a general lengthening of the sealed buds. The height increment that did occur in the growth rooms was essentially the elongation of only a single shoot cycle. As in the large cuttings, responses in height increment up to the 24-week point could be related to the photoperiod treatment provided in the first half of the study. Where an increasing photoperiod was provided in the first 16 weeks, greatest height increment occurred
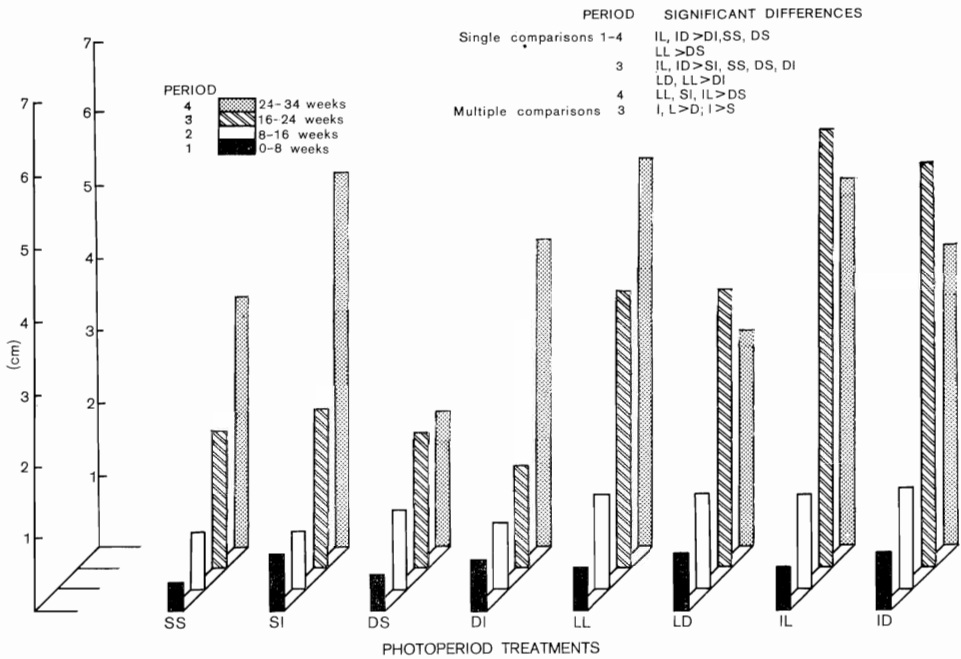
FIG. 2—Height increments — small cuttings. The significance differences in the multiple comparisons refer to final treatments.

in the third 8-week period, and this growth was significantly greater than with the initial short or decreasing photoperiods. Initial long photoperiods were associated with intermediate height increments which were significantly greater than the increments of plants given decreasing photoperiods in the first half of the experiment. In period 4 the LL, IL, and SI treatments produced the greatest height increments, while increment in the DS treatment was very low. Total height increment was greatest in the IL, ID, and LL treatments, and least in the DI, SS, and DS ones (Fig. 3).

Seedlings

Only a single shoot cycle elongated in the growth rooms. In contrast to the other material the seedlings showed pronounced treatment responses by the end of period 2, despite very slow initial growth (Fig. 4). By this stage the seedlings under the long and increasing photoperiods had grown more than twice as much as the seedlings given a short photoperiod. As with the cuttings, the responses during period 3 related strongly to the initial 16-week treatments. Initial long-day and increasing-photoperiod treatments gave significantly greater increment than initial decreasing treatments. The greatest height increment in period 4 occurred in the DI and IL treatments, while much slower height increment occurred with DS, LD, and ID treatments. In multiple contrast tests final long-day and final increasing-photoperiod treatments were superior to final decreasing treatments. Total height increment was significantly greater in the IL treatment than in the DS treatment (Fig. 5). None of the treatments, however, prevented the onset of a fairly well-defined growth flush.

