

BUD MORPHOGENESIS OF *PINUS RADIATA* IN NEW ZEALAND

II. THE SEASONAL SHOOT GROWTH PATTERN OF SEVEN CLONES AT FOUR SITES

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ABSTRACT

Primordial initiation and development of branch buds were studied in seven clones at each of four locations in the North Island of New Zealand.

Initiation of the annual shoot primordia had started by mid-September at all sites. Growth differences due to site began to appear in January, when extension and primordial differentiation of the new season's shoot was starting.

At the warmer sites initiation continued until late autumn or early winter while at the colder sites it ceased earlier. Consequently the annual shoots collected in September from the coastal Te Teko seed orchard contained 220 to 241 more primordia than those from the other three sites. Shoot extension by September was also higher there (1.3 mm per internode as compared with 0.5 mm at the inland location of Waimihia). Te Teko was also the site where needle growth was most rapid and the number of cycles in the annual shoot was greatest.

The results generally confirm the pattern of shoot growth previously demonstrated for the leading shoot of a single clone.

INTRODUCTION

The first paper in this series (Bollmann and Sweet, 1976) described in detail the seasonal pattern of primordial initiation and subsequent development and growth of the annual shoot of a single clone of *Pinus radiata* D. Don. It also indicated how this varied between two sites differing in temperature by 2° to 3° throughout the year.

This paper extends these data to 7 clones and 4 sites. For reasons of availability of material, first order branch shoots were examined rather than the leading shoots used in Part I of this study.

MATERIALS AND METHODS

The material used in this study was from grafts of seven clones (including No. 7 on which Paper I of this series was based) planted in four North Island seed orchards. The orchards are located near Te Teko (in coastal Bay of Plenty, and owned by the Tasman Pulp and Paper Company), in Kaingaroa and Waimihia State Forests (on the central volcanic plateau), and in Gwavas State Forest (in southern Hawkes Bay). Geographic and climatic details of the sites are given in Table 1. All sites, as part of

TABLE 1—Geography and climate of the seed orchard sites

	TE TEKŌ					KAINGAROA					WAIMIHIA					GWAVAS				
Latitude (South)	38°02'					38°24'					38°50'					39°44'				
Altitude (mm)	8					544					743					355				
CLIMATE — ANNUAL																				
Mean average daily temperature (°C)	14.0					11.0					9.3					11.0				
Mean precipitation (mm)	1512					1548					1704					1224				
% of growing season with deficit of 75 mm (150 mm)	70(20)					60(0)					60(0)					70(20)				
CLIMATE — MONTHLY																				
Month before and at the time of harvest	Nov Dec	Jan Feb	Mar Apr	May Jul	Aug Sept	Nov Dec	Jan Feb	Mar Apr	May Jul	Aug Sept	Nov Dec	Jan Feb	Mar Apr	May Jul	Aug Sept	Nov Dec	Jan Feb	Mar Apr	May Jul	Aug Sept
Mean temperature in year of harvest (°C)	16.6 19.3	21.0 20.9	n.a.* 16.1	12.8 8.3	11.2 12.0	13.3 16.3	17.1 17.8	15.3 12.2	9.6 4.8	7.0 8.4	11.8 14.5	15.1 15.2	13.9 9.9	7.9 2.7	4.9 6.2	13.3 15.5	16.7 17.6	15.0 12.5	10.7 6.0	7.4 8.4
Mean temperature for all years of record (°C)	15.2 17.3	18.5 18.9	n.a.* 14.6	11.7 9.1	9.9 11.4	12.4 14.4	15.1 15.8	14.5 11.4	8.5 5.7	6.7 8.5	11.2 12.9	14.3 14.7	12.8 9.7	6.7 4.1	5.0 6.8	13.2 14.5	15.5 16.3	14.4 11.3	9.2 5.9	6.8 8.7
Precipitation in year of harvest (mm)	47 229	135 89	35 114	258 44	112 70	31 294	140 76	44 106	202 99	190 62	60 220	150 28	19 105	221 159	229 96	20 93	156 64	57 40	150 71	104 108
Mean precipitation for all years of record (mm)	94 119	94 114	122 124	163 160	157 114	109 127	114 132	112 114	150 142	142 135	135 145	112 132	109 132	177 163	157 142	76 117	99 99	109 89	106 114	78 74

n.a.* = not available. Climate is of the nearest meteorological station — in all cases within 10 km of the orchard site.

production seed orchards, received fertiliser (mainly superphosphate and urea) annually. The application (based on foliage analysis) was aimed at achieving foliar levels of N, P, K and Mg above 2.0, 0.2, 0.8 and 0.12% respectively (Kellison, unpubl.). At the time of harvest Ca and Mg had reached these levels, but N (1.7%) and P (0.12%) levels were still below the target. Nutrient levels were comparable at all orchards.

The grafts from which the material was collected were planted in 1964 (Kaingaroa and Waimihia), 1965 (Gwavas), and 1966 (Te Teko).

Five potentially cone-bearing first order branches, two to three years old, were selected on each of two ramets per clone at each site. The branches were located in the upper crown of the trees at a part of the stem four to twelve cycles below the leading bud. One branch per ramet was sampled (14 total) in each of five months: December 1974 and January, February, April and September 1975. Collections were made during the third week of each month. Table 1 indicates the extent to which the weather in the months of harvests differed from the long term means.

At each collection the shoot was harvested at the point where initiation for the 1974-75 part of the shoot had started. In the elongated part of this shoot the length of each cycle was measured and counts were made of bracts without axillary buds (i.e., sterile cataphylls), what appeared to be dormant short shoots, needle fascicles, seed cones (receptive or in bud) and of second order branches or their buds. The main bud was then dissected and all its components, cataphylls and the various kinds of axillary primordia, counted. The primordia in the area of the long shoot clusters in this study were dissected and preserved in FAA for microscopic examination. The primordia were dehydrated in a TBA series, embedded in Poly-Ester wax and stained in Haematoxylin and Orange-G.

The preceding annual shoot on part of the branch below the point of harvest was also assessed. Its length was measured, and its long shoot clusters counted and the numbers of their components (branches, one year old or mature seed cones and dormant buds) determined.

Basically the design consisted of harvesting two shoots and/or buds from each of seven clones at four sites on five different dates. The experiment was not completely balanced however. At Kaingaroa clone 81 was represented by only one tree and none could be found of clone 101 (this clone suffers from graft incompatibility). During a storm the crown broke out of one ramet of clone 81 at Te Teko and one of clone 108 at Kaingaroa.

Because few of the parameters examined were present at all five harvests, separate analyses of variance were made for each harvest. These were two-way factorial analyses to test the significance of differences among clones (random effects) and sites (fixed effects). The analysis coped with the minor imbalance (up to five missing shoots of a total of 56), in that F tests for main effects were virtually unbiased, even in the presence of some interaction.

RESULTS

The variability in branch shoot initiation and development, between sites and clones, at five dates during the 1974-75 growing season, is illustrated in Fig. 1. Table 2 gives more details and information on cataphyll initiation by the apical meristem, subsequent cataphyll development and elongation of the shoot.

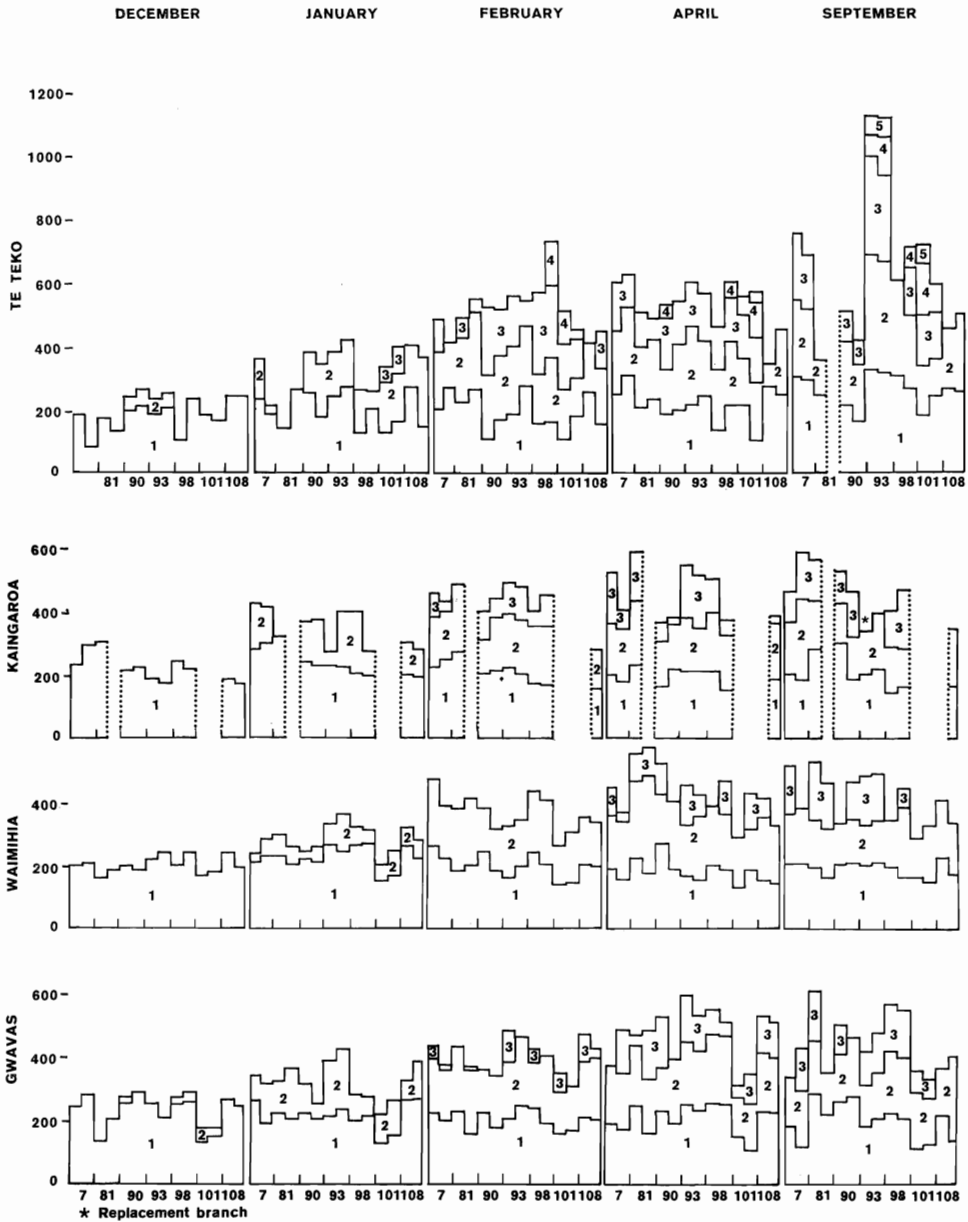


FIG. 1—Cataphyll initiation of branch shoots from four seed orchard sites at five harvest dates.

The Shoot in Early Summer (December)

Initiation of the new season's bud scales and axillary primordia was well under way at all sites. Some clones at Te Teko (Nos. 90 and 93) and at Gwavas (Nos. 90, 98, and 101) showed a second cycle being initiated including, at Te Teko, some axillary

TABLE 2—Cataphyll initiation and subsequent growth

Initiation				Development				Shoot Elongation				
Growth cycle being initiated ⁽¹⁾				Mean No. of total cataphylls	Mean No. of cataphylls inside the buds	Mean percentage of cataphylls outside the buds (2)	Mean percentage of short shoots with emerged needles (3)	Mean length of cycle 1 (cm)	Mean length of cycle 2 (cm)	Mean length of cycle 3 (cm)	Mean total length of shoot (cm)	
Cycle No.	Mean No. of cataphylls	Cycle No.	Mean No. of cataphylls									
DECEMBER												
Te Teko	1	185	2	17	202	181	10.4	—	0.9	—	—	0.9
Kaingarooa	1	229			229	213	7.0	—	0.7	—	—	0.7
Waimihia	1	210			210	200	4.9	—	0.5	—	—	0.5
Gwavas	1	229	2	9	238	223	6.3	—	0.9	—	—	0.9
JANUARY												
Te Teko	2	115	3	19	332	227	31.6	3.3	8	—	—	8
Kaingarooa	2	109			350	305	12.9	0.8	5	—	—	5
Waimihia	2	57			290	282	2.8	—	0.6	—	—	0.6
Gwavas	2	95			320	302	5.9	0.9	2	—	—	2
FEBRUARY												
Te Teko	3	133	4	126	505	266	44	35	24	5	—	29
Kaingarooa	2	158	3	61	431	311	28	13	7	—	—	7
Waimihia	2	166			358	292	18	5	5	—	—	5
Gwavas	2	167	3	27	404	276	32	7	8	—	—	8
APRIL												
Te Teko	3	118	4	72	568	260	54	36	32	8	—	40
Kaingarooa	3	88			448	286	36	19	12	3	—	15
Waimihia	3	62			436	273	37	18	9	1	—	10
Gwavas	3	90			474	293	38	11	12	(0.3)	—	13
SEPTEMBER												
Te Teko	1A ⁽⁴⁾	78			658	113	85	91	42	28	14	84
Kaingarooa	1A	80			438	130	70	74	20	10	1	31
Waimihia	1A	63			417	191	53	34	16	6	—	22
Gwavas	1A	80			436	120	73	68	23	17	2	42

(1) Frequently at any one site, different shoots were initiating different cycles. Hence two columns.

(2) Number of cataphylls of the extended part of the shoot
 $\frac{\text{Total number of cataphylls}}{\text{Total number of cataphylls}} \times 100$

(3) Number of short shoots with emerged needles
 $\frac{\text{Total numbers of short shoots}}{\text{Total numbers of short shoots}} \times 100$

(4) Cycle 1 of the following season.

TABLE 3—Mean number of cataphylls per completed cycle of harvested branches

	Te Teko	Kaingaroa	Waimihia	Gwavas
Cycle 1	223 (63)	215 (47)	206 (66)	216 (68)
Cycle 2	168 (44)	160 (32)	165 (42)	168 (42)
Cycle 3	161* (28)	124 (11)	124 (12)	123 (18)
Cycle 4	104 (8)			
Cycle 5	77 (3)			

Numbers in brackets are the mean number of shoots on which the sample was based.

* Significantly different (1% level) from cycle 3 values at the other 3 sites.

primordia. At this stage long shoot primordia could only be identified by their large size and the occurrence of sterile cataphylls above them. Shoot elongation (cycle 1) had just started at all sites.

The Shoot in Mid-Summer (January and February)

By mid-January the initiation of cycle 1 was completed at all sites with a few possible exceptions where long shoots could not yet be identified.

Clone No. 101 at Te Teko had buds with components of cycle 3 present. There were no significant differences between sites in the total number of cataphylls initiated. ($P = 0.077$.) Long shoot primordia had not yet differentiated into seed cone and branch primordia and they were still recognisable only by their size. An exception was Te Teko, where some seed cone primordia could be identified (Table 4). Shoot extension was well under way at Te Teko and Kaingaroa (Fig. 2).

February is the warmest and often the driest month in New Zealand, and initiation, development and extension continued at all sites. By then many long shoots of cycle 1 had differentiated into seed cone primordia and branches but those of cycle 2 were still largely undifferentiated (Table 4). Cataphyll initiation, needle emergence and shoot extension were most advanced at Te Teko; Waimihia buds had the fewest cataphylls.

The Shoot in Autumn (April)

The mid-April collection was near the end of the growing season in most places. Temperatures were about 5° lower than at the previous (February) collection.

The buds collected at Te Teko were more advanced than those at the other sites in terms of total initiation, shoot primordia development and shoot extension (Table 2). Several clones at Te Teko (Nos. 90, 98, and 101) had laid down a fourth cycle not present at any other site (Fig. 1). At that stage the shoots from Waimihia had initiated only slightly fewer cataphylls than those from Kaingaroa and Gwavas. At all sites somewhat fewer first cycle long shoots were present than the previous month (Table 4). Trees at Te Teko had more identifiable seed cone primordia of the second cycle than those at Kaingaroa, Waimihia and Gwavas indicating that seed cone determination of cycle 2 at the latter sites was probably still in progress.

The Shoot in Spring (September)

Branches collected in September were on the average slightly less vigorous than those of the previous collections. It was seldom possible to find five comparable branches

TABLE 4—Longshoot development and differentiation (mean numbers)

	Te Teko					Kaingaroa					Waimihia					Gwavas				
	Dec	Jan	Feb	Apr	Sep	Dec	Jan	Feb	Apr	Sep	Dec	Jan	Feb	Apr	Sep	Dec	Jan	Feb	Apr	Sep
CYCLE 1																				
Branches	0	1.9	4.8	4.6	6.3	—	0	4.7	2.1	3.9	—	0	5.9	2.9	3.1	—	0	4.9	2.7	3.6
Seed cones	0	0.6	2.6	2.6	2.8	—	0	1.9	4.4	2.3	—	0	1.2	3.5	2.3	—	0	2.1	3.7	2.9
Undifferentiated buds	10.8	7.5	2.6	1.6	0.7	—	11.5	7.1	3.9	1.1	—	10.3	7.3	3.9	0.4	10.6	10.0	6.9	4.2	0.2
Total longshoots	10.8	10.0	10.0	8.8	9.8	—	11.5	13.7	10.4	7.3	—	10.3	14.4	10.3	5.8	10.6	10.0	13.9	10.6	6.7
CYCLE 2																				
Branches	—		4.0	4.1	5.5	—		1.2	1.7	5.5	—		0	2.9	6.4	—		0	1.2	5.2
Seed cones	—		0	2.6	0.3	—		0	0.5	0.6	—		0	0.3	0.1	—		0	0.4	1.0
Undifferentiated buds	2.9		2.9	5.4	1.3	—		8.2	5.7	0.1	—		1.3	7.3	0.4	—		7.1	9.7	0.8
Total longshoots	2.9		9.9	12.1	6.1	—		9.4	9.9	6.2	—		1.3	10.5	6.9	—		7.1	11.3	7.0

Significant differences occur between sites with respect to:

Number of	Cycle 1	Cycle 2
Branches	Apr (0.1%) Sep (5%)	NS
Seed cones	NS	Apr (0.1%)
Undifferentiated buds	Apr (5%)	Apr (1%)
Total long shoots	Feb (5%), Sep (5%)	NS

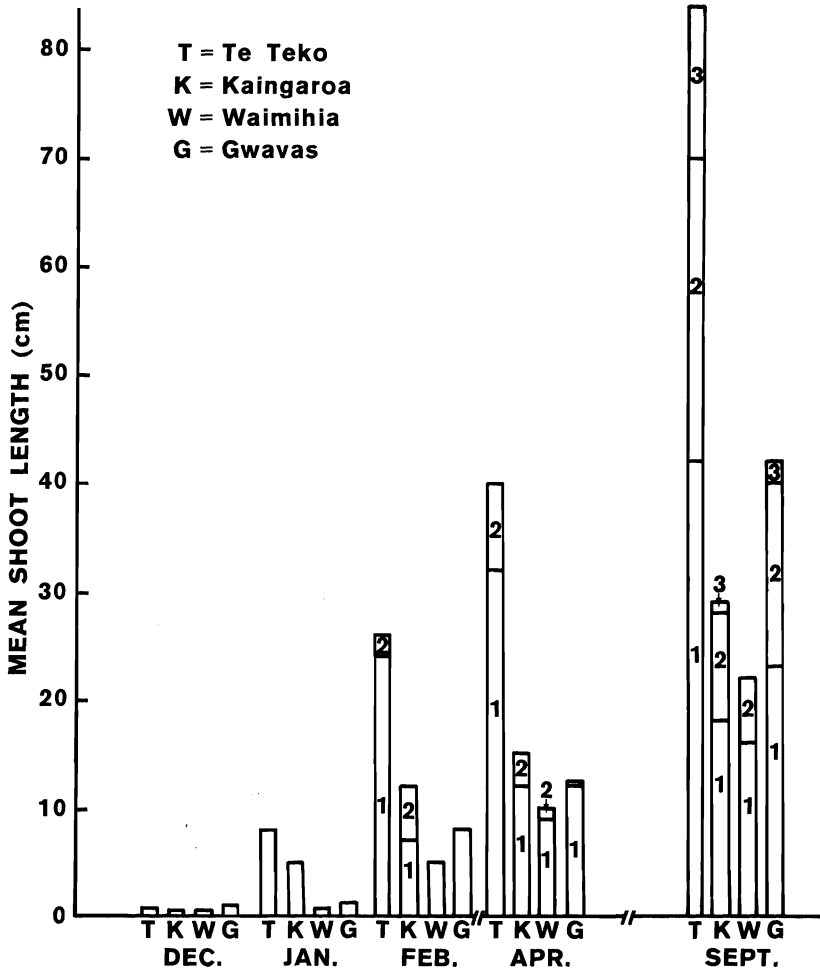


FIG. 2—Shoot extension in four seed orchard sites at five harvest dates.

in the same cluster and for most ramets this sample was obtained from slightly younger branch material.

The September shoot contains all of the previous season's initiation plus, in its bud tip, some of the primordia for cycle 1 of next year (Fig. 3).

Most clones had initiated more cataphylls and primordia at Te Teko than elsewhere and three of the seven clones (93, 98, and 101) had also produced at least one more cycle of growth there (Table 2, Fig. 1). Needle emergence was most advanced at Te Teko (see Table 2) and this was shared by all the clones. Whereas cycle 1 seed cones were fully receptive at Kaingaroa and Gwavas, they had generally closed at Te Teko. At Waimihia the seed cone buds had just started to open. There were no significant differences in numbers of cycle 1 or cycle 2 seed cones between the four sites (Table 4).

In September the annual shoot was not yet fully extended, with part of it still

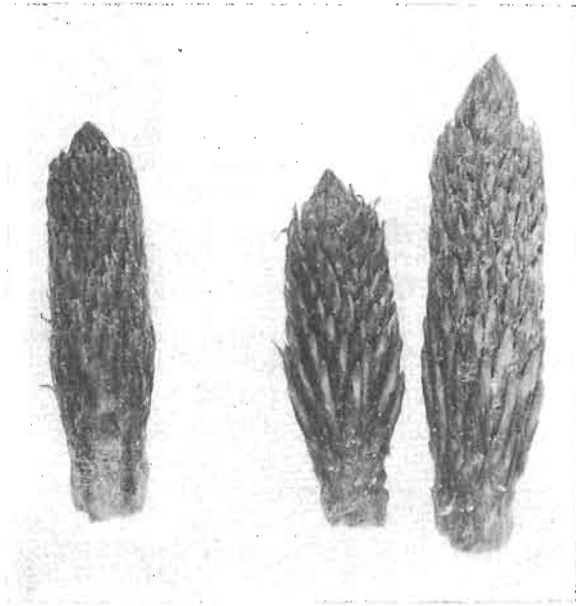


FIG. 3—Buds at the beginning of the growing season in September. The buds (tightly sealed distal region of the shoots), from Waimihia (left) and Kaingaroa (right, pair) seed orchard branch shoots contain the sterile cataphylls of the new season's initiation. Note that the long shoot buds of the last cycle of the previous season have developed little and are hidden under the rapidly developing needle fascicles.

contained inside the bud. Since no additional branches were collected after September data on fully extended shoot length are not available to assess site differences in this respect. However, based on the number of primordia initiated and the regression of numbers of primordia on total shoot length for cycle 1, it was calculated that Te Teko and Gwavas shoots had 87% of their growth potential realised by September, as against only 67% for the Waimihia shoots. This compares very well with indications given by bud size.

Initiation

The beginning of the initiation phase of shoot development is characterised by two features: (a) the long shoots which terminate the last cycle in the annual shoots are, in contrast to those of the earlier cycles, much smaller in size compared with the short shoots below them, and (b) the presence of unusually large numbers of sterile cataphylls (apical cataphylls, which protect the apex during the winter, and newly formed ones) which can be seen at the base of the first cycle of the new season's shoot (Bollmann and Sweet, 1976). The initials of the new shoot are contained in the tips of the September buds (see Fig. 3). Mean cataphyll counts in September of 80 at Gwavas, 78 at Te Teko, 79 at Kaingaroa, and 63 at Waimihia, indicate that while initiation may have started a little later at Waimihia than at the other sites, there were no statistically significant

differences between sites ($P = 0.139$). Differences between clones however were significant at the 5% level, indicating some clonal differences in the start of initiation in the new season's shoot.

Total numbers of cataphylls initiated by the shoots sampled in December and January (Table 2) were not significantly different at the four sites. In the January shoots the mean counts ranged from 332 in Te Teko (coastal) to 290 in Waimihia (altitude of 743 m). Of the branches collected in February, April and September however total initiation was significantly higher at Te Teko than at the other sites; 147 more cataphylls than Waimihia in February, 132 more in April and 241 more in September (significance levels were 0.1, 5 and 1% respectively).

There were no significant differences between sites in the number of primordia in cycles 1 and 2, but cycle 3 at Te Teko had more cataphylls initiated than at the other seed orchards (Table 3). Overall, cycle 1 had significantly more cataphylls than cycle 2 which in turn produced more initials than cycle 3. This difference in mean cataphyll numbers between cycles 1 and 2 was apparent in *all* of the 7 clones. There were several individual shoots however, in which cycle 1 had fewer cataphylls than cycle 2 (Fig. 1).

The number of cycles laid down in the annual shoot was greatest at Te Teko where one-third of the shoots harvested in September had either 4 or 5 cycles (clones 93, 98 and 101). Elsewhere no shoots had more than 3 cycles (see Fig. 1). At Waimihia many of the shoots had only two cycles. The higher number of growth cycles of the September branches at Te Teko was confirmed by a count made of cycles laid down the previous year on all the branches sampled. At Te Teko 41% of the branches had more than 3 cycles the previous year compared with 13%, 10% and 17% at Kaingaroa, Waimihia and Gwavas.

Year to year variation in the number of cycles initiated by a shoot has been reported previously (Bollmann and Sweet, 1976; Bannister, 1962). It was demonstrated also by the branch shoots in this study. Comparison with the number of cycles laid down the previous year by the same branches shows a reduction at all sites. The mean number of cycles recorded in April and September with the corresponding numbers of the previous year's shoots shown between brackets are: Te Teko 3.3 (3.5), Kaingaroa 2.8 (3.1), Waimihia 2.5 (2.9), and Gwavas 2.8 (3.1).

Shoot Elongation

The pattern of shoot extension is shown in Fig. 2. In interpreting this figure it should be realised that the data for each harvest were obtained from different branches between which a degree of variability existed. It should also be noted that the figure only shows shoot elongation until September and does not include the large proportion of the spring growth that takes place from September (when the last shoots were harvested) until December. Figure 2 illustrates that shoot elongation was much more prompt at Te Teko than at the other sites. There is also an indication that extension growth of a branch, as of leader shoots (paper I, Fig. 7, Table 5), occurs simultaneously to some extent in consecutive shoot cycles.

A strong correlation was found between the length of a fully extended shoot and the numbers of cataphylls it contained. Over all the ramets at all sites, the correlation coefficient between numbers of first cycle cataphylls and length in September of the

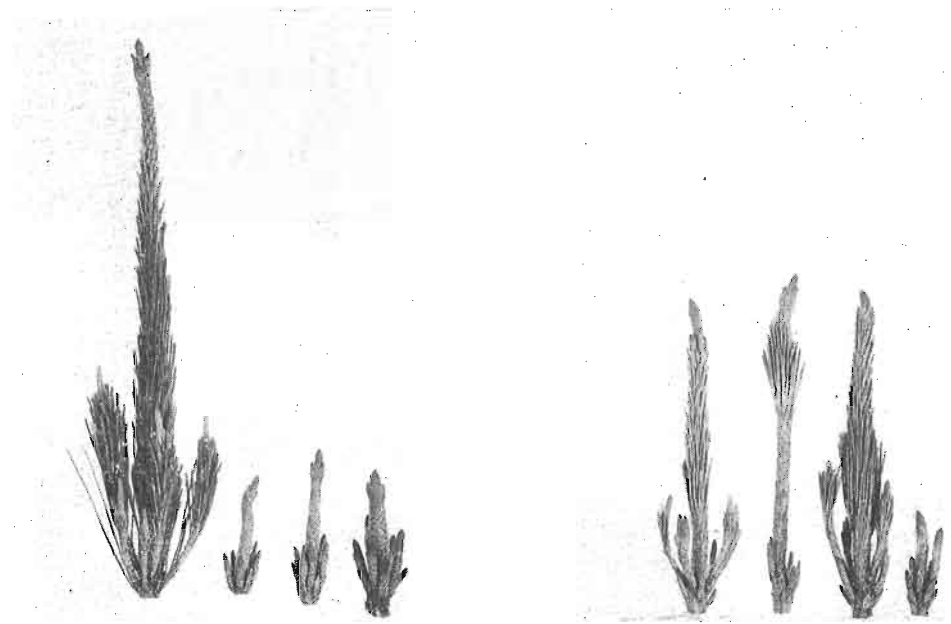


FIG. 4—The shoots of two clones at four sites in autumn (April).

Clone 7 is the group on the left, and Clone 90 the group on the right.

In each case shoots are, from left to right, from: Te Teko, Kaingaroa, Waimihia, and Gwavas.

The total number of cataphylls initiated at that time (with those of cycle 1 in parentheses) were, in the same order:

Clone 7: 654 (331), 417 (192), 431 (187), 375 (163).

Clone 90: 491 (193), 393 (225), 527 (227), 404 (190).

fully extended first cycle was 0.7 ($P < 0.01$). The fact that the mean length of cycle 1 in September was greatest at Te Teko despite a comparable number of cataphylls (Fig. 2) indicates that the first cycle of some shoots from the other areas were not yet fully extended. However site \times clone interactions and variability between individual shoots (see Fig. 4) were evident.

Long Shoot Development

During recent studies of flowering it became apparent that long shoot differentiation can have considerable quantitative variation between branches within a ramet (authors, unpubl.). Although the branches for the five harvests were matched as carefully as possible the general pattern of long shoot development presented in Table 4 must therefore be regarded with caution.

In cycle 1, there was a progressive decrease with time in the number of primordia that remained undifferentiated. The increase in the numbers of recognisable seed cone primordia from February to April at Kaingaroa, Waimihia and Gwavas indicates the time involved in the differentiation process. The number of seed cone primordia decreased from April to September at Kaingaroa, Waimihia and Gwavas, pointing to pre-anthesis abortion at these sites. This is confirmed by the decline in the total number

of long shoots over that period. Abortion of seed cone primordia however does not account for all the loss of long shoots. Some, which were originally classified as undifferentiated long shoots, may subsequently have developed as needle fascicles. (In fully developed shoots atypically short needle fascicles often occur just below a set of branches, indicating that they may have been differentiated at a later date.)

Further examination of Table 4 shows that at the three sites other than Te Teko the mean numbers of cycle 1 branches decreased between February and April, and increased again subsequently. While the increase by September can be explained by differentiation of previously undifferentiated long shoot primordia, the sudden drop in April is more difficult to explain. Identification of early-formed (February) cycle 1 long shoots was made externally under the stereo microscope largely on the basis of size and in retrospect it is apparent that the total long shoot count and numbers of these identified as branches in February were over-estimated.

More detailed data on differentiation within the long shoot (branches and seed cones) and short shoot (pollen cones and needles) regions of *Pinus radiata* shoots will be published in a separate paper.

SUMMARY AND DISCUSSION

In this study the data presented in the first paper of the series have been extended to demonstrate further site effects and clonal variability.

The major effect of site was on the number of growth cycles in the annual shoot and, as a result of this, on primordial initiation, long shoot differentiation, and extension growth.

At the warmest site (Te Teko), 5 out of 13 trees had annual shoots with more than 3 cycles, while at the other seed orchards no shoots had more than 3. Also more primordia were initiated in the Te Teko annual shoot (725 compared with a mean of 503 at the other sites). Since the number of cataphylls of the first two cycles were comparable at the four sites the increased primordial initiation at Te Teko must therefore have resulted mostly from the higher number of growth cycles.

In terms of long shoot initiation and development the effect of site also related to the increased number of cycles in the annual shoot at Te Teko. More cycles clearly mean increased total numbers of long shoots initiated.

Within any one cycle however site affected long shoot differentiation rather than initiation. Of the total numbers of first cycle long shoots in September a higher proportion developed into branches at Te Teko than at the other location.

The finding that the numbers of receptive (September) seed cones per cycle was comparable at the four locations was unexpected as the Te Teko orchard does in fact have a much higher annual seed production than the other sites, at least during the first 10 years of life (Sweet, 1977). Information suggests that variation between seed orchards exists in the number of branch shoots with three or more growth cycles, the number of seed cone-bearing shoots in the crown at a given age (Sweet, 1977), levels of cone abortion (Sweet, 1973), and seed yield per cone (Sweet, 1977). These factors, rather than the number of seed cones differentiated per cycle, must have represented the main effects of site on seed production.

It was not possible to examine the shoots when fully extended. Shoot measurements in September, however, suggest that elongation was more prompt at the warmer location. There 87% of the estimated total length of the shoot was realised by September as compared with 67% at the cooler climate sites.

The data presented here confirm that geography influenced the initiation of shoot components and their subsequent development and growth. As natural soil nutrient levels had been modified at all sites with fertiliser schedules aimed at producing a set of common foliar nutrient levels, the expectation is that climate has provided the main geographical influence. The role of temperature in affecting primordial initiation is currently under investigation in a growth room study.

Part I of this series of papers examined the growth pattern of the leading shoot of radiata pine. The information in this paper relates to the growth of vigorous first-order shoots from the upper part of the crown. Branches lower in the crown tend to initiate fewer cycles in the annual shoot (often only one) and there the axillary primordia that differentiate reproductively develop into pollen cones rather than seed cones. It is planned to publish information on pollen cone differentiation and development in a separate paper in this series.

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REFERENCES

- BANNