

## FOLIAGE DEVELOPMENT WITHIN THE CROWNS OF PINUS RADIATA TREES AT TWO SPACINGS

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### ABSTRACT

Needle production, development, and abscission in *Pinus radiata* D. Don trees were examined on branches of different ages and orders over an 8-month growing season in two stands of different spacing (6700 and 760 stems/ha) and age (7 and 9 years) growing on a fertile site.

Trees of the more open stand consistently had three orders of branching and living branches up to 6 years old, while the close-spaced stand had only two orders of branching and living branches up to 4 years old. The main period of needle emergence was from August to November, although a few fascicles in the topmost crown level continued to emerge until March. Final needle length decreased with depth in the crown and generally with increasing branch order. Needle length of fascicles which emerged early in spring were in only a few cases significantly greater than those of summer-emerging needle fascicles. Generally needle elongation had ceased by mid-February while the main period of branch elongation was considerably less, i.e., from September to early November, and coincided with the period of needle emergence. The close-spaced trees showed net gains in numbers of fascicles in the first-order branches in the upper two crown levels at the end of the season. Trees of the medium-spaced stand showed greatest net foliage gains in the second- and third-order branches and losses in the first-order branches; the upper two crown levels, however, could not be reached. Values for specific needle areas of the needles, measured in May only, ranged from 121 to 293 cm<sup>2</sup>/g and increased with crown depth and decreased with needle age.

**Keywords:** needle numbers; needle emergence; needle elongation; abscission; branch age; branch order; *Pinus radiata*.

### INTRODUCTION

One of the main limitations to the development of reliable mechanistic models designed to predict the yields of coniferous forest crops is the ability to estimate tree crown or crop canopy development (Landsberg 1986). Predictions of canopy development should predict both the development of leaf area index (LAI) of the stand (Gholz 1986) and the vertical distribution of the foliage within the crowns (McMurtrie *et al.* 1986). Three types of models of tree crown development have been published, none of which, however, meets the requirements of predicting canopy area development in time and space.

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Most of the data of tree crown and canopy development of coniferous forest crops are of changes in dry weight of crown components (e.g., Madgwick 1981, 1983; Tadaki 1986). Unfortunately there are seldom data of specific needle area available, nor is there knowledge of the factors which cause changes in specific leaf area so that data on foliage dry weights can be converted reliably to areas.

Maillette (1982) presented a demographical model which provides detailed information on survival of needles of *Pinus nigra* var. *maritima* (Ait.) Melville in different parts of the crown with climatic conditions, tree age, and growth pattern, but these data of foliage numbers need to be combined with leaf area data to be useful in predicting rates of canopy processes.

The model of needle area development for *Pinus radiata* of McMurtrie *et al.* (1986) is claimed to be a dynamic mechanistic model in which shoot production is a function of photosynthesis at each crown level. The authors conceded that, although relatively realistic predictions of crown development were achieved, major improvements were needed which required information of the level and patterns of variation of growth of needles and branches with position in the crowns of trees. There is little information on this in the published literature.

In this study, data are presented which will assist in the further development of these three types of models or a more comprehensive model which includes components of all three. The information presented is concerned with variation in different attributes of needle (specific needle areas, numbers of fascicles per branch, rates of growth, length) and branch growth with depth in the crown of *P. radiata* trees.

Two stands of *P. radiata* were selected, both of which had closed canopies and natural mortality of the basal branches but showed contrasts in respect to live branch development. The two stands were growing adjacent to each other on a fertile site.

The objectives of the study were to:

- (1) Describe the effects of branch age and order on number of needle fascicles initiated and abscised, and the elongation of new needles within the crowns of *P. radiata* trees;
- (2) Compare the effect of tree spacing on within-crown patterns of needle production, elongation, and loss;
- (3) Examine changes in specific needle area with crown position and needle age.

## MATERIAL AND METHODS

*Pinus radiata* trees were sampled from two adjacent stands at the Long Mile Experimental Site in the grounds of the Forest Research Institute, Rotorua (lat. 38° 10'S, long. 176° 16'E).

*Stand 1* – Medium-spaced stand, about 0.5 ha in area, 9 years old, with 760 stems/ha and average height of 13.5 m. This stand was established using the same planting stock and at the same time as the main experimental forest in the Puruki subcatchment, 30 km south of Rotorua (Beets & Brownlie 1987); its close proximity to the Forest Research

Institute facilitated studies involving daily and intensive measurements. Growth of the Rotorua trees was approximately similar to those at Puruki. Both sites are fertile and well-drained, but the mean annual air temperature at Rotorua is some 2°C warmer than at Puruki.

*Stand 2* – Close-spaced stand, 0.8 ha in area, 7 years old, with a spacing of approximately 6700 stems/ha and average height of 12 m. Details of this stand have been given by Madgwick (1981).