FIG. 3—Representative individuals of small cuttings from the eight treatments, shown just
prior to final harvest. Total height increment of individuals in IL, LL, and ID
treatments was significantly greater than in DI, SS, and DS treatments. Marks
show approximate height at beginning of the study. Plants are photographed against
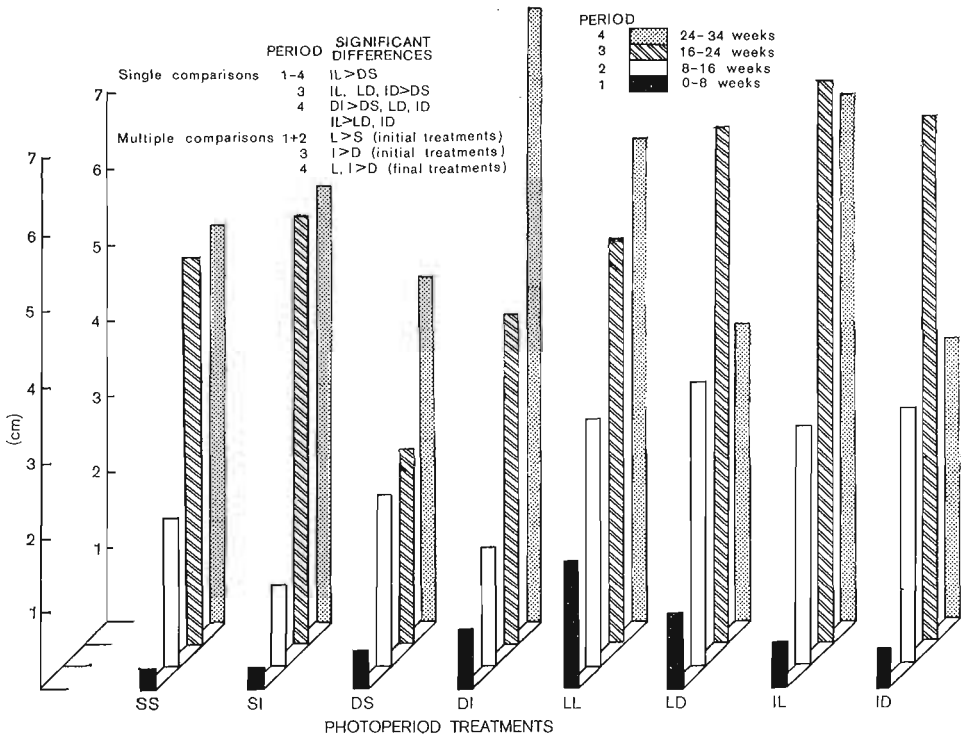a 10-cm grid.

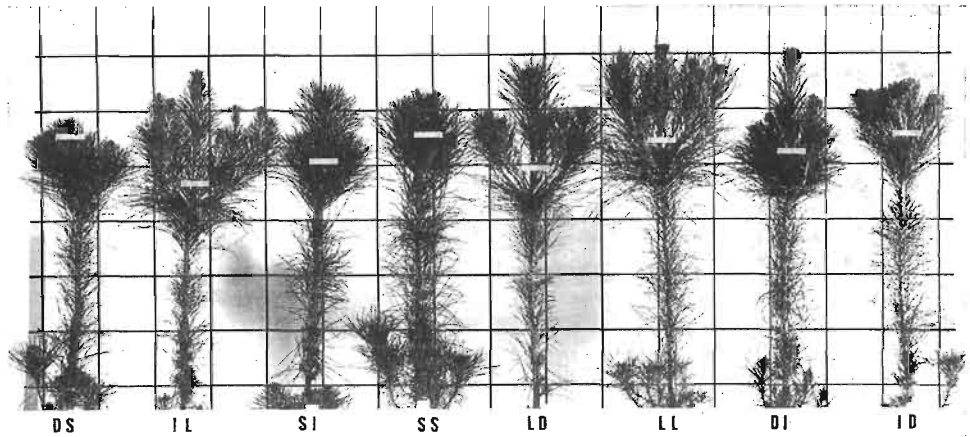FIG. 4—Height increments — seedlings.

FIG. 5—Representative seedlings from the eight treatments in the experiment, shown just
       prior to final harvest. Total height increment was significantly greater in the
       IL treatment than in the DS treatment. Branch growth was greatest in the IL
       and LL treatments.

Diameter Increment

Even though all the diameter measurements were made on each plant at a position
marked on the stem, repeatability of measurements was poor, especially in cuttings.
This variability was attributable to the rough bark and some resin flow.

There were no significant differences in diameter increment with photoperiod for
the small cuttings. Trees in the large-cuttings group, under a decreasing photoperiod,
produced significantly greater diameter increments than did those under short or long
photoperiods in the second quarter of the study. There were no significant differences
in the latter half of the study for the large cuttings.

Diameter growth on seedlings in the first half of the experiment tended to be
greater under both the decreasing and increasing photoperiods than the long photo-
period (Fig. 6) although differences were not satistically significant. However, for
the latter half of the study, seedlings in the DI, LD, and ID treatments had the largest
diameter increments, being significantly more than in SS or DS treatments.

Lengths of Needles, Shoot Cycles, and Branches

There were no significant differences in needle and shoot cycle characters for large
cuttings. For the small cuttings the IL treatment, although resulting in significantly
longer shoot cycles than the DS and SS photoperiods, gave no corresponding differences
in fascicle numbers (Table 2). Nevertheless, the differences in needle density were
not significant. Although the needle lengths had been measured on the small cuttings on
the second elongated shoot cycle from the apex, these needles had undergone partial
expansion prior to the start of the experiment. Long days appeared to give longer
needles than short days.

At the final harvest, branches of the IL-treated seedlings were particularly long,

being significantly longer than those of all the other treatments except those of the LL treatment (Table 2, Fig. 5). Seedlings from the latter treatment had significantly longer branches than did those from the SI treatment.
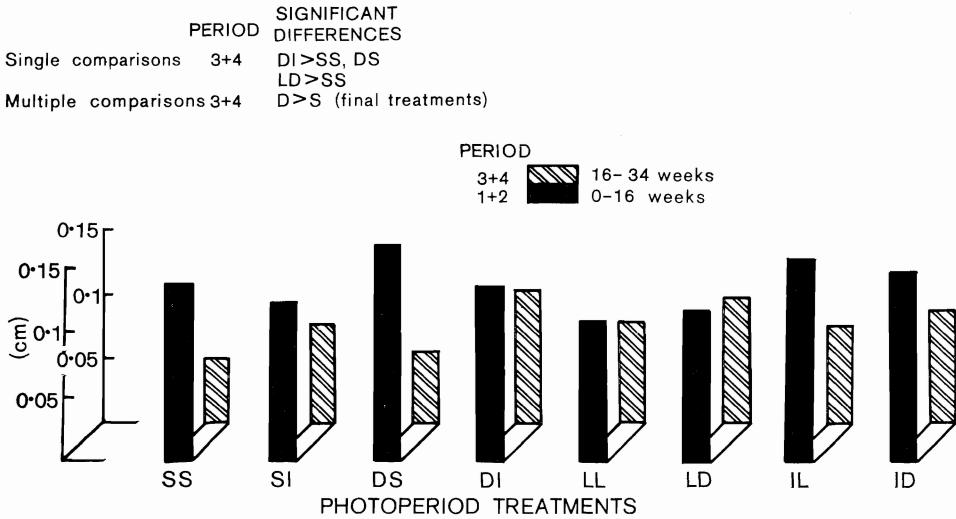

FIG. 6—Diameter increments — seedlings.

TABLE 2—Effect of photoperiod on shoot and needle growth of the small cuttings and on branch growth of the seedlings

Treatment	Small Cuttings			Seedlings
	Length (mm) of shoot cycle elongated during treatment	Needle density on cycle (fascicles/mm)	Fascicle length (mm)	Branch length (mm)
SS	66	1.60	85	95
SI	95	1.09	95	75
DS	50	1.93	108	112
DI	80	1.42	109	107
LL	106	1.18	—	144
LD	71	1.78	125	120
IL	148	.84	—	188
ID	112	.96	90	119
Significant differences (Tukey 5%)	IL>DS, SS	N.S.*	LD>SS, SI	IL>SI, DI, SS, DS, LD, ID, LL>SI

* N.S. denotes not significant ($P > 0.05$)

Root Growth

Scoring on a three-point scale of relative abundance of white root tips at the soil/pot interface failed to show significant differences for the seedlings. However, the plants in the SI treatment appeared to have the most abundant new root growth. Actual counts showed that these seedlings did have a large number of roots (average = 160) at the soil surface, which was significantly more than seedlings in the SS (82) and DI (71) treatments, but not significantly different from the DS (122) treatment. This result accords with the high root/shoot ratios obtained in the SI photoperiod treatment (Table 3). With the great variability within treatments for both types of cuttings there were no significant treatment differences.

TABLE 3—Oven dry weights (g) of seedling components (averages from 12 seedlings except where ‡ indicates averages from 6 seedlings)

A. Mid-term Harvest

Treatment	Foliage (incl. branches)	Stemwood	Stem bark	Stem	Roots	Root/shoot ratio	Shoot	Total
S	9.5	3.7	2.2	5.9	7.5	0.50	15.4	22.9
D	12.2	4.6	2.3	6.9	7.6	0.42	19.1	26.7
L	14.5	5.0	2.5	7.5	8.4	0.39	22.0	30.4
I	10.9	4.1	2.3	6.4	7.6	0.45	17.3	25.0
Significant differences (Tukey 5%)	L>I, S	N.S.	N.S.	N.S.	N.S.	S>L	L>S	L>S

B. Final Harvest

Treatment	Foliage	Stem-wood‡	Stem bark‡	Branches‡ (wood plus bark)	Stem plus branches*	Roots	Root/shoot ratio	Shoot	Total
SS	18.7	5.8	3.2	1.4	10.8	11.5	0.39	29.5	41.1
SI	19.8	7.3	3.7	1.4	11.4	13.7	0.44	31.2	44.9
DS	19.0	7.3	4.3	1.9	11.7	12.5	0.41	30.7	43.3
DI	19.8	7.9	4.5	1.8	12.9	11.3	0.35	32.7	43.9
LL	23.1	8.6	4.7	3.4	14.1	12.1	0.33	37.2	49.3
LD	20.2	7.1	3.9	1.9	12.3	10.4	0.33	32.5	42.9
IL	22.1	7.1	4.0	2.2	13.5	12.2	0.34	35.6	47.7
ID	21.6	7.6	4.1	2.2	14.2	12.1	0.34	35.8	48.0
Significant differences (Tukey 5%)	N.S.	DI, LL>SS	LL, DI>SS	LL>all	ID, LL>SS	N.S.	SI>LL, LD	LL>SS	N.S.

* Preceding columns do not sum to this value because of different sample sizes

Total Seedling Dry Weight

Mid-term harvest

At this stage branchwood was a very minor part of the total dry weight of the seedlings, and was included with the foliage component (Table 3). The short-day treatment tended to give less weight in all components, but had the highest root/shoot ratios. Plants grown under long days had a significantly greater weight of foliage than those grown under increasing or short photoperiods.

Final harvest

For stem, bark, and branch components, dry weight was greatest in the LL photoperiod treatment. The DI, ID, and IL treatments also tended to give above-average dry weights. Seedlings from the SS treatment had the least dry weight for these components. In the branchwood component the superiority under the LL treatment was very marked. The total above-ground dry weight fraction was greatest in the seedlings grown with the LL photoperiod, followed by those in the ID and IL conditions. Root/shoot ratios were highest in seedlings of the SI, SS, and DS treatments, but only the extreme differences, SI *v.* LL and LD, were significant.

Wood Properties

Large cuttings

The plants from the IL photoperiod treatment had relatively thin cell walls and large lumens with the result that ratios of cell wall thickness/lumen diameter (wall/lumen) and cell wall thickness/cell diameter (wall/diameter) were low for this treatment (Table 4). This last ratio was significantly lower than found under the DS and SS treatments. By Mork's (1928) definition of latewood, three treatments caused latewood formation (i.e., wall/lumen ratios greater than 0.5) with the DS treatment causing the most-marked latewood formation, followed by the SS and LD treatments. Results of contrasting treatments are illustrated in Fig. 7. Wall thickness and wall/lumen and wall/diameter ratios were negatively correlated with height increment, lumen positively correlated, and cell diameter showed no clear trend. With analyses of co-variance, adjusting for preceding height increments, none of the treatment differences was statistically significant ($P \geq 0.2$).

Small cuttings

At the final harvest the measurements of the cross-sectional xylem cell dimensions showed that the clones selected for high wood density had significantly smaller cell diameters than the low-density clones (Table 4). Cell walls tended to be thicker and lumens smaller in the high-density clones, and the wall/lumen and wall/diameter ratios were significantly higher than in the low-density clones.

The responses to photoperiod were similar for both the high- and low-density clones. Between treatments the only significant differences were in the cell wall/diameter ratio, where the LD treatment gave a significantly higher ratio than the IL, SI, and LL treatments. There were also significantly higher ratios in the plants of the DI photoperiod treatment than in those of the SI treatment.

All tracheid dimensions showed significant average regressions on preceding height increment within treatment/density subclasses, these being positive for lumen and

TABLE 4—Xylem cell dimensions at final harvest

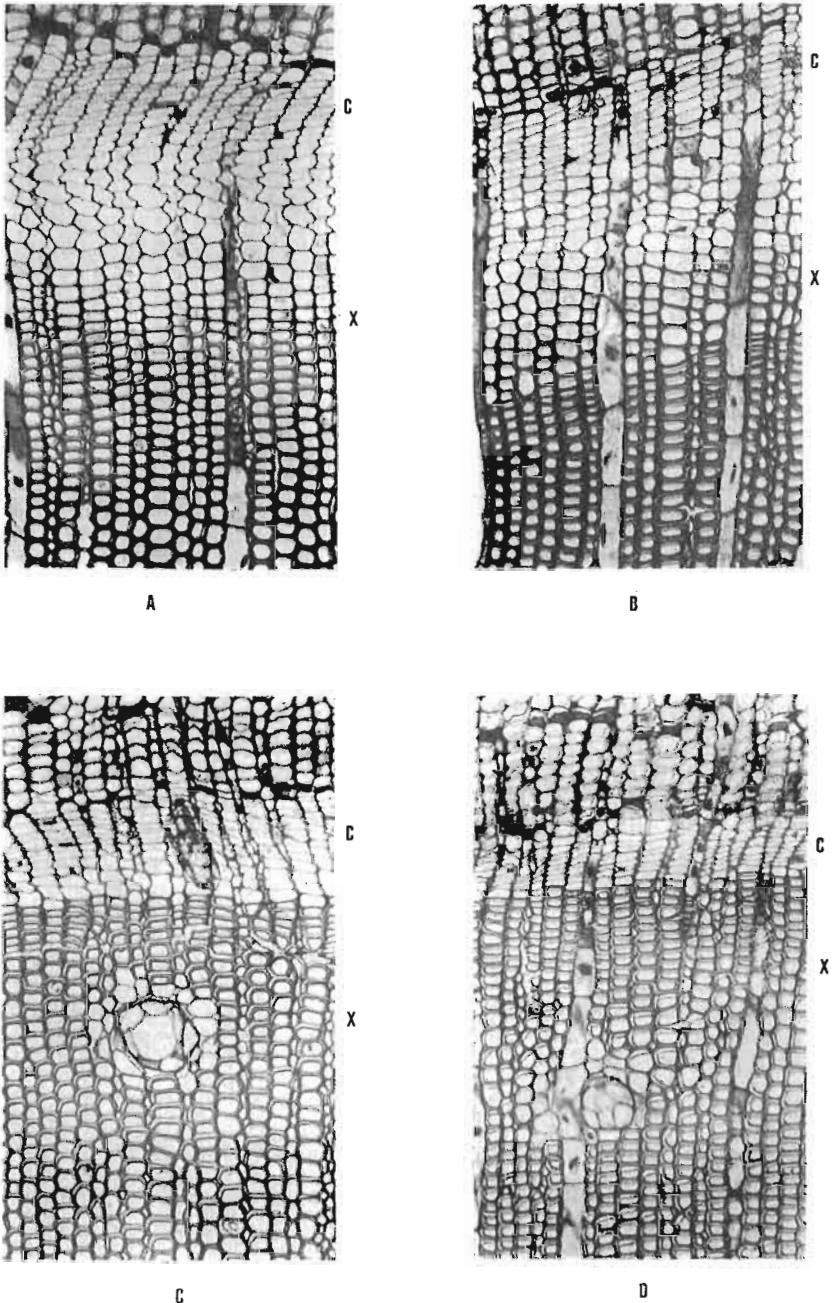| Treatments	Double wall thickness	Lumen	Diameter	Wall/lumen ratio	Wall/diameter ratio
	— — — — — μm — — — — —				
A. Large cuttings					
SS	4.77	8.6	13.3	0.56	0.36
SI	4.60	10.5	15.1	0.49	0.32
DS	4.75	8.2	13.0	0.62	0.38
DI	4.11	9.5	13.6	0.45	0.31
LL	3.80	8.7	12.5	0.46	0.31
LD	3.93	8.0	11.9	0.51	0.33
IL	3.50	11.7	15.2	0.31	0.23
ID	3.91	10.0	13.9	0.42	0.29
Significant differences (Tukey 5%)	N.S.	N.S.	N.S.	N.S.	SS, DS>IL
B. Small cuttings					
Density					
High	3.22⎤ N.S.	9.8⎤ N.S.	13.0⎤ *	0.337⎤ *	0.250⎤ *
Low	3.12⎦	11.3⎦	14.4⎦	0.268⎦	0.211⎦
Treatments					
SS	3.23	10.8	14.0	0.31	0.243
SI	2.95	11.4	14.3	0.27	0.220
DS	3.28	10.7	13.9	0.31	0.231
DI	3.21	9.7	12.9	0.34	0.241
LL	3.20	12.0	15.1	0.27	0.217
LD	3.32	9.1	12.4	0.38	0.259
IL	3.17	11.5	14.7	0.28	0.214
ID	3.01	9.3	12.4	0.34	0.251
Significant differences (Tukey 5%)	N.S.	N.S.	N.S.	N.S.	DI>SI, LD>IL, LL, SI
C. Seedlings					
SS	3.71	13.02	16.73	0.29	0.22
SI	3.56	13.95	17.50	0.26	0.21
DS	3.71	12.65	16.36	0.30	0.23
DI	3.45	15.67	19.13	0.22	0.18
LL	3.72	12.90	16.62	0.30	0.23
LD	3.76	12.56	16.33	0.31	0.23
IL	4.50	14.23	18.74	0.32	0.24
ID	3.77	11.75	15.50	0.32	0.24
Significant differences (Tukey 5%)	IL>all	DI>ID	N.S.	DS, LD, IL, ID>DI	
Multiple contrasts Scheffe 5%)	L>I	—	—	D>I	

* Denotes significant differences P < 0.05

FIG. 7—Photomicrographs of stem sections showing the cambial zone (C)
and xylem cells (X) matured during the treatment in a large cutting.
(Magnification 180 ×)
A. Treatment IL, earlywood formation and an active cambial zone
B. Treatment SI, change in type of wood formation is evident with this
   treatment
C. Treatment DS showing recent formation of latewood-type cells
D. Treatment LD showing recent formation of latewood-type cells

cell diameter, and negative for wall thickness, and wall/lumen and wall/diameter ratios. These regressions were particularly marked for wall/lumen and wall/diameter ratios ($R^2 > 0.4$, $P < 0.001$). With analysis of covariance the significance of treatment differences actually increased. However, the adjusted means for wall/lumen and wall/diameter ratios were not closely related to the unadjusted means, and did not appear to fall into any coherent pattern of response.

Cell number in the cambial region at the final harvest showed that the plants of the SS treatment had fewer new xylem cells than those of any other treatment. However, the differences were not statistically significant.

Seedlings

Wall thickness was significantly greater in the seedlings of the IL treatment than in seedlings of all other treatments (Table 4). Overall, seedlings that had been under the long days for the second half of the experiment had thicker cell walls than plants that had been under final increasing photoperiod. Wall/lumen and wall/diameter ratios were higher in the LL, DS, LD, IL, and ID treatments than in the seedlings of the DI treatment in which relatively thin cell walls were combined with relatively large cell diameters. Both ratios were significantly higher in the final decreasing than in the final increasing photoperiod treatments. The final long-day treatment resulted in wall thicknesses being significantly greater than those formed under final increasing photoperiod. There were no significant differences in cell diameter, but the lumens were largest in the plants of the DI treatment and smallest in the ID photoperiodic treatments.

Wall thickness showed an appreciable positive association with preceding height increment ($R^2 \cong 0.15$), lumen size and cell diameter weak positive correlations ($R^2 \leq 0.1$), and wall/lumen and wall/diameter ratios almost none. With the covariances adjustment, treatment differences in lumen size and cell diameter were non-significant ($P > 0.2$), but for wall thickness and wall/lumen and wall/diameter ratios the significance was almost unaltered.

DISCUSSION

The various photoperiod treatments influenced almost all parameters of plant growth. Despite differences in the patterns of growth and in the phase of flushing rhythm, the responses to photoperiod in the three types of propagule showed definite similarities. The total height increment made by the large cuttings in the growth rooms was disappointing for such material, and growth may have been affected by the roots being partially root-bound. Alternatively, the night temperature chosen might have been too low for rapid height increment. The treatment comparisons in this material, however, are considered valid, largely because they accord well with treatment differences in the other plants. Height increment showed strong differences between treatments, long days and increasing photoperiod generally giving greater growth than short days and decreasing photoperiod. Despite these differences the photoperiod response appears to be quantitative, rather than the qualitative response which has been observed in certain other conifers (Wareing, 1950; Downs, 1962; Romberger, 1963). None of the treatments prevented the onset of a definite flush in the seedlings, the effect being more on the timing and intensity of the flush. Nor did the seedlings produce sealed buds, in contrast to most temperate conifers kept in short days (Downs, 1962). In the cuttings appreciable

shoot elongation was observed in all treatments, and the large cuttings continued rapid height increment for some time after being placed in even the least favourable treatment. The capacity to maintain height increment under all daylength conditions and therefore at all times of the year (when temperature is not immediately limiting) undoubtedly contributes to the rapid growth generally shown by *P. radiata*.

The sustained 16-h (LL) photoperiod treatment gave greater total height increment than the sustained 8-h (SS) treatment by factors of 1.8 for large cuttings, 1.6 for small cuttings, and 1.3 for seedlings. These results agree generally with the previous studies by Richardson (1964), Sweet (1966), Florence and Malajczuk (1970), and Hellmers and Rook (unpubl. data), although the difference in relative response was less in our investigation than in these previous studies. However, the response in our present study was greater than in those by Vaartaja (1959) and Downs (1962).

These quantitative discrepancies may be unimportant, however, because height increment responses must be considered in relation to the nature and condition of the material, its previous treatment, and the underlying tendency of pines to grow in a series of flushes. The continued rapid height increment of the large cuttings during period 1 suggests that any photoperiodic checking of height growth occurs only after an appreciable time lag. The delayed height growth of the small cuttings and, to a lesser extent, of the seedlings, meant a considerable time lag in photoperiodic stimulation. In the small cuttings, in particular, this probably resulted from their being in a resting phase when the experiment began. The small cuttings had very small buds at the start, and it was presumably only when the buds were developed sufficiently to provide the basis of a growth flush that the material became responsive to photoperiodic stimulation. Responsiveness in the small cuttings and the seedlings may have been affected by the recent transplanting but, against this, quite rapid photoperiodic response has been observed in material with large, well-formed buds despite very recent transplanting (Burdon, 1974).

In the seedlings total height increment was less markedly influenced by treatment than was increment during individual periods. Hence a lack of height growth during one period may reflect the stimulation of a vigorous flush during the previous period rather than current conditions. Conversely, a vigorous flush may really reflect conditions which effected a temporary suppression of growth during the preceding period (cf. Burdon, 1974, Expt 4).

Overall, the results indicate that there is a response to daylength shift *per se*, with increasing daylength favouring active shoot elongation. The evidence for this lies in the consistency of response among the different classes of plant and not in conclusive results for any one category. Height increment during period 3 was greater (by 18-51%) in all three classes after initial increasing photoperiod than after initial long days. During the same period the increment in each class was less (by 23-37%) after initial decreasing photoperiod than after initial short days. These differences do not appear to be a readjustment after height increment response evoked in the initial stages of the experiment. Total height increment was consistently greater (by 16-17%) under the IL treatment than under LL, while it tended to be less under DS than under SS (the exception being the anomalous early height increment of the large cuttings allocated to the DS treatment). If these particular treatment differences are genuine the only

satisfactory explanation is daylength shift response, of which the mechanism is conjectural.

Of note was the very marked promotion of branch elongation as well as leader elongation in the seedlings under the IL treatment. This may relate to the observation by Cremer (1974) that vegetative elongation of small laterals of *P. radiata* in the field occurs almost entirely during the spring, when photoperiod is increasing.

In the small cuttings no treatment differences were detected in fascicle number within the shoot cycle which elongated during the treatments. Moreover, all these fascicle primordia may have been initiated before the treatments began (cf. Bollmann and Sweet, 1976). Evidently the treatment differences in height increment were essentially elongation responses rather than effects on numbers of primordia. Results for primordial counts in the large cuttings (Jenkins *et al.*, 1976) are fragmentary, but support this interpretation. There is no real evidence as to whether the treatments influenced the rate of primordial initiation in the apical region.

Diameter growth responses, insofar as they were significant, did not show a consistent pattern, excepting perhaps a trend for greatest increment to occur under decreasing photoperiod. The relationship between diameter increment responses and height increment responses was also inconsistent. Xylem increment in woody plants is generally promoted by long days (see Borger and Kozlowski, 1972), but these longer photoperiods are generally associated with higher energy inputs. Although there are obviously situations when height and diameter increment are positively coupled there are also situations where they appear to be competitively interrelated (e.g., Jackson *et al.*, 1976; Habjørg, 1972; Jenkins, 1975), hence a consistent relationship between these two growth parameters is hardly to be expected.

Dry weight measurements of seedlings showed a reduction of above-ground dry weight by short days compared with long days. This can be attributed to the initial effect of treatment on the rate of extension of new photosynthetic tissue and thence on photosynthetic capacity of plants, or to an effect on the degree of mutual shading among leaves. Although Hellmers and Rook (unpubl. data) found little difference in root/shoot ratios between short and long photoperiods, the short-day treatment in the present study gave the largest root/shoot ratios after 16 weeks. At the final harvest the plants in the SI treatment showed more roots at the soil surface and had a large root/shoot ratio.

Tracheid diameters tended to be smaller with decreasing photoperiod and short-day treatments, and larger with long days or increasing photoperiod, at the time of tracheid formation. Correspondingly, wall/lumen and wall/diameter ratios tended to be higher in the cuttings with decreasing daylength and short days. These effects, however, were not as pronounced as in many other conifer species where short days cause marked reductions in cell radial diameters (Larson, 1962; Wodzicki, 1964; Denne and Smith, 1971; Heide, 1974), but in these published studies photoperiod effects were confounded with differences in total daily irradiance.

Tracheid dimensions generally tended towards earlywood characteristics in the treatments which gave greater height increment, but a notable exception was the thick cell walls in the seedlings in the IL treatment, this being coupled with a positive within-treatment association between wall thickness and height increment. Previous

work with conifers, however, has given widely variable responses of wall thickness to short days (Larson, 1962; Wodzicki, 1964; Richardson, 1964; Denne and Smith, 1971; Smith, 1975).

Only part of the observed variation in tracheid dimensions could be interpreted as an immediate effect of the degree of shoot elongation. Unexplained variation may reflect direct effects of photoperiod which are independent of the shoot elongation response, or imperfections in the measure of shoot elongation.

Relative Importance of Daylength Shift Compared with Absolute Daylength

Although there is some evidence for a response to daylength shift, the relative importance of shifts compared with absolute daylength in governing shoot extension within this study is by no means clear. For one thing, there was the confounding of almost inevitable effects of abrupt initial shifts in daylength (as in initial I and S treatments) with the subsequent conditions. For another, there is the problem that laboratory conditions cannot fully simulate natural conditions; because of this the possibility should not be overlooked that uniform daylength conditions as provided in a laboratory might well trigger daylength shift responses.

In the field there are various growth phenomena, including timing of the growth resurgence after the winter solstice, latewood-earlywood differentiation, and final flower development (Lill and Sweet, 1977; Burdon, 1974; 1977), which can be explained very satisfactorily by a response to daylength shift. Its significance for co-ordinating and synchronising growth, in comparison with any response to absolute daylength, may be greater than laboratory experiments have suggested. This is because after the winter solstice, when the characteristic spring flush begins, increasing daylength occurs in conjunction with cool soil temperatures and low night temperatures, which appear to allow in particular the extension of the leading shoot axes in adult trees (Rook and Hobbs, 1976). Conversely, after the summer solstice shortening days, although still long, occur in conjunction with higher night temperatures. Hence it is possible that daylength shift effects rather than absolute daylength effects are reinforced by temperature. Moreover, the response needed to maintain an existing entrainment of the flushing rhythm to the seasonal climatic cycle may be relatively weak. At the same time one cannot discount the possibility of a synergism, as distinct from a simple effect, between daylength shift and temperature. This study, of course, concerned only vegetative response, yet the indications are that final flower development may be under much stricter environmental control (Burdon, 1974; 1977).

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