

# ENVIRONMENTAL VARIABLES INFLUENCING THE INCREMENT OF *PINUS RADIATA*: (2) EFFECTS OF SEASONAL DROUGHT ON HEIGHT AND DIAMETER INCREMENT

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(Received for publication 23 May 1975)

## ABSTRACT

Comparisons between well-watered and experimentally droughted trees of identical genotype, over a period of 5 years, showed that height and diameter growth of unstressed trees continued throughout the year at Rotorua, N.Z. Height increment attained maximum levels during October/November, followed by a peak of cross-sectional-area growth in February, and a secondary peak of height increment during March/April.

Drought imposed during winter/spring reduced height growth considerably during late spring, resulting in an apparent shift of peak growth; while summer/autumn drought virtually eliminated the secondary peak of height increment. Cross-sectional-area increment was most strongly reduced by imposed drought during the summer and autumn, and showed marked but over-compensating rehydration responses following removal of drought stress. However, the adverse effects of sustained drought on height increment continued for some time after rewatering. Effects on bud and shoot development are also discussed.

## INTRODUCTION

The intermittent nature of both height and diameter increment is now generally recognised (Kozlowski, 1964). *Pinus radiata* provides no exception to this generalisation, either in relation to diurnal/nocturnal patterns (Fielding and Millett, 1941) or when growth is measured over an interval of several days. However, it has long been apparent to foresters that there are several anomalies in the seasonal growth pattern(s) of *P. radiata*: that while it may in some regions exhibit a distinct period of dormancy, with an associated resting bud (e.g. in the south of New Zealand, or in South Australia—*vide* Fig. 1), yet it does not invariably conform with the pattern of a long dormant period and brief period of rapid spring/summer growth, so characteristic of most of the temperate zone species (Kozlowski, 1964) that have been introduced into New Zealand. Thus, in Hawaii vegetative growth of *P. radiata* is continuous throughout the year, and flowering almost so (Lanner, 1966), while in northern New Zealand both height and basal area increment may be almost continuous (Fig. 1). In Australia, Fielding (1955) considered that *P. radiata* has both the "potential of growing in height virtually through-

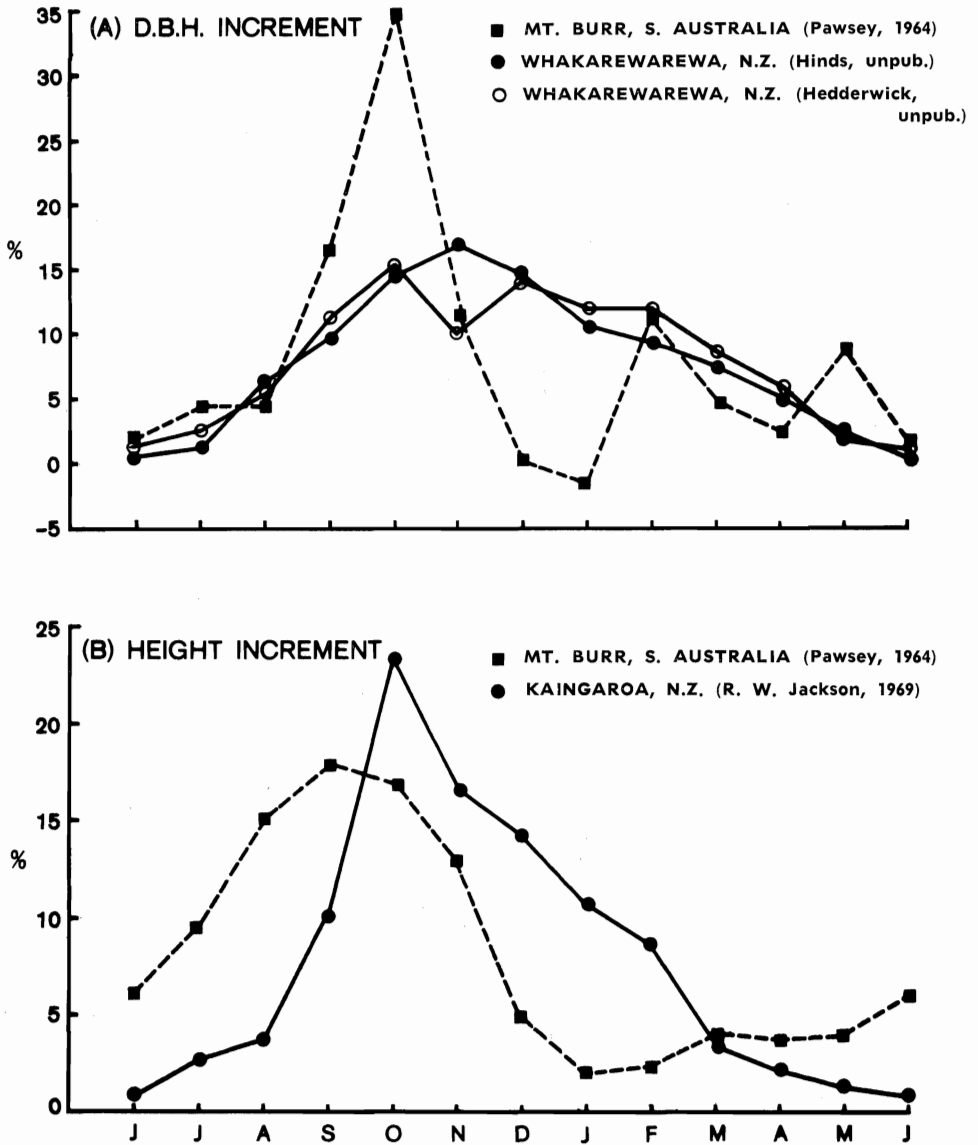


FIG. 1—Monthly increment for *P. radiata* recalculated as percent of annual total: seasonal curves for South Australia (trees 11-20 years old) and New Zealand (Kaingaroa trees 3-6; Whaka trees 13-16 and 33-40 years old).

out the year” and a “capacity to make diameter growth at any season of the year, provided moisture and temperature conditions are not limiting”. These observations are supported by Bollmann (1974) in a recent morphological study of polycyclic activity in the species’ apical bud and by the demonstration of cambial activity during midwinter (Barnett, 1971).

The question of whether the endogenous pattern for *P. radiata* is, or is not, recurrent has important implications for our understanding of environmental influences on growth, and in considering practical and experimental means of manipulating productivity. Thus Kozlowski (1964) provides a summary of the many patterns of shoot growth apparent among woody species. His survey indicates that whereas growth of those species with primordia of the axial extension already predetermined in the resting bud are mainly influenced by weather of the season prior to shoot extension, those with recurrent bud formation and growth are more influenced by current weather conditions

The responsiveness of stem dimensions (by shrinkage) to periods of temporary water stress is now well documented (Fielding and Millett, 1941; Van Laar, 1967) and there is abundant experimental evidence (MacDougal, 1938; Fielding and Millett, 1941; Waring, 1971) as well as circumstantial data for the depressive effect of drought on diameter growth. Fig. 1 A illustrates these features for monthly d.b.h. increment at Mt Burr, South Australia and at Whakarewarewa, N.Z. Fielding and Millett (op. cit.) considered that the secondary period of autumn diameter growth at Mt Burr was contingent on the occurrence of autumn rains, since the only clearly defined period of diameter growth at Canberra was during the spring. In both localities bursts of growth may follow heavy rain during summer and autumn, and Cremer (1972) has demonstrated the rapidity with which *P. radiata* may resume diameter growth after an extended period of drought. As shown by more comprehensive data of Pawsey (1964), the summer reduction of cross-sectional increment is less apparent at higher levels in the green crown, and Fielding (1955) states that any cessation occurs later there than at lower levels in the stem.

There is also circumstantial evidence for effects of annual weather variations on height increment (Fig. 1 B), although Fielding (1955) recorded that it had not yet been possible to relate them definitely to such differences. He characterised the pattern of apical extension of seven-year-old trees near Canberra by a period of rapid spring growth, followed by negligible or very slow extension during the rest of the year. He also remarked that the only period when all terminal shoots could be considered dormant was for a few weeks following the spring growth flush, although the timing of this varied (between individuals and between years). Loughton (1937) similarly mentioned the burst of growth in spring, usually reaching a climax during September to November (in South Africa), and he maintained that soil-moisture was the factor governing the duration of this period of rapid growth; while Cremer (1973) found that up to 38% of the annual height growth could occur during January to June, but was strongly related to the current intensity of drought. Finally, Lanner (1966) discusses examples of continuous height growth by *P. radiata* in the tropical climate of Hawaii (viz. individuals with a "fox-tailing" habit) and presents data indicating that the frequency of such individuals is markedly increased by high rainfall, while the habit is curtailed by drought.