Six trees which could be reached from a mobile elevated platform were selected in the close-spaced stand and three in the medium-spaced stand. Trees in the close-spaced stand were the second row in from the common side between the stands. On each sample tree, an average-sized branch from each whorl of live branches was selected. The age of the branch, seasonal order of production (i.e., formed in the first, second, or third cycle of shoot growth of that year – Bollmann & Sweet 1976), height of branch insertion into the stem, and branch length were noted (Fig. 1). Measurements of needle emergence and length and shoot elongation, and estimates of needle abscission were recorded throughout the main growing season, i.e., from September to May. Previous work on *P. radiata* in the central North Island of New Zealand (Bollmann & Sweet 1976) showed that negligible numbers of new stem units are laid down and only minor amounts of shoot elongation occur between June and August.

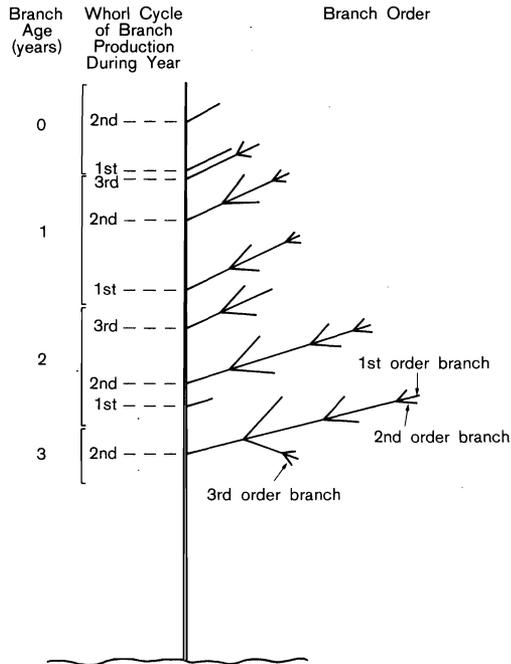


FIG. 1—Method used to classify branches according to age, whorl cycle of production, and order of branching.

Measurements of needle elongation were taken and estimates of abscission and shoot elongation made on first-, second-, and third-order branches, when present, at 4-weekly intervals from September to January and thereafter (when growth rates had decreased) every 8 weeks. It was intended to select three fascicles with needles emerging from fascicle sheaths and to apply dots of acrylic paint to the needle bases at each measurement date throughout the study in order to mark the size of the needles at that time. Different colours of paint identified points of the different measurement dates. However, application of too much paint (e.g., during windy conditions at the top of trees) tended to cause the young emerging needles to stick either together or to the fascicle sheath, thereby causing inhibition or distortion of their growth. Where needle growth appeared to be so affected, neighbouring fascicles were selected and substituted for the damaged fascicle at the next measurement date.

At each measurement date, the lengths of the branches and the average-sized (based on length and diameter) higher-order branchlet per whorl were also recorded (Fig. 1). Number of fascicles which had abscised was estimated by eye by the same observer throughout the study and the length of shoot, or its equivalent length where foliage loss was patchy, was marked with black ink.

At the end of May the first-order sample branches of each tree were harvested. Total branch length was recorded. In that part of the shoot which had elongated during the course of this study, the length of each cycle was measured. Total number of stem units (Bollmann & Sweet 1976) and numbers of needle fascicles and their scars on the defoliated sections of shoot were estimated using the phyllotaxis method described for *P. radiata* shoots by Bannister (1962); second- and, where present, third-order branches were handled in a similar manner.

The needles marked with paint were located at different positions along axes of the shoots depending on time of emergence. Such needles were removed and the lengths of three needles per sampling position were recorded for each shoot. The length of a needle at any particular date was determined by the distance between the paint dot and needle tip plus the length of the fascicle sheath. Needle elongation in pines takes place mainly owing to the activity of the basal intercalary meristem (Romberger 1963).

A non-linear model

$$Y = \frac{A}{(1 + B \cdot C^x)}$$

was found to provide the best fit for the data of needle elongation, and model,

$$Y = A - B \cdot C^x$$

for branch elongation with time. In comparing the regressions of needle growth by branch order, crown level (branch age), and tree spacing, the data were restricted to fascicles which had emerged before 19 October (Fig. 2 and 3), except those of the bottom crown levels of both stands in which fascicles emerged before 9 November were accepted. Regressions were also fitted to the branch elongation data by branch age and tree spacing. GENSTAT (Lawes Agricultural Trust 1983) was used for regression analyses and comparison of regressions.

In May, 10 mature fascicles per age-class of needle per sample branch were collected to measure specific needle area (total surface area/oven-dried weight). Total surface area of the needles was estimated by the volume displacement technique (Beets 1977). The fascicles were oven-dried at 80°C until a constant weight was attained. Detailed statistical analyses were not possible because of the unbalanced nature of the data resulting from the individual trees having different numbers of growth cycles and branches per year, and from some damaged shoots and fascicles requiring substitution of others. Coefficients of variation were calculated.

## RESULTS

### Needle Emergence and Elongation

Trees of the more-open medium-spaced stand consistently had three orders of branches, whereas the trees of the close-spaced stand carried only two orders. Trees of the former stand had foliage-bearing live branches up to 6 years old, i.e., Crown Level 6, while only one of the six trees of the latter stand had such branches as old as 4 years (Table 1). No data are available for the upper two crown levels of the medium-spaced stand as they were out of reach.