These interpretations are supported by the obvious differences between the patterns of growth in the summer-drought climates of Australia, and the considerably more humid climates of New Zealand (c.f. Fig. 1). However it is necessary, in comparing such data from different regions, to temper the interpretation by several qualifications. These relate to the changes of phenotypic expression that occur as a tree ages, and also the very marked differences in seasonal growth pattern between different genotypes. Samples of

a few trees are likely to differ substantially in regard to mean phenotypic expression, even from within one local population, and Kozlowski and Ward (1961) consider that the endogenous pattern for different genotypes is frequently so different that it is wholly misleading to average them.

For these several reasons, the experiment reported in this paper was designed around a series of treatments imposed on trees of identical age and genotype. It was assumed, from the outset, that there would be large clone  $\times$  treatment interactions, and in the layout of the experiment clonal effects were deliberately confounded with anticipated positional effects in the plantation. This was done for reasons of economy, since the main objective was to determine the effect of seasonal water deficits on the common growth pattern of the selected genotypes.

### METHODS

The experiment was established at the Forest Research Institute, Rotorua, during early August 1967, when individual evapotranspirometer units of 2.72 m<sup>3</sup> capacity (spaced at 4 m  $\times$  5 m) were planted with two 27-month-old rooted cuttings of one of three clones (FRI Nos. 450, 451, 460). These ramets were derived from 12-month-old grafted material off 6-month-old seedlings sown in the Forest Research Institute nursery in October 1963. During the 1967-68 growing season all units were maintained in an unstressed condition, in order to maximize growth, and in June 1968 one tree of each pair was removed from each unit, to secure uniformity throughout each clone. The treatment sequences were then begun.

The basic pattern imposed was a simple 2  $\times$  2 factorial, combining drought *v.* no drought with seasonal incidence, *i.e.* winter-spring *v.* summer-autumn. There were thus four treatments, defined by the annual pattern of drought, as follows:

- (nil) — NO DEFICIT: free access to rainfall throughout the year,
- (ws) — WINTER/SPRING DEFICIT: No rainfall access from June to November inclusive;
- (sa) — SUMMER/AUTUMN DEFICIT: No rainfall access from December to May inclusive;
- (wssa) — YEAR-ROUND DEFICIT: Rainfall excluded throughout the year.

During the 6-month period when any particular unit was not scheduled to be on a deficit, the level of soil moisture was allowed to fluctuate in accordance with the amount of rain falling on the 1.49 m<sup>2</sup> cross-section of the evapotranspirometer. During natural drought periods, however, it was necessary to maintain the contrast between treatments by supplementary watering to sustain a minimum soil moisture level of about 40% by volume, with a corresponding soil water potential of -0.5 bars. For the units on a current deficit regime, rainfall was totally excluded by covering the surface of the unit with polythene sheeting, sealed around the base of the tree. Interception of rain by the crown was not prevented. In order to prevent trees dying during periods of intense evapotranspiration, particularly those on the (wssa) regime, it was necessary to specify a minimum soil moisture level that should be maintained. This was set at 15% by volume (with a corresponding s.w.p. of -10 bars), but occasionally the droughted units accidentally became drier than this. The amount of surface water to be applied to any unit was calculated by a water-budget (Jackson, Gifford and Hobbs, 1973), which was

balanced for every 2 cm of open-tank evaporation. Readjustments were made as necessary, when indicated by routine weekly monitoring of soil moisture content with a neutron probe, using the access tube installed in each unit. Fig. 2 illustrates typical soil-moisture profiles for each month during the final year of the experiment, and Fig. 3 represents a diurnal series of measurements of leaf water potential for each treatment, grouped by individual clones.

In order to prevent treatments producing a cumulative effect (analogous with that resulting from climatic differences), they were interchanged in successive years according to a cross-over design, which would also permit the analysis of after-effects due to treatment in the preceding year. With 3 replications (comprising 4 trees of each of 3 clones) the annual sequence of treatments became:

CLONE:	REPLICATION			YEAR AND TREATMENT				
	450	460	451	1968/69	1969/70	1970/71	1971/72	1972/73
UNIT NO.	3	6	22	(nil)	(ws)	(wssa)	(sa)	(sa)
	1	7	20	(sa)	(wssa)	(ws)	(nil)	(nil)
	2	8	18	(wssa)	(nil)	(sa)	(ws)	(ws)
	4	10	21	(ws)	(sa)	(nil)	(wssa)	(wssa)

Each clone was regarded as a block (thus deliberately confounding genotype and positional block effects). Within clones each treatment sequence was allocated at random to any particular unit, and these were randomly located within blocks.

Height growth of each tree was measured to the nearest cm every 10 days from May 1968 until 1972, when for practical reasons the intervals were extended to 30 days. Until May 1969 the trees had been too small to instal dendrometer bands, but after this date girth increment at breast height and stump height (15 cm above soil-level) was also measured to the nearest mm at 10-day intervals. On termination of the experiment in June 1973, the trees were harvested and sectioned for a complete dry-matter analysis of the crowns, stems and root-systems. Prior to foliage stripping, the longest branch and that nearest to the mean in each branch cluster were repositioned on the stem against a metre-square grid, to provide a permanent photographic record of each tree (See Figs. 4, 5, 6). Stem cross-sections were also taken at stump, at breast-height and at the point reached by the terminal bud in June each year. A photograph of the breast-height discs of all 12 trees is provided by Fig. 7.

### RESULTS

Absolute monthly values of height and cross-sectional increment for each unit are tabulated in Appendix 1. A visual representation of the annual increments, together with their associated treatment regimes, is also provided by Figs. 4, 5, 6 and 7. It is apparent from these figures that there are considerable absolute differences in the amount of annual increment between clones and between years. In order to reduce these influences on the analysis, all monthly increments are expressed as percent of the mean annual total for the pertinent clone in each year.

The first year's data were discarded, because the trees were still too small to measure cross-sectional growth accurately enough and because the main purpose of the 1968/69

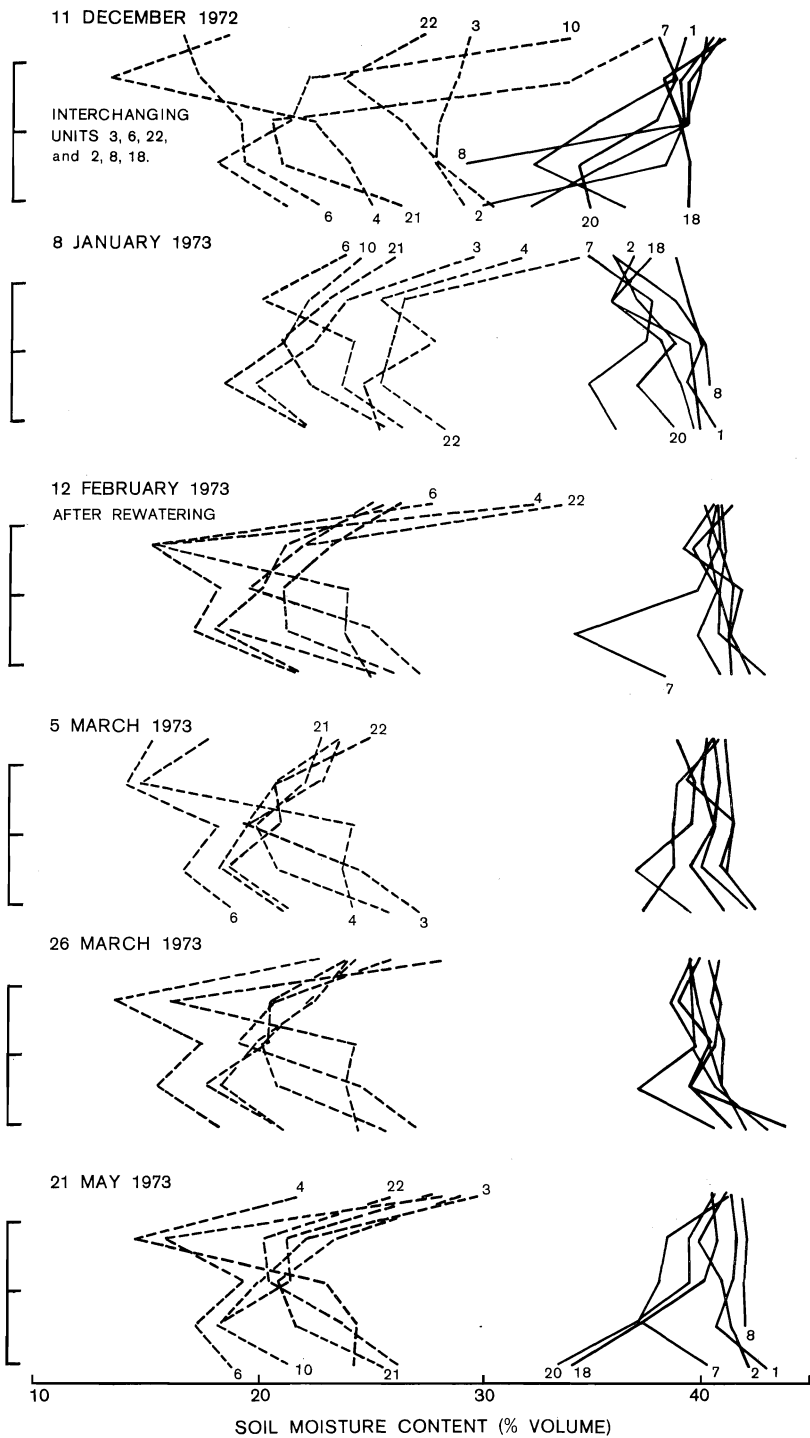
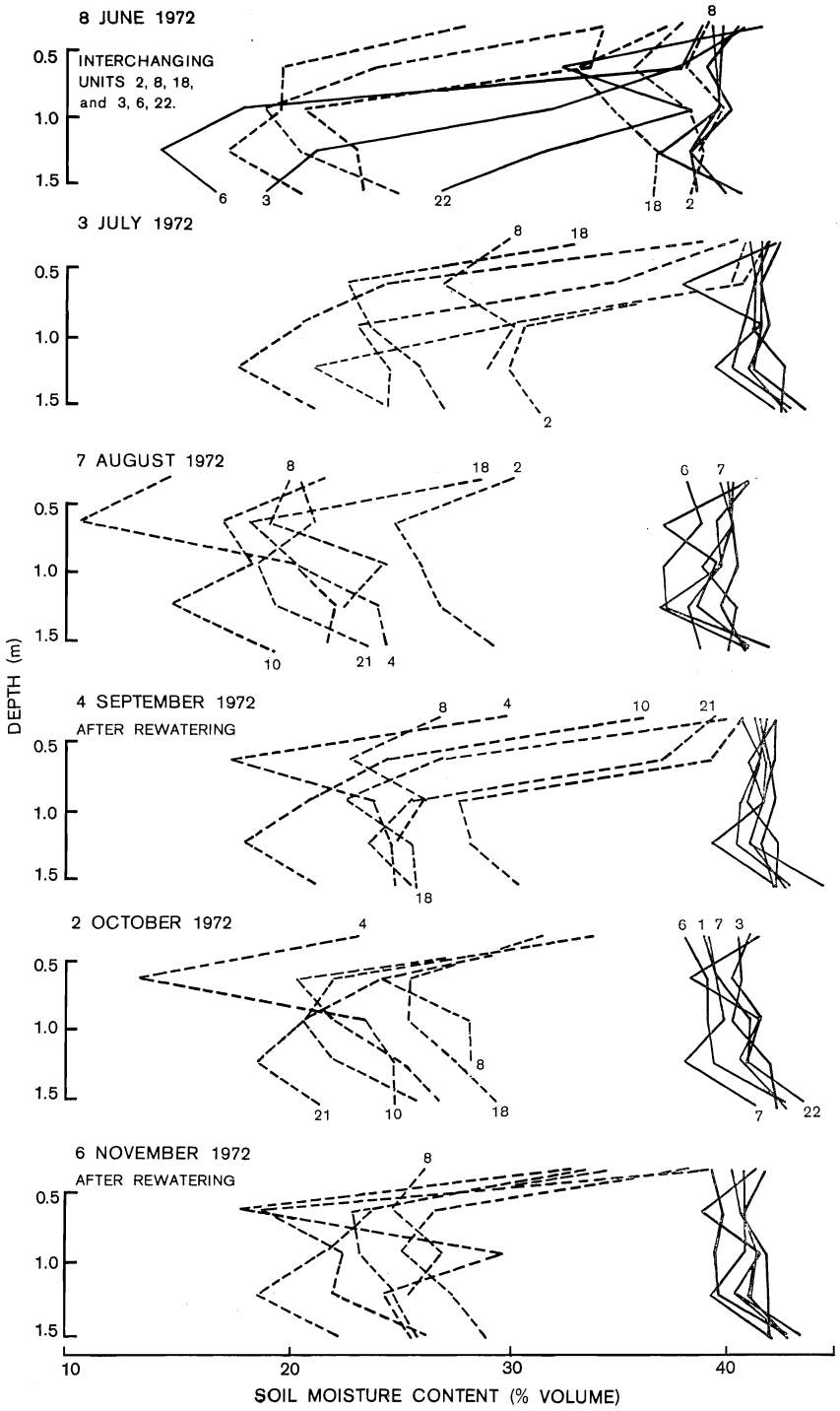


FIG. 2—Soil moisture status for each month during the final growing-season, showing grouping by treatment and transitional effects of treatment interchanges in



June and December. Solid lines represent unstressed units; pecked lines, the units under current deficit.

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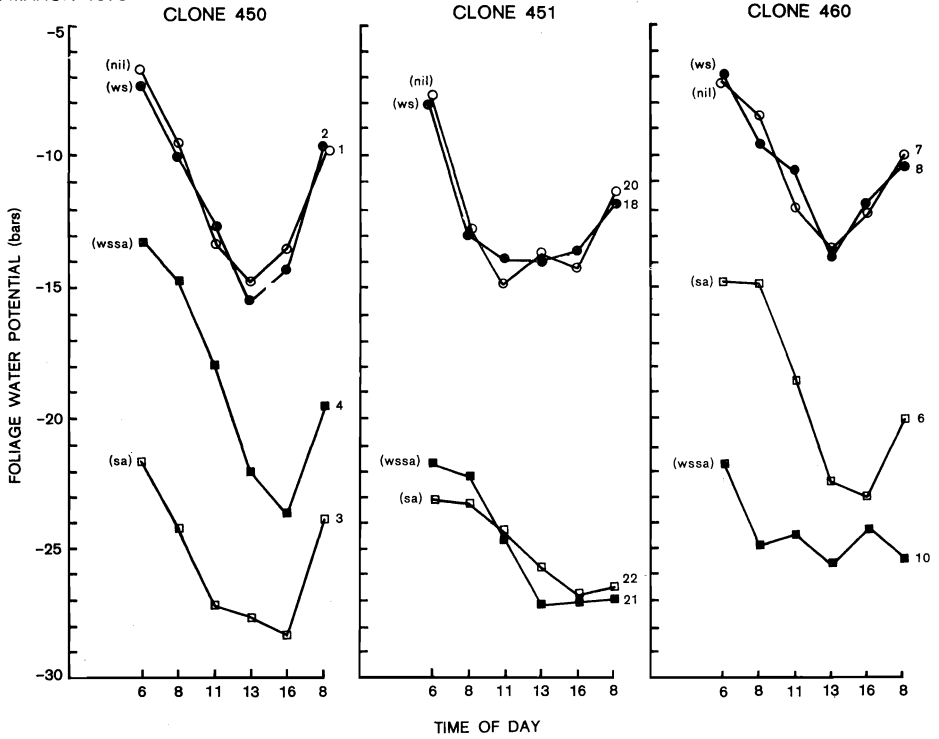


FIG. 3—Comparison of diurnal leaf water potentials between treatments on 28 March 1973, and at 0800 hours the following morning.

treatments was to balance the design for treatment after-affects as well as direct effects in the four following growing-seasons, from June 1969 to May 1973.

Then, denoting each of the four treatments by subscript  $i$ , each of the four growing-seasons by  $j$  and each of the three clones by  $k$ , let:

$I_{ijk}$  = increment in any month for a particular treatment/clone combination in year  $j$

$G$  = overall total of 48 increment values  $I_{ijk}$  in any month

$T_i$  = total of increment values for treatment  $i$  in the current year

$A_i$  = total of increment values for years preceded by treatment  $i$

$P_j$  = total for year  $j$  over all treatments and clones

$C_k$  = total for clone  $k$  over all treatments and years

$CT_{ik}$  = total for clone  $k$  in each year subjected to treatment  $i$

$CA_{ik}$  = total for clone  $k$  in years preceded by treatment  $i$



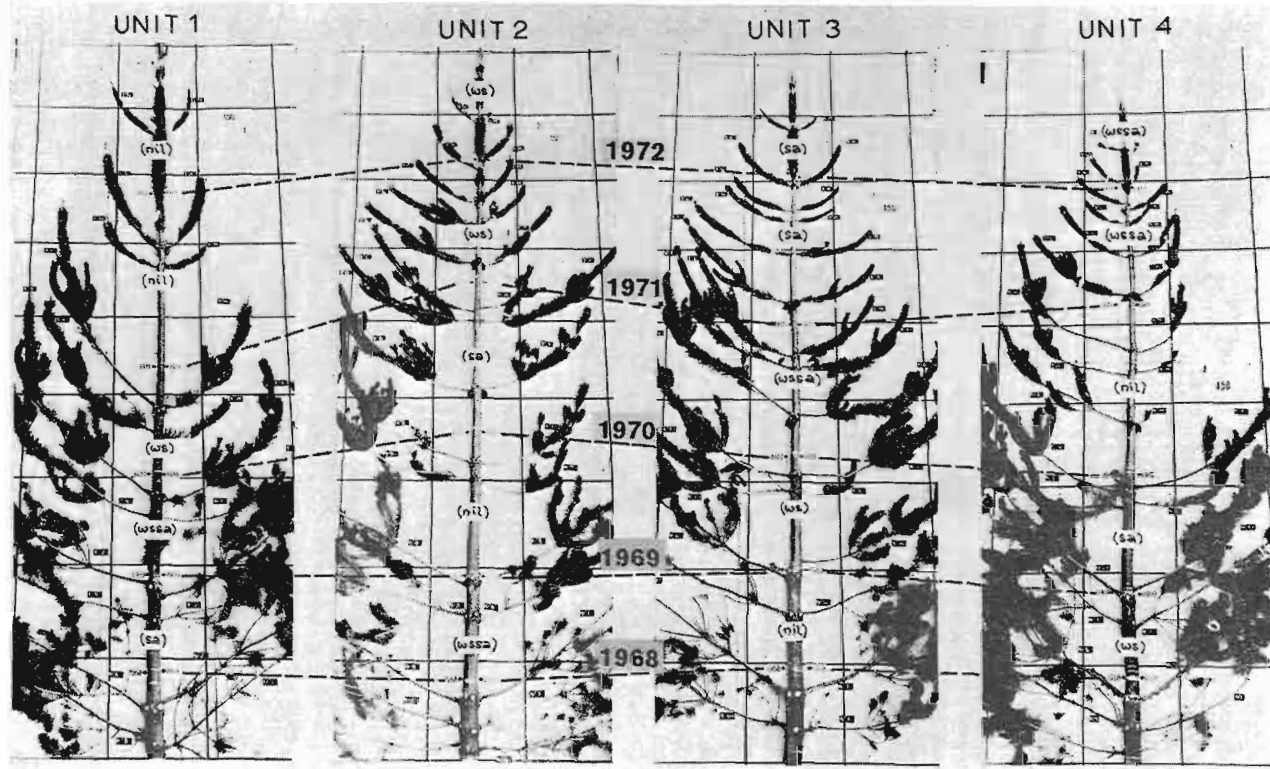


FIG. 4—Form and branching habit of each unit in Clone 450 on termination of experiment (June, 1973). Position of terminal bud at beginning of June in each year is marked by dotted line, together with intervening treatment regimes. Background grid is 1 m × 1 m.

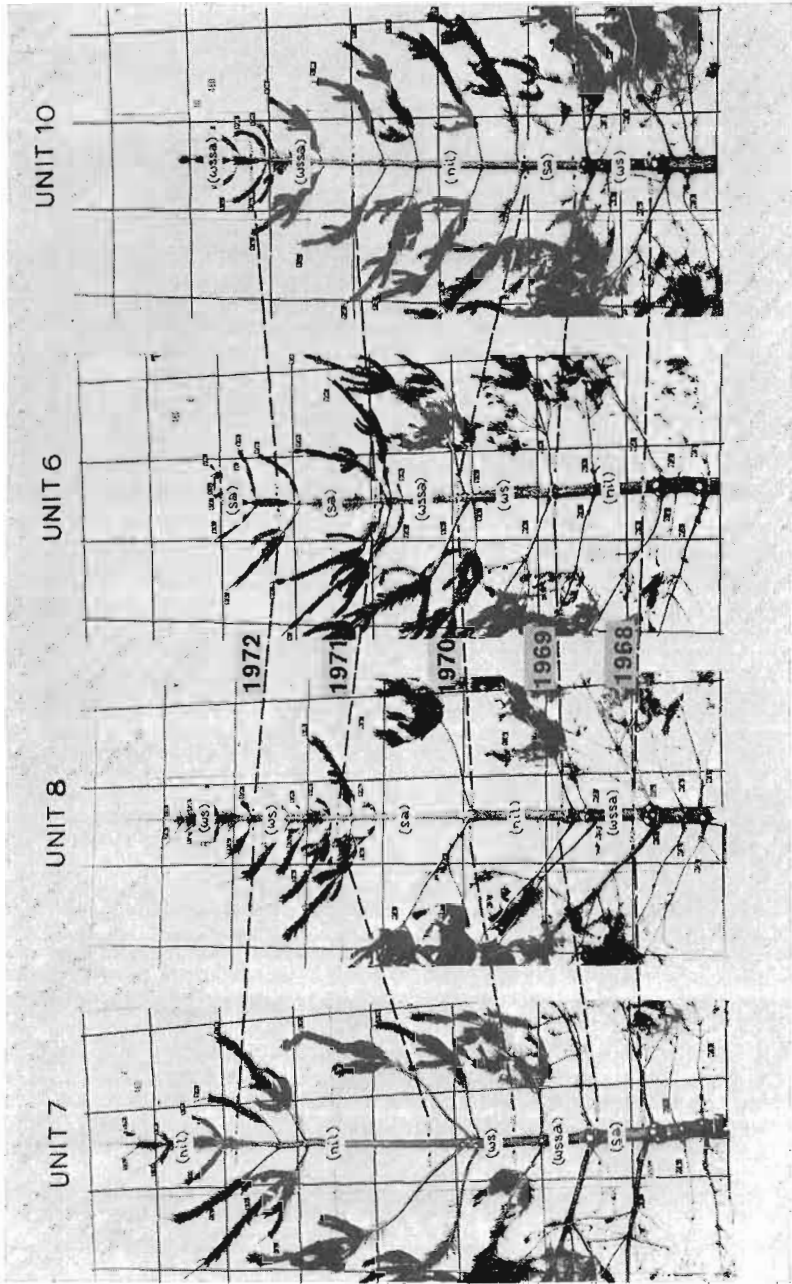


FIG. 5—Form and branching habit of each unit in Clone 460 on termination of experiment.

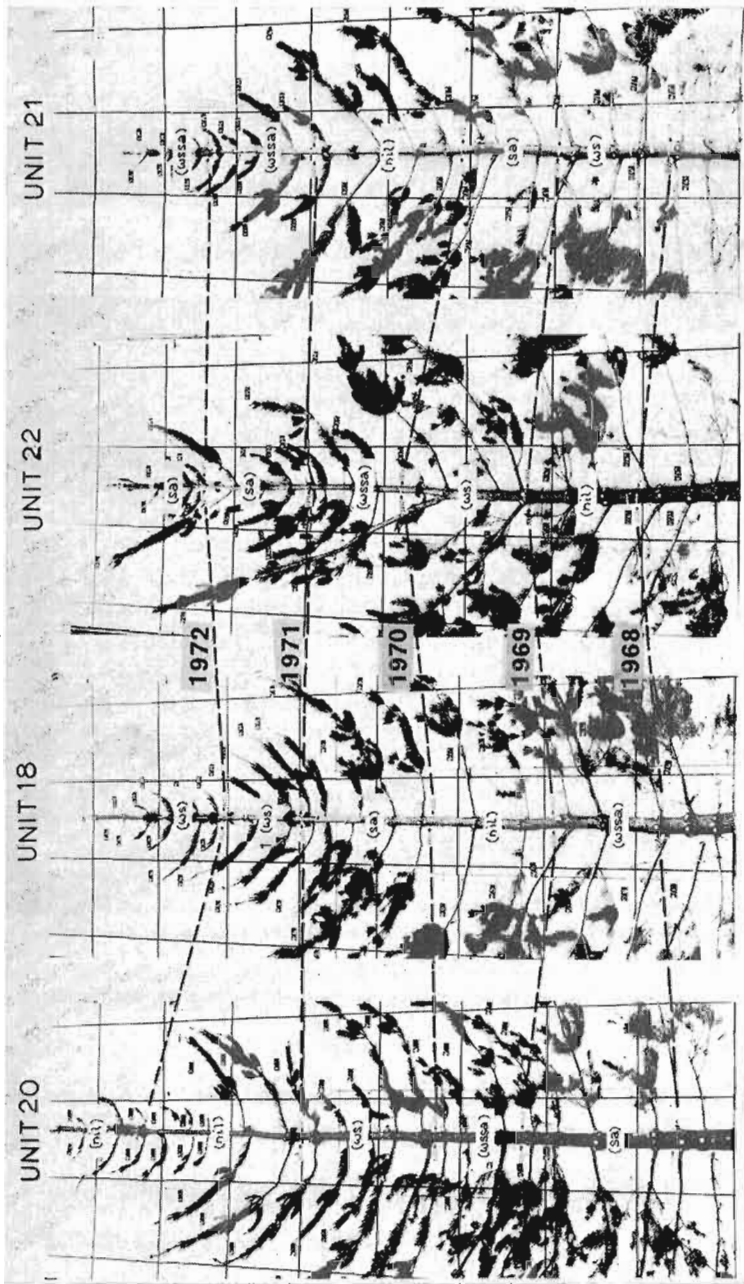


FIG. 6—Form and branching habit of each unit in Clone 451 on termination of experiment.

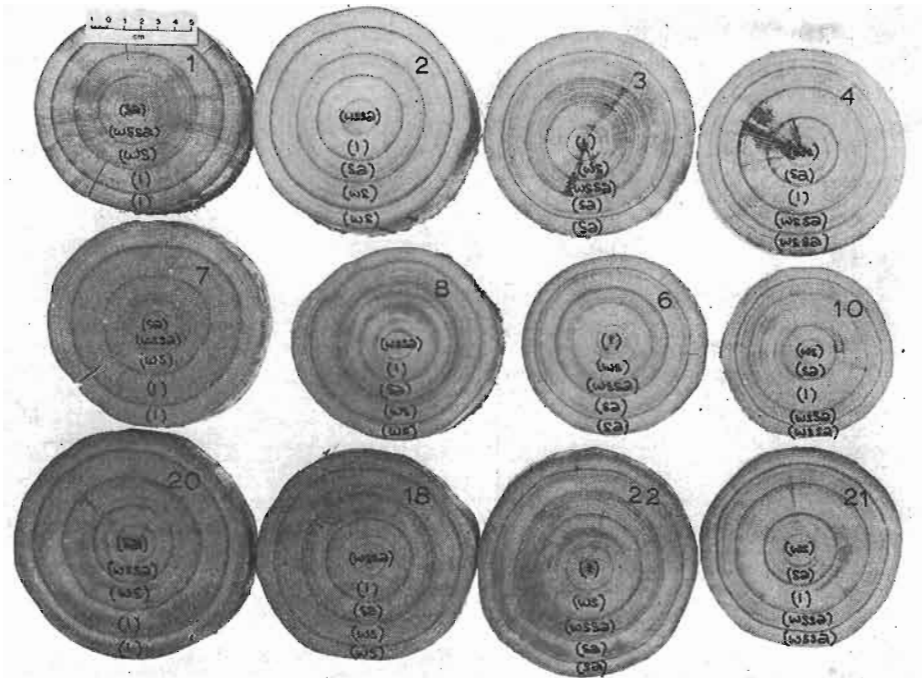


FIG. 7—Patterns of false rings and relative cross-sectional increment at breast-height for each regime of seasonal drought throughout the experiment. Numbers denote unit identity.

The analysis of variance of effects on increment in any month was then calculated as follows:

SOURCE OF VARIATION	d.f.	SUM OF SQUARES
Between clones	2	$(3 \sum C_k^2 - G^2)/48$
<i>Treatments:</i>		
Direct effects	3	$(4 \sum T_i^2 - G^2)/48$
T * C interaction	6	$(12 \sum CT_{ik}^2 - 4 \sum T_i^2 - 3 \sum C_k^2 - 3 G^2)/48$
After-effects	3	$(4 \sum A_i^2 - G^2)/48$
A * C interaction	6	$(12 \sum CA_{ik}^2 - 4 \sum A_i^2 - 3 \sum C_k^2 - 3 G^2)/48$
Between years	3	$(4 \sum P_j^2 - G^2)/48$
Residual error	24	Difference
TOTAL	47	$\sum I_{ijk}^2 - G^2/48$

Each of the direct effects is associated once with each of the after-effects of treatment in the preceding year, and each of these after-effects is associated once with each of the

direct effects in the succeeding year. Thus, given the orthogonal comparisons:

$$(X_2 + X_4 - X_1 - X_3)^2/48 : (WS) \text{ EFFECT}$$

$$(X_3 + X_4 - X_1 - X_2)^2/48 : (SA) \text{ EFFECT}$$

$$(X_1 + X_4 - X_2 - X_3)^2/48 : \text{INTERACTION (WS} \times \text{SA)}$$

these may be used to subdivide the treatment sum of squares for direct effects ( $X_i = T_i$ ), freed from the influence of treatments in the preceding year, or for after-effects ( $X_i = A_i$ ), from which the influence of current year treatments upon increment have likewise been eliminated. Each of these comparisons will have but one degree of freedom, The appropriate test of significance is provided by the treatment/clone interaction, with six degrees of freedom. No provision is made for testing for differences between clones or between years.

Results of the analysis for each month, in the form of partitioned sums of squares, are tabulated in Appendix 2 for height and cross-sectional area increment separately. The three degrees of freedom for treatments are further broken down into the variances attributable to each of the orthogonal comparisons. When these are tested against the appropriate treatment/clone interaction, the significances of the corresponding F ratios for direct effects may be tabulated for each month as in Table 1.

## DISCUSSION

### *Cross-sectional Increment*

It is obvious from Fig. 8A, and statistically confirmed by Table 1A, that cross-sectional increment is highly vulnerable to current moisture stress during the period December through April. This coincides very neatly with the evidence summarised earlier, particularly Pawsey's curve for Mt Burr (Fig. 1A). It may be noted in this

TABLE 1—Significance of effects of seasonal water deficits on monthly increment, expressed as percent of total for the year

(A) Direct effects on Cross-sectional Increment												
	J	J	A	S	O	N	D	J	F	M	A	M
(WS) EFFECT:	NS	NS	*	**	NS	**	**	NS	NS	NS	NS	NS
(SA) EFFECT:	NS	NS	NS	NS	NS	*	**	**	**	**	**	NS
INTERACTION:	NS	NS	NS	NS	NS	*	*	NS	NS	NS	NS	NS
(B) Direct effects on Height Increment												
	J	J	A	S	O	N	D	J	F	M	A	M
(WS) EFFECT:	NS	*	*	**	NS	**	NS	NS	NS	NS	NS	NS
(SA) EFFECT:	NS	NS	NS	NS	NS	NS	*	NS	**	**	**	**
INTERACTION:	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	*	NS

\* Significant at 5% level

\*\* Significant at 1% level

} on 1 and 6 d.f.

N.S. denotes not significant.

connection that the mean rainfall aggregates for June-October and December-April are 447/213 mm at Mt Burr and 678/579 mm at Whakarewarewa. Highly significant reductions of increment may also be produced by drought during September and November, and, to a lesser extent, in August. This, again, is well in accord with Waring's (1971) statement that annual basal area increment was closely correlated with rainfall during September through April, and that it will cease any time after November if precipitation becomes inadequate. However, it is evident that the spring/early summer phase of the endogenous cycle of cross-sectional development is much less readily modified in spring/early summer than later in the growing-season, and that the magnitude of any reduction is less. It is questionable how much of the apparent reduction during August and September is in fact due to diminished cambial activity and growth or whether it is mainly attributable to tissue dehydration. The very large surge in cross-sectional area that occurs between November and December following rewatering of the previously drought-influenced (ws) treatment must be mainly due to rehydration. Moreover, it is adequate to account for most of the accumulated loss during the preceding five months, and the substantial increase of (ws) over the (nil) regime in the ensuing three months (January, February and March) must be due to increased growth.

This is a curious result, and would appear to indicate that a rainfall regime with a dry spring and wet summer and autumn is more favourable for maximum basal area increment than one with good rainfall distributed throughout this period.

The decrements of cross-sectional area that have been frequently reported by earlier investigators as occurring during summer drought, show up only once in the data (in January 1973 for Unit 21), although there are several occurrences for the (ws) and (wssa) regimes in June and July. Haasis (1932) recorded similar shrinkages in the spring of 1931, and Fielding and Millett (1941) state that they are not uncommon during spring and autumn at Canberra. However, such decrements were more frequent in the original data, measured at 10-day intervals: over a 30-day period such temporary shrinkage due to tissue dehydration is more readily masked by the continuing trend of growth. The best evidence for such episodes of stress is provided by Fig. 7, which represents the appropriate treatment, as applied, against each annual ring. Inspection of this figure reveals the exact coincidence of repeated false rings with the periods of water-stress (c.f. Shepherd, 1964), regardless of whether such occurred during the winter/spring or summer/autumn.

The occurrence of a significant (sa) effect in November, prior to actual imposition of this treatment, is regarded as a fortuitous result of the analysis.

Inspection of the corresponding curves in Fig. 8 shows that most of this effect is in fact associated with the year-long deficit (wssa). Moreover, November is the month when height increment culminates and there appears to be a concurrent slight downturn in cambial activity. It is possible that this would be accelerated by the (wssa) treatment.

#### *Height Increment*

Fig. 8B and Table 1B indicate the highly significant effects of current rainfall deficits on height increment during September, November and the four successive autumn months February to May. Although the analysis indicates that the October differences are not significant, the trend is obvious from the graph (Fig. 8B), and the F ratio for (ws) effects, at 5.66, is in fact very close to being significant. Examination of the partitioned

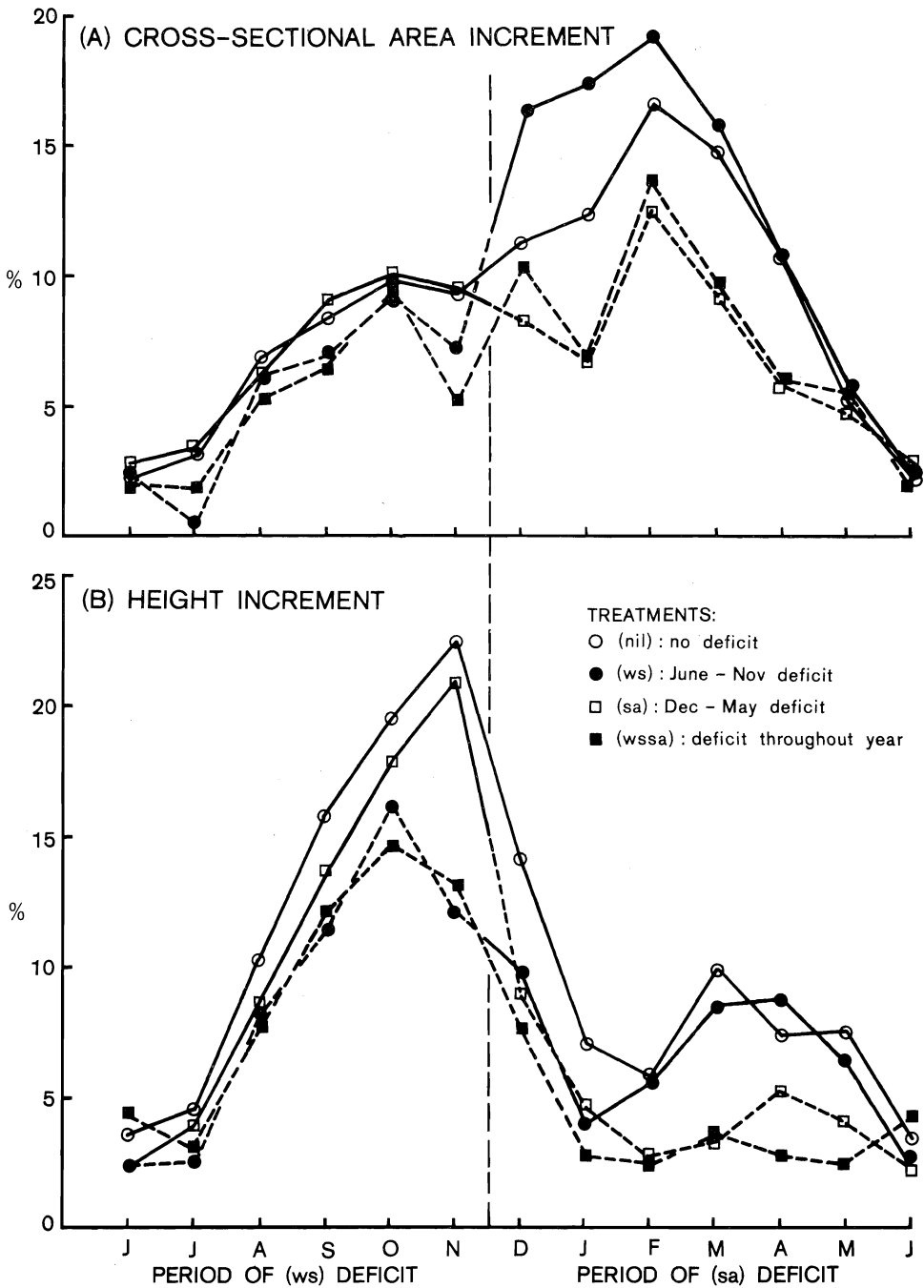


FIG. 8—Monthly increment percentage means for each treatment over all four years of the analysis. Absolute differences between clones and years are eliminated by expressing values as a percentage of total growth of each clone for the year.

sums of squares (S.S.) for October, in Appendix 2B, shows that the reason for this apparent anomaly is the exceptionally high error term (in relation to the treatment S.S.) — indicating that variation among the clones was greater than usual in this month.

Three particular features of the height increment curves demand comment:

(1) The very strong reduction of height increment during November, resulting from a current winter/spring rainfall deficit, and the consequent shift in the primary peak of growth. Such a shift is particularly apparent in the curve of height growth for Mt Burr (Fig. 1B), indicating a corresponding deficiency of rainfall even so early in the growing-season.

(2) In marked contrast to diameter increment, apical extension failed to 'pick-up' again until February, following the release from water deficits at the end of November. The negative effect of (ws) deficit on increment in December is very nearly significant ( $F = 4.80$ ).

(3) The secondary peak of height increment during March/April, and its vulnerability to concurrent drought. Notwithstanding Kozłowski and Ward's (1961) caution that an apparent midsummer depression is frequently attributable to the averaging of curves of intrinsically different form, there is evidence that it is a genuine characteristic of the annual cycle of extension growth in *P. radiata*. Thus Fielding (1966) commented that the rate of height growth tended to be minimal during the late summer (in southern Australia), and cited Pawsey's data showing that periods of nil height in all of the sampled trees occurred only during the summer. In the New Zealand provinces of Hawke's Bay and Canterbury, which are similarly prone to late summer/autumn drought, foresters are familiar with this as the typical pattern. Much of the confusion over the reality or otherwise of the double-peaked height growth curve is due to the fact that it is not invariable, but apparently subject to influence within the current growing-season. This raises some interesting questions about the nature and extent of development of the primordia within the terminal bud, which will be discussed in the final section below.

#### *After-effects of Treatments*

An orthogonal comparison among the factorial effects is presented in Table 2, with the significant values indicated by parentheses. There are, in fact, only four significant effects. One would be inclined to dismiss them as a statistical consequence of the criteria used in validation, were it not for the obvious consistency of the analysis for the (sa) effect. This is interpreted as indicating a positive effect of summer/autumn drought on cross-sectional increment during the following September through April, and a consistently negative effect on height increment for the 10 months (June until March) immediately ensuing. This negative influence is particularly apparent in the increment for the following December.

#### *Bud and Shoot Development*

An hypothesis that *Pinus radiata* is a polycyclic species (Bollmann, 1974) with an indeterminate period or periods of quiescence, would seem to provide a simpler basis for interpreting the various modifications of pattern that occur, than Cremer's (1973) postulate that the regular, determinate annual pattern of the subordinate shoots is basic for this species. Although this corresponds more closely with the 'typical' cool-temperate sigmoid pattern of seasonal development, the latter is usually very stable when trans-



TABLE 2—After-effects of water-deficits during the following growing-season

(A) After-effects on Cross-sectional Increment												
	J	J	A	S	O	N	D	J	F	M	A	M
(WS) EFFECT:	-1.25	-2.97	1.32	-2.67	-0.34	-0.96	0.37	-0.05	-0.16	-0.58	0.61	1.49
(SA) EFFECT:	0.68	1.84	-0.52	2.07	((2.58))	1.53	2.64	2.02	(3.37)	1.45	1.66	-0.26
INTERACTION:	0.68	2.04	0.19	0.60	((2.26))	-0.10	-0.19	-1.02	-0.01	1.67	-1.09	1.52

(B) After-effects on Height Increment												
	J	J	A	S	O	N	D	J	F	M	A	M
(WS) EFFECT:	-1.23	0.09	-0.75	-1.96	0.39	-3.13	0.05	-0.35	1.34	3.70	-1.44	-1.75
(SA) EFFECT:	-1.65	-0.67	-3.96	-1.15	-3.20	-2.20	((-7.64))	-2.68	-1.41	-3.00	3.29	-1.25
INTERACTION:	-0.46	0.57	1.33	2.53	0.75	7.05	-0.92	0.25	-1.14	0.38	-2.12	-2.09

( ) Significant at 5% level }  
 (( )) Significant at 1% level } on 1 and 6 d.f.

planted to alien climatic regimes. Thus Lanner (1966) records that, while several such representative species (*Pinus echinata*, *P. sylvestris*, *P. ponderosa*, *P. pinaster*) retained their distinctive dormant season in Hawaii, *P. radiata* was "unusual in having no defined dormant season". Evidence has been provided that it retains this capacity for recurrent activity in the most diverse climates.

While concurring with Cremer's (1973) statement (regarding the leading bud) that "new internodes may be initiated through most or all of the year. The complete annual shoot is certainly not present in condensed form in the overwintering bud", it is still an open question whether the primordia in the bud at mid-winter represent the first cycles of a new series, or the last of the old. Bollmann (op. cit.) indicates that the cycle of apical initiation begins in late spring (i.e. September/November, depending on genotype) and continues through the following winter, even into July or August. There is considerable genotypic variability in the timing of growth flushes and of periods of reduced growth, but in colder climates and in cooler years a greater proportion of the population appears to exhibit winter dormancy, and for a longer period. Typically, for an individual forming 3 or 4 clusters of branches in a year, extension-growth is seldom, if ever, more than 1 or 2 cycles behind initiation. Thus, both initiation and extension may be influenced by weather within the current season. However, although we have repeatedly observed the omission of complete branch clusters from the seasonal sequence for a particular genotype, our data regarding the influence of water stress were conflicting. Thus, Fig. 9 shows the omission of branch clusters in two successive years for the stressed ramets of Clone 451, but comparison with the corresponding ramets of Clone 450 (i.e. Units 1 and 4 of Fig. 4) shows exactly the opposite effect. Other examples may be found by comparing Figs. 4, 5 and 6. Such modifications of the basic pattern could be produced by one of several currently accepted mechanisms, involving competition between meristematic tissues in dominant and subordinate shoots, particularly under conditions of water or nutrient stress, or correlative inhibition by growth-substances; but it is evident that there is no simple correlation with water-stress.

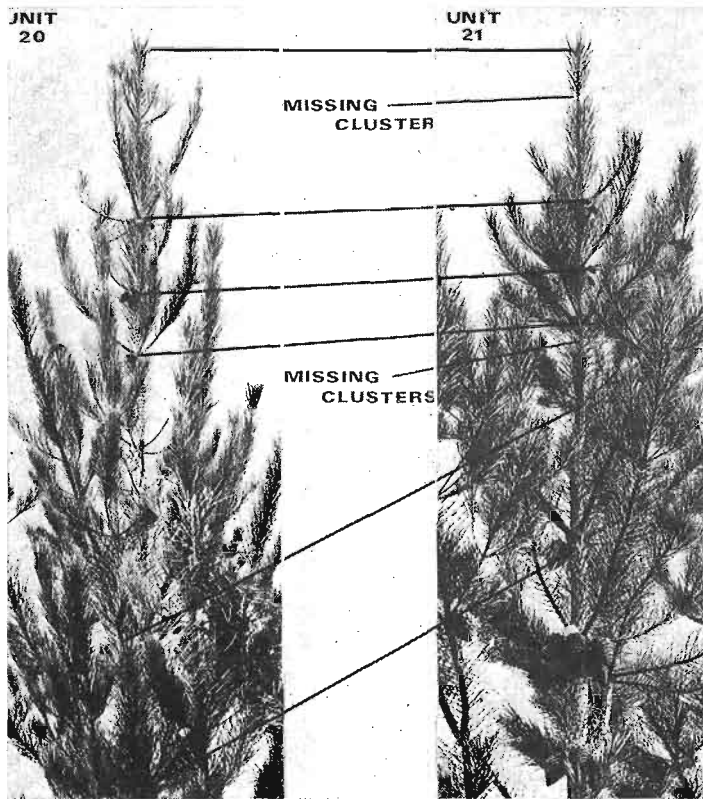


FIG. 9—Showing omission of clusters of lateral branches in summer of 1972 and again in summer of 1973 for Unit 20 of clone 451. Corresponding branch clusters are linked across the figure. Photographed on 5 March 1973.

In sum, it is considered that such polycyclic development, combined with a capacity for continuing cambial development during midwinter, permits unusually flexible responses to environmental fluctuations, and accounts for the markedly different patterns of seasonal growth that have been reported for *Pinus radiata*.

#### ACKNOWLEDGMENTS

We record our appreciation of the practical aid given by Mrs Elizabeth A. Jackson and Mrs Elizabeth A. Povey (née Haggart) in the critical early stages of this experiment, to Mrs Wynne Hobbs for assistance during its operation, and to Mr H. Hemming for the photographic records.

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APPENDIX 1 (A): Summary of Monthly Cross-sectional Increments,  
in sq mm, for each Unit

(B): Summary of Monthly Height Increments,  
in cm, for each Unit

Unit Year	J	J	A	S	O	N	D	J	F	M	A	M	A	M	A	M	A	M						
1 1969/70	60	31	251	297	243	179	258	386	572	477	316	185	3	3	6	17	15	26	21	9	4	1	4	4
1970/71	62	313	452	537	558	267	1438	1306	1124	903	1129	387	2	7	19	18	21	15	7	4	10	9	11	5
1971/72	133	179	316	318	369	373	472	382	632	493	500	101	9	6	21	24	32	37	31	19	12	20	20	7
1972/73	0	93	281	759	1068	694	808	719	625	953	430	108	2	17	22	40	33	49	28	11	18	9	8	20
2 1969/70	61	62	287	369	498	452	475	499	1068	764	651	362	3	4	10	19	27	38	27	5	6	10	13	9
1970/71	183	465	769	801	832	645	1000	689	1308	1115	636	780	8	13	25	21	35	39	13	6	11	2	8	8
1971/72	232	234	282	237	334	433	831	597	758	564	572	210	13	4	24	16	25	28	18	11	9	15	17	6
1972/73	0	110	332	672	910	810	1298	1208	1233	1259	511	386	0	7	19	29	35	25	17	8	15	16	13	15
3 1969/70	29	29	210	249	260	305	464	454	935	702	601	239	2	2	7	17	16	27	25	13	4	6	11	3
1970/71	217	295	454	625	567	332	1118	628	1213	581	694	919	8	8	18	19	36	20	16	5	6	9	10	4
1971/72	307	88	399	404	410	461	468	237	478	483	195	147	10	9	21	30	36	42	21	18	9	19	5	0
1972/73	191	192	289	880	1102	716	518	524	1066	870	662	222	4	14	12	38	38	27	15	0	2	8	24	10
4 1969/70	0	28	175	212	189	330	207	249	643	444	337	173	2	3	6	16	24	35	22	8	3	3	5	7
1970/71	116	235	486	570	596	764	1179	1099	1592	1065	1205	381	4	8	22	26	23	30	24	13	5	17	15	11
1971/72	217	175	219	265	357	361	502	185	372	329	142	238	15	6	12	29	28	28	19	13	4	6	3	5
1972/73	0	0	182	644	1035	479	779	994	1120	937	635	213	2	7	17	31	33	19	4	9	4	11	8	3
6 1969/70	111	113	310	321	334	345	678	819	1068	939	695	417	2	0	7	19	20	20	24	8	3	2	3	2
1970/71	194	329	400	408	485	211	937	221	828	462	391	396	3	6	18	14	26	3	6	2	0	5	3	4
1971/72	357	361	438	742	605	772	392	316	560	650	412	499	2	5	6	17	26	46	5	10	1	2	6	8
1972/73	0	181	181	826	842	570	577	682	493	598	402	304	1	6	13	30	36	29	4	0	0	10	18	14
7 1969/70	32	64	228	270	353	182	414	313	488	424	306	134	3	0	5	13	13	14	9	0	2	1	0	2
1970/71	202	154	313	320	493	224	1108	1114	978	745	556	354	0	2	12	9	19	11	13	0	1	6	15	10
1971/72	171	172	524	444	361	549	653	667	878	1104	720	313	12	9	24	20	40	49	34	23	4	13	15	13
1972/73	247	166	334	676	687	348	439	621	539	913	463	467	3	7	13	23	43	42	3	13	3	33	15	9

8	1969/70	111	150	388	282	374	389	448	754	1038	912	617	404	2	3	7	22	25	30	19	6	1	2	2	1
	1970/71	242	430	565	516	594	404	549	491	644	218	146	369	4	6	27	28	39	32	12	2	5	1	1	3
	1971/72	424	257	259	790	537	545	1497	1557	1617	1146	530	321	8	7	11	10	26	13	4	5	3	3	17	18
	1972/73	116	-922	574	116	818	355	717	1340	1121	760	641	518	1	2	10	18	35	16	19	3	12	29	13	13
10	1969/70	87	59	273	189	261	410	178	293	420	398	206	209	0	1	3	7	8	14	18	11	3	0	1	2
	1970/71	185	284	487	506	633	604	802	716	1063	783	810	486	4	2	15	28	32	28	22	22	7	3	8	10
	1971/72	348	70	212	428	435	367	447	379	924	710	320	161	21	6	19	13	29	17	9	7	0	4	2	3
	1972/73	0	-211	317	320	976	220	669	339	1266	945	360	362	0	6	8	20	28	26	2	3	1	0	0	1
18	1969/70	99	134	383	292	419	605	600	727	1071	724	592	221	2	3	10	16	16	25	19	2	9	18	15	8
	1970/71	350	357	487	562	772	530	610	415	1068	219	516	449	1	7	20	21	26	32	21	12	2	5	7	4
	1971/72	401	81	407	661	846	779	1333	1379	1813	1483	504	407	10	5	10	12	25	14	5	6	11	8	10	8
	1972/73	-222	-440	551	669	906	689	933	1187	1089	1358	753	126	3	2	14	23	38	11	9	4	18	26	19	14
20	1969/70	62	94	324	272	355	296	385	526	731	591	283	240	1	1	9	17	9	22	16	0	9	9	8	5
	1970/71	257	475	435	304	577	236	1163	1297	1091	778	654	519	6	10	13	16	20	15	4	10	18	21	19	13
	1971/72	371	300	531	774	632	643	821	923	1382	1066	543	457	16	9	18	29	26	31	34	6	14	31	4	19
	1972/73	0	0	440	892	1023	810	823	956	850	1360	629	0	4	8	19	26	33	29	10	4	19	15	8	28
21	1969/70	27	83	230	179	280	360	381	401	781	415	257	175	3	5	11	17	17	28	11	6	8	3	1	7
	1970/71	233	383	545	357	636	661	1041	1038	1223	670	549	349	7	11	14	15	25	22	7	9	16	18	17	10
	1971/72	274	276	349	424	720	514	598	685	1015	558	0	322	11	1	12	14	11	37	22	11	3	9	10	4
	1972/73	-94	94	380	674	1182	603	714	-103	933	739	320	646	6	6	13	19	29	19	6	0	7	6	0	10
22	1969/70	66	101	313	254	379	356	891	878	1153	1027	626	351	1	3	8	18	15	23	22	2	4	20	16	3
	1970/71	212	323	548	392	632	175	958	618	698	324	723	469	9	10	15	20	20	14	11	0	6	7	5	1
	1971/72	297	376	609	700	955	898	1089	772	785	710	90	270	10	5	13	23	21	29	8	10	7	17	14	0
	1972/73	102	206	414	1051	1073	765	442	0	1121	798	577	116	3	3	4	14	32	34	8	0	2	0	16	11

APPENDIX 2: Analyses of Variance for Monthly Increment: Tabulated Summary of Partitioned Sum of Squares

<b>(A) Effects on Cross-sectional increment</b>												
<b>Source of variation</b>	<b>J</b>	<b>J</b>	<b>A</b>	<b>S</b>	<b>O</b>	<b>N</b>	<b>D</b>	<b>J</b>	<b>F</b>	<b>M</b>	<b>A</b>	<b>M</b>
Between clones	7.57	8.38	5.07	0.78	9.47	15.0	3.83	15.9	3.12	4.41	40.6	18.9
Direct treatments	3.98	57.5	15.9	47.4	6.14	129.1	432.7	930.5	335.5	419.4	278.2	7.43
T * C Interaction	7.40	47.3	6.49	5.72	11.51	7.48	18.0	108.8	100.6	74.6	9.64	33.5
(WS) effect	1.38	45.7	10.9	43.2	4.06	104.7	148.3	85.1	40.0	7.39	0.22	6.13
(SA) effect	0.32	9.52	4.78	0.85	1.96	14.1	255.7	769.0	288.1	410.8	277.9	1.30
Interaction	2.28	2.30	0.25	3.41	0.12	10.3	28.7	76.4	7.33	1.19	0.01	0.00
Treatment after-effects	7.52	49.1	6.18	35.4	35.7	9.82	21.5	15.3	34.3	15.7	12.9	13.8
A * C Interaction	6.82	33.0	9.59	28.6	5.09	7.07	27.8	32.5	33.8	18.5	23.3	7.84
(WS) effect	4.71	26.5	5.27	21.4	0.35	2.76	0.41	0.01	0.08	1.03	1.10	6.64
(SA) effect	1.40	10.2	0.81	12.9	20.0	7.02	21.0	12.2	34.2	6.31	8.26	0.20
Interaction	1.40	12.5	0.11	1.07	15.4	0.03	0.10	3.12	0.00	8.36	3.55	6.95
Between years	133.5	200.4	14.14	109.7	363.4	69.2	104.9	9.49	140.0	231.9	92.8	41.6
Residual	51.0	193.7	80.9	81.0	57.8	79.3	129.7	145.4	371.7	100.5	135.1	108.0
Total sum of squares	217.8	594.5	138.3	345.5	489.1	317.1	764.3	1361.9	1051.0	904.0	635.5	263.2

<b>(B) Effects on Height Increment</b>												
<b>Source of variation</b>	<b>J</b>	<b>J</b>	<b>A</b>	<b>S</b>	<b>O</b>	<b>N</b>	<b>D</b>	<b>J</b>	<b>F</b>	<b>M</b>	<b>A</b>	<b>M</b>
Between clones	6.37	10.9	4.43	18.6	266.7	38.9	43.4	47.3	137.3	151.5	32.0	43.4
Direct treatments	29.0	25.7	33.7	137.1	159.4	990.3	273.1	114.0	112.0	409.1	250.5	188.6
T * C Interaction	15.9	9.88	14.2	36.9	141.9	218.6	110.6	122.4	35.6	61.0	24.9	55.1
(WS) effect	1.57	22.4	21.2	110.3	134.0	967.7	88.5	70.4	1.40	4.44	4.14	20.9
(SA) effect	1.21	0.02	8.37	4.73	25.1	0.91	156.4	39.3	110.5	397.7	201.0	167.3
Interaction	26.2	3.26	9.13	22.1	0.37	21.6	28.1	4.25	0.01	6.97	45.3	0.35
Treatment after-effects	13.4	2.37	53.9	34.6	32.9	193.2	177.8	22.1	15.2	68.6	52.3	27.0
A * C Interaction	37.4	10.1	47.8	100.5	97.0	84.4	66.3	25.3	29.5	107.2	34.1	53.5
(WS) effect	4.52	0.02	1.68	11.5	0.45	29.5	0.01	0.36	5.40	41.1	6.2	9.23
(SA) effect	8.20	1.36	47.0	3.95	30.8	14.6	175.3	21.5	6.00	27.0	32.5	4.69
Interaction	0.64	0.98	5.30	19.2	1.67	149.2	2.53	0.18	3.88	0.43	13.5	13.1
Between years	195.9	56.5	215.4	100.8	226.7	317.5	754.6	93.4	15.2	71.9	21.1	74.4
Residual	37.1	38.6	137.0	360.8	315.6	311.5	374.4	220.2	132.4	264.8	240.3	76.8
Total sum of squares	346.1	188.6	554.6	789.4	1240.3	2154.3	1900.5	684.1	484.9	1348.2	720.0	598.7