TABLE 1—Mean heights above ground and lengths of branches of trees of the medium- and close-spaced stands

Stand	Branch age (years)	Mean height above ground (m)	Mean branch length (mm)	Branch length bearing foliage (mm)
Medium-spaced	2	7.5	2030	1350
	3	7.4	2770	1200
	4	6.3	2100	880
	5	3.7	3690	700
	6	2.9	2680	180
Close-spaced	0	8.8	530	510
	1	8.0	820	700
	2	6.5	1250	580
	3	5.5	1200	630
	4	5.1	1540	330

Needles were emerging by early September and most elongation had ceased by mid-February. The three upper crown levels (0 to 2), including foliage borne on the terminal shoot, of the trees in the close-spaced stand showed a wider range of needle emergence dates than foliage produced in the lower two levels (3 and 4) of that stand or Levels 2 to 6 of the medium-spaced stand. Foliage at Crown Level 0 continued to emerge until 7 March, while foliage arising from the stem and first-order branches of Crown Level 1 emerged in December, although most foliage had emerged before November (Fig. 2 and 3). The time of emergence was similar for the needles in the five lower crown levels of trees of the medium-spaced stand.

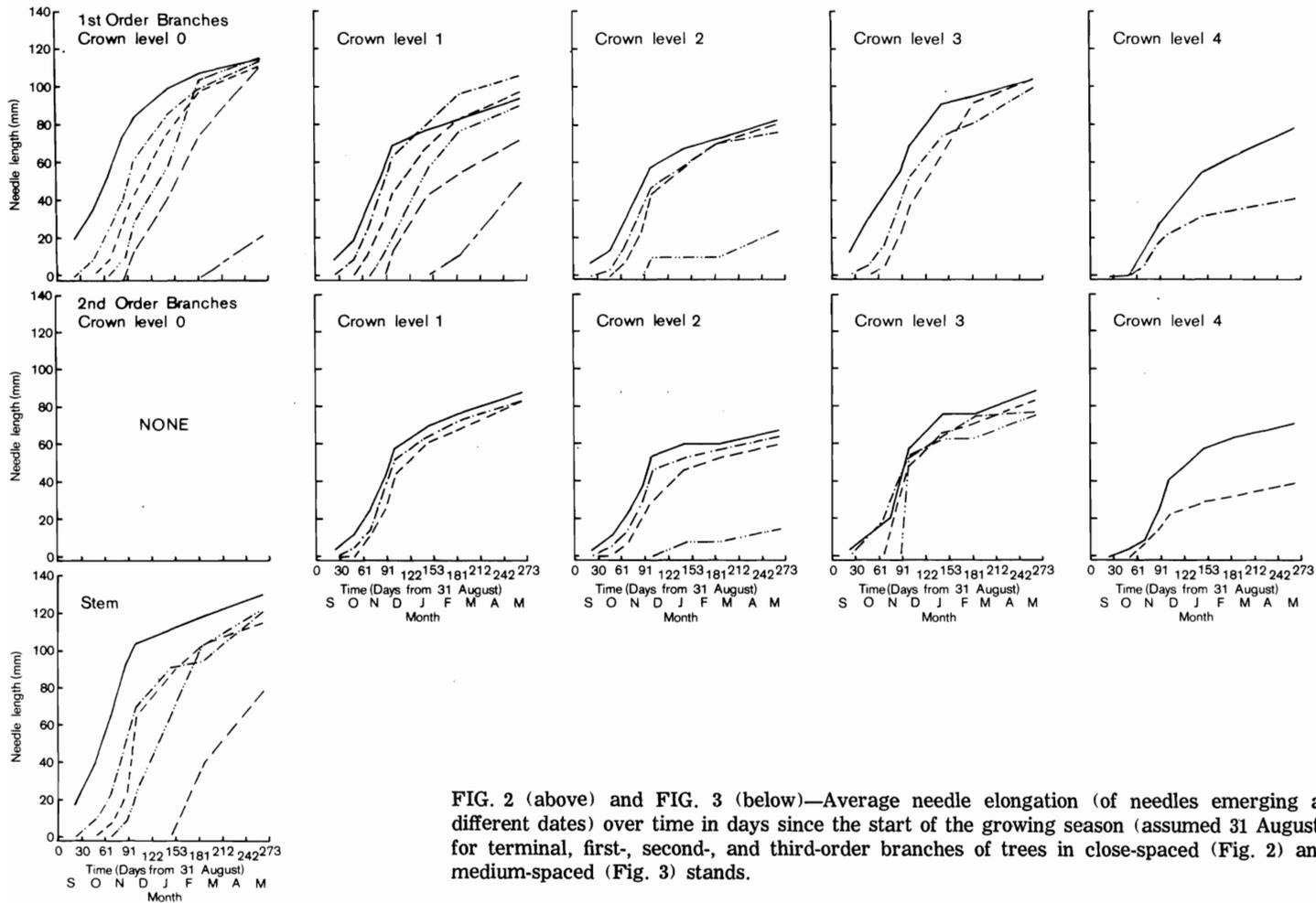
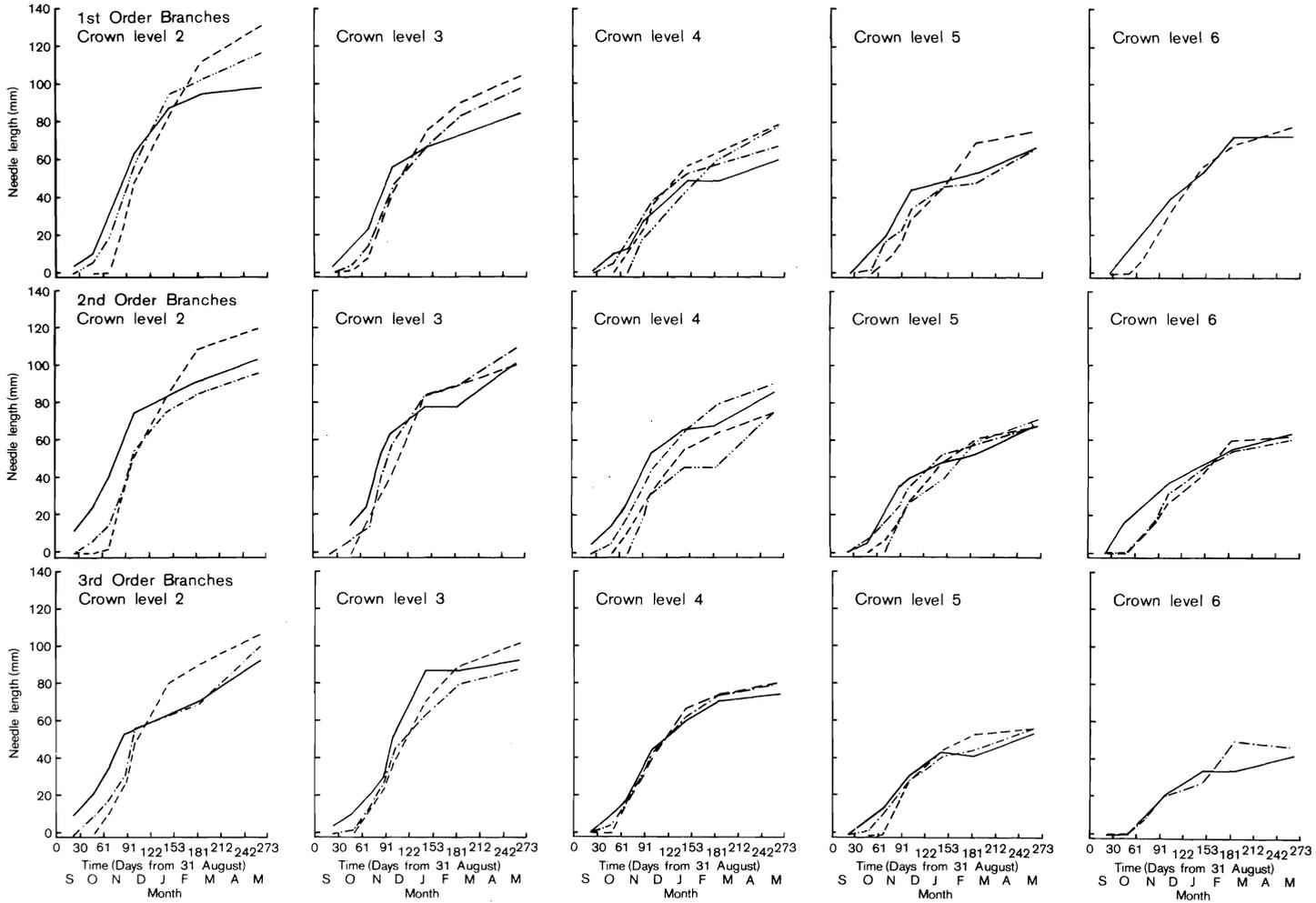


FIG. 2 (above) and FIG. 3 (below)—Average needle elongation (of needles emerging at different dates) over time in days since the start of the growing season (assumed 31 August) for terminal, first-, second-, and third-order branches of trees in close-spaced (Fig. 2) and medium-spaced (Fig. 3) stands.



The values of the parameters of the non-linear model,  $Y = A/(1 + B \cdot C^x)$  and coefficients of determination ( $r^2$ ) are presented for each stand type, branch order, and crown level in Table 2. The  $r^2$  values are generally high, indicating that the regressions satisfactorily fit the data.

TABLE 2—Parameters of the needle growth model,  $Y=A/(1+B.C^x)$ , at different crown positions, where A, B, and C are an asymptote, a scale factor, and a slope factor, respectively

Order of branch	Crown level	Parameters			Coeff. det. $r^2$
		A	B	C	
<b>Medium-spaced stand</b>					
First	2	102.458	72.933	0.956	0.98
	3	95.652	23.527	0.966	0.92
	4	57.098	40.513	0.961	0.94
	5	57.768	56.344	0.956	0.93
	6	74.279	56.130	0.965	0.98
Second	2	93.237	38.473	0.959	0.93
	3	80.750	42.184	0.962	0.93
	4	82.347	26.405	0.967	0.96
	5	61.087	38.719	0.963	0.96
	6	59.945	34.377	0.966	0.95
Third	2	85.445	17.901	0.969	0.91
	3	84.820	119.359	0.953	0.97
	4	73.366	58.536	0.959	0.99
	5	52.573	21.287	0.969	0.92
	6	43.063	53.981	0.964	0.94
<b>Close-spaced stand</b>					
First	0	108.981	17.773	0.968	0.91
	1	91.893	38.899	0.958	0.97
	2	72.846	52.460	0.955	0.95
	3	92.405	119.044	0.949	0.94
	4	73.648	46.499	0.966	0.98
Second	1	77.412	86.673	0.952	0.97
	2	60.889	156.729	0.942	0.97
	3	76.544	163.766	0.944	0.97
	4	64.910	259.305	0.944	0.99
Stem		112.679	29.170	0.958	0.85

In Table 3, non-linear regressions of needle growth are compared between crown levels of each branch order for both stands separately, and also between branch order for the same crown level, i.e., branch age, of both stands. The significant differences noted in these analyses were differences in asymptotic values, i.e., needle length, and not rates of elongation.

In the first-order branches of the medium-spaced stand, needle growth was mostly significantly different among crown levels except between Levels 2 and 3, and 4 and 5. The second-order branches were similar to first-order branches except for Levels 3 and 4 or Levels 5 and 6 which were not different. In the third-order branches, Level 2 was not different from Levels 3 and 4 but the others were all different.

TABLE 3—Comparison of needle growth between crown levels at each branch order

Medium-spaced stand														
First-order branch					Second-order branch				Third-order branch					
Crown level	3	4	5	6	Crown level	3	4	5	6	Crown level	3	4	5	6
2	ns	**	**	**	2	*	*	**	**	2	ns	ns	**	**
3		**	**	**	3		ns	**	**	3		**	**	**
4			ns	**	4			**	**	4			**	**
5				**	5				ns	5				*

Close-spaced stand												
First-order branch						Second-order branch						
Crown level	1	2	3	4	Stem	Crown level	2	3	4	Stem		
0	*	**	ns	**	ns							
1		**	ns	**	*	1	**	ns	**	**		
2			**	ns	**	2		**	ns	**		
3				**	*	3			**	**		
4					**	4				**		

\* significant at the 5% level  
 \*\* significant at the 1% level  
 ns not significant at the 5% level

In the first-order branches of the close-spaced stand, needle length at Crown Level 0 was significantly greater than that of Levels 1, 2, and 4, but not of Level 3. No differences were found between Levels 1 and 3 or Levels 2 and 4 in both second- and third-order branches. Needle growth of stem was different from that of branches of all crown levels, except Level 0 of first-order branches.

In the close-spaced stand there were significant differences in needle growth between different branch orders at the same level in the crown, i.e., branch age, except in Crown Level 4 where there was no difference between first- and second-order branches. In the medium-spaced stand Crown Level 3 did not show the differences between branch orders that the other levels showed (Table 4).

Using data from Crown Levels 0 and 1 of the first-order branches only for the close-spaced stand (Table 5), i.e., the most complete set of data, comparisons were also made between the growth of needles which had emerged at different times. The regression comparisons showed that needles which emerged earlier were not significantly different from those of the later emerging needles in Crown Level 0. On the other hand, the later-emerging needles of Crown Level 1 differed significantly from the earlier needles but the differences were due mainly to final needle length.

#### Numbers of Needle Fascicles Present per Branch

At the end of May when the branches were harvested estimates were made of (a) the number of fascicles present per sample branch of each crown level and branch order at the beginning of the season, and (b) number of fascicles produced during the growing season. The sum of these make up the total number of fascicles present during the

TABLE 4—Comparison of needle growth between branch orders at each crown level

		Crown level 1											
		Branch order										2	
		1					**						
Branch order		Crown level 2				Crown level 3				Crown level 4			
		Close	Medium			Close	Medium			Close	Medium		
		2	1	2	3	2	1	2	3	2	1	2	3
Close	1	**	**	**	ns	**	ns	*	ns	ns	**	ns	ns
	2		**	**	**		*	ns	ns		*	**	ns
Medium	1			ns	**			ns	ns			**	**
	2				ns				ns				ns

		Crown level 5 (medium-spaced only)				Crown level 6 (medium-spaced only)			
		2		3		2		3	
Branch order									
	1		ns		ns		**		**
	2				**				**

\*\* significant at the 1% level  
 ns not significant at the 5% level

TABLE 5—Comparison between growth of needles emerged at five different times within a crown level in closed-spaced stand

Emerged time	Crown level 0				Crown level 1			
	2	3	4	5	2	3	4	5
1	ns	ns	ns	ns	*	ns	ns	*
2		ns	ns	ns		ns	ns	**
3			ns	ns			ns	*
4				ns				*

\* significant at the 5% level  
 \*\* significant at the 1% level  
 ns not significant at the 5% level

Note: The values of "Emerged time" are relative, e.g., needles of 1 emerged earlier than those of 2.

season; the actual number of fascicles at any one time was, of course, less since production and loss occurred simultaneously. Production occurred at the apices of the branches and loss in the older ages. These were estimated separately. The number of fascicles abscised during the 8-month study was also estimated and the balance of numbers of fascicles remaining was calculated. The values presented in Table 6 are means and ranges of numbers of fascicles between samples for branches of each stand type, crown level, and branch order. The number of samples of each branch category is noted in the bottom part of the table.

TABLE 6—Changes in number of fascicles per branch over the growing season by crown level for medium- and close-spaced stands (*see* text for explanation of table)

Numbers of fascicles per branch	Branch order	Crown level										
		Medium-spaced stand					Close-spaced stand					
		2	3	4	5	6	0	1	2	3	4	
At beginning of growing season	1	Mean	368	422	442	362	56	0	148	194	260	150
		Range	186–550	372–490	171–887	99–887	12–100	0	0–482	11–526	69–549	108–192
	2	Mean	130	93	133	120	47	–	0	50	94	50
		Range	0–360	0–181	0–380	0–365	31–66	–	0	0–191	0–166	0–77
	3	Mean	72	21	39	48	23	–	–	–	–	–
		Range	0–144	0–76	0–151	0–153	12–37	–	–	–	–	–
Produced during growing season	1	Mean	169	284	126	76	82	256	188	109	19	36
		Range	125–212	189–392	94–171	48–114	65–99	137–431	99–355	17–214	0–113	13–58
	2	Mean	107	78	63	40	46	–	71	46	18	22
		Range	48–181	0–136	0–172	0–84	0–95	–	46–120	0–105	0–58	0–55
	3	Mean	74	38	22	15	15	–	–	–	–	–
		Range	60–83	17–56	0–42	7–31	12–38	–	–	–	–	–
Total present during growing season	1	Mean	537	706	568	438	138	256	336	303	279	186
		Range	311–762	576–764	271–668	147–893	77–199	137–431	114–685	28–740	69–662	166–205
	2	Mean	237	171	196	160	93	–	71	96	112	72
		Range	48–509	74–285	38–411	21–365	40–141	–	46–120	13–296	50–207	42–115
	3	Mean	146	59	61	63	38	–	–	–	–	–
		Range	65–227	17–132	0–151	8–153	12–79	–	–	–	–	–
Abscised during growing season	1	Mean	247	202	226	330	41	0	39	106	53	147
		Range	184–310	0–334	0–667	133–451	0–81	0	0–127	0–348	0–222	12–281
	2	Mean	32	56	24	31	27	–	0	11	5	9
		Range	0–92	0–206	0–212	0–164	0–59	–	0	0–58	0–23	0–31
	3	Mean	0	0	0	8	16	–	–	–	–	–
		Range	0	0	0–7	0–78	0–31	–	–	–	–	–
Balance end of season	1	–78	+82	–100	–254	+41	+256	+149	+3	–34	–111	
	2	+75	+22	+39	+9	+19	–	+71	+35	+13	+13	
	3	+74	+38	+22	+7	–1	–	–	–	–	–	
Number of branches in sample	1	2	3	6	3	2	6	13	10	6	2	
	2	4	9	24	14	7	–	11	18	7	5	
	3	2	6	19	18	7	–	–	–	–	–	

Trees of the medium-spaced stand showed considerable growth in terms of fascicles produced in the three branch orders, even in 6-year-old branches, while trees of the close-spaced stand produced most of their fascicles on the first-order branches of the youngest branch age-class.

Trees of the medium-spaced stand showed considerable gains in needle fascicle numbers over the season in the second- and third-order branches, but net losses in the first-order (Table 6). The first-order branches, however, still retained a considerable end-of-season balance residual number and had more foliage per branch than the higher order branches. Trees in the close-spaced stand showed considerable net gains in numbers of fascicles of the first-order branches only in the top two crown levels and showed net losses in Crown Levels 3 and 4 (Table 6). The second-order branches showed net gains in Crown Levels 1 to 4. The numbers of fascicles produced per branch in both the first- and second-order branches, however, were relatively few.

### Specific Needle Area

Where there were fewer than three fascicles per branch class and per needle age, samples of different branch orders were combined in Table 7 to provide a mean value

TABLE 7—Effect of crown level, branch order, and foliage age on specific needle leaf area ( $\text{cm}^2/\text{g}$ ) of needles collected from (a) medium-spaced stand and (b) close-spaced stand. Values are means of 3 to 6 samples and values in parentheses are coefficients of variations expressed as percentage of mean value

Crown level	Branch order	Needle age			
		Current	1-year-old	2-year-old	3-year-old
<b>(a) Medium-spaced stand</b>					
3	1	235.1 (9)	162.5 (3)	147.2 (8)	None
	2				
4	1	234.1 (16)	144.4 (4)	123.4 (2)	121.3 (5)
	2	259.6 (5)	183.0 (22)	138.8 (8)	None
	3		215.1 (15)	176.1 (8)	None
5	1	292.9 (11)	204.4 (29)	148.8 (20)	130.2 (16)
	2				
	3		227.8 (13)	160.0 (11)	None
6	1	1 sample only		None	None
	2	None	207.0 (11)	2 samples	None
	3	None		None	None
<b>(b) Closed-spaced stand</b>					
1	1	246.1 (17)	187.7 (12)	148.7 (21)	None
	2			None	None
2	1	232.3 (8)	160.8 (13)	147.2 (13)	None
	2	245.3 (2)	181.4 (11)	None	None
3	1	254.2 (19)	189.0 (19)	156.1 (17)	None
	2		209.7 (17)	197.2 (13)	None
4	1	292.2 (11)	223.6 (21)	171.5 (11)	None

and coefficient of variation for the combined samples. Both stands showed trends of (i) increasing values for specific needle area with increasing branch age, i.e., crown depth, and (ii) decreasing values with increasing needle age.

### Branch Elongation

In contrast to needle growth, branch elongation of the close-spaced trees occurred only over a 2-month period from early September (Fig. 4). A different model from that used for needle growth was used to describe branch growth. The model fitted to the branch elongation data had coefficients of determination greater than 0.98; the parameters are listed in Table 8a for each age of branch and there were significant differences between all branch ages (Tables 8b, Fig. 4).

Data collected from trees of the medium-spaced stand indicated that the fact that their crowns were wider than trees of the close-spaced stand resulted, at least in part, from

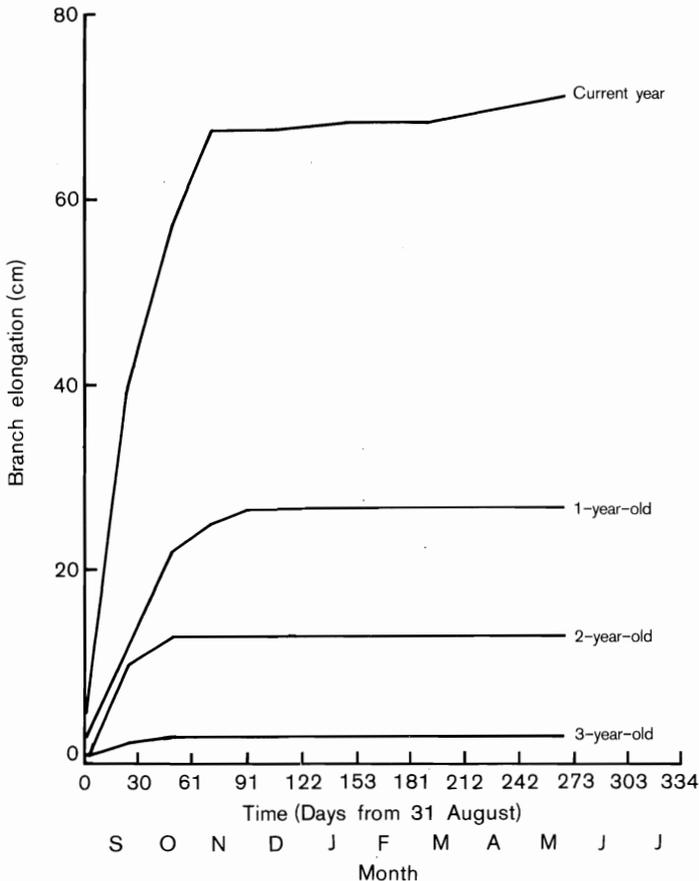


FIG. 4—Average branch elongation of different-aged branches over time in days since 31 August for trees of close-spaced stand.

TABLE 8a—Parameters of the model of branch elongation  $Y = A \cdot B \cdot C^x$ , at different branch-age, where A, B and C are an asymptote, a scale factor and a slope factor, respectively

Branch age (year)	Parameters			Coeff. det. $r^2$
	A	B	C	
Current	69.818	68.032	0.964	0.99
1	27.472	27.042	0.971	0.98
2	12.981	13.893	0.936	0.99
3	2.025	2.148	0.947	0.99
4	5.075	5.397	0.952	0.99

TABLE 8b—Comparison of branch elongation at different branch-age

Branch order	1	2	3
Current	**	**	**
1		*	**
2			*

\* significant at the 5% level

\*\* significant at the 1% level

the longer duration of growth of the branches over a period of years. The 4-, 5-, and 6-year-old branches of the medium-spaced stand continued to elongate 70 to 100 mm per year.

In the trees of the close-spaced stand, branch elongation was more vigorous and continued over a longer duration at the top of the tree crown than at the bottom (Fig. 4). Branch growth exceeded 10 cm only in the upper three crown levels. The two older age-classes of branches made negligible elongation. Branches at the top crown level showed some renewed elongation from late March to May in addition to the spring elongation. This late season growth, however, constituted less than 10% of the total annual elongation.

## DISCUSSION

The measurements reported here are from the average-sized living branch of each whorl from each of the sample trees. Values for means and the ranges of the needle attributes measured per branch sample type show considerable, but not unexpected, variation (Tables 3, 4, and 6) as the plant material comprised a mixture of genotypes which showed large differences in branch frequency and size. Significant clonal variations in branch numbers have previously been reported for *P. radiata* (Burdon 1971; Madgwick 1983), as well as other species, e.g., *Pinus contorta* Loudon (O'Reilly 1986).

Although our study started in September, it was apparent that some fascicles had emerged and our data suggest that the main period of needle emergence was over 2 months from approximately mid-August (Fig. 2 and 3). The terminal shoot and branches of the two youngest-aged branches of trees of the close-spaced stand continued to have

a few needle fascicles emerging through summer (December and January) and there was an autumn flush in March in the topmost branches.

There was a general pattern of decreasing needle length with increasing branch age, i.e., depth in crown, and with increasing branch order in trees of both stands (Fig. 2 and 3). Comparison of the linearised regressions of needle growth indicated that generally rates of growth were not significantly different, but rather the differences were due to duration of growth as final needle lengths were significantly different. The study site was fertile and moist and there was no suggestion of any nutritional or moisture stress inhibition of growth (cf. Linder *et al.* 1987). In addition to needle length decreasing with crown depth and increasing branch order, numbers of new fascicles (Table 6) and branch elongation (Fig. 4) decreased and specific needle area increased (Table 7) with crown depth. Kellomäki (1980) noted that the amount of needle biomass produced per branch in *Pinus sylvestris* L. depended on the crown position and the photosynthetic production of the branch. The changes in needle and branch growth noted above may also be associated with changes in red:far-red ratio of light (Morgan *et al.* 1985). Unfortunately, insufficient knowledge of the irradiance profiles in these spatially complex stands and lack of data of needle biomass and density precluded any attempts to relate growth of the branches and needles to environmental conditions within the crowns.

The 8-month study covered those times of the year when almost all needle initiation and elongation in *P. radiata* trees growing in the Rotorua area occurs (Bollmann & Sweet 1976; Bollmann *et al.* 1986). Madgwick's (1983) data of changes in canopy needle dry weights show a sigmoid form of dry matter increment occurring over 4 months in late spring to summer. Our data generally agree with this, but suggest that needle elongation may continue for another month. Linder *et al.* (1987) reported on an irrigation and fertilisation experiment with 10-year-old *P. radiata* in Australia in which there were four-fold differences in needle length with treatment. They noted that needles of trees of all treatments stopped growing by mid-February, which is in agreement with our New Zealand data. We observed that final needle length in most shoots was not significantly related to date of needle emergence during the period from August to November; however, the needles of less vigorous shoots (Fig. 2) which emerged in September appeared shorter than those emerging in August. O'Reilly (1986) presented data, and a descriptive model, for the elongation of needles at the proximal and distal ends of first-order branches from the fourth whorl of *P. contorta* trees of different provenances. He noted that the patterns of growth initiation were similar for both distal and proximal needles, but there were differences among provenances. O'Reilly noted that, although growth of proximal needles ceased earlier than did distal needle growth, the differences were slight; there were highly significant differences among provenances. He ascribed most of the differences in final needle length to duration of elongation.

The values of numbers of needles initiated in Table 6 provide a reasonable estimate of the annual production, but the values of winter leaf abscission in the literature are too uncertain to allow a reliable estimate of net changes in foliage numbers over the whole year to be attempted. Will (1959) and Linder *et al.* (1987) claimed that needle fall in *P. radiata* peaks during winter on sites not limited by water. Madgwick (1983) observed static values of canopy needle mass during winter which would indicate that leaf fall is comparable to needle growth at that time. The "growth", however, may be

mainly increased needle dry weight rather than increased needle numbers or further needle elongation at this time. The general picture of net changes in needle numbers per branch was of net losses of needles on first-order branches of second to fifth crown levels and slight gains in the bottom level of trees in the medium-spaced stand. The second- and third-order branches in all six levels generally showed slight gains. This is in general agreement with Madgwick's (1983) observation that foliage amounts were tending to decrease more in the mid-crown region than at the base of the crown. Trees of the close-spaced stand had major foliage increases only in the top two crown levels where first- and second-order branches were present. Generally the close-spaced stand was not making major over-all gains in foliage amounts and if numbers of branches at different levels were taken into account there could well have been a net loss of foliage. Madgwick & Oliver (1985) estimated that foliage production peaked in the close-spaced stand at age 7 at 10.55 t/ha where total canopy foliage biomass was 14.81 t/ha and that by age 8 production fell by 17%.

Specific needle area data are important in estimating needle area of tree crowns and LAI from needle dry weight. Kellomäki & Oker-Blom (1981) noted that specific needle areas increase with crown depth and decrease with increasing needle age in stands of *P. sylvestris*. Our data (Table 7) concur. To convert canopy dry weights to needle areas it is important to record needle weight by crown level and needle age.

Madgwick (1981) estimated branch production of the close-spaced stand at age 7 to be 6.5 t/ha. Most branch elongation takes place during September and October (Fig. 4), but the major period of height growth extends from August to January (Jackson *et al.* 1976; Rook & Whyte 1976). Radial stem growth of *P. radiata* occurs over a longer period, i.e., at least from August to May, and presumably radial branch growth too occurs over a longer period than extension growth.

The data presented describe needle development in terms of numbers of needles produced per branch type and their elongation, within the crowns of *P. radiata* grown at widely different spacings. The information, however, is not available in absolute units of needle area production in space over time, which is needed for realistic canopy development models. Our data, together with data of other studies of foliage biomass changes (Madgwick 1981, 1983; Madgwick & Oliver 1985; Linder *et al.* 1987), however, will assist in the extrapolation of canopy models developed from simpler crop structures to older and a wider architectural range of *P. radiata* stands.

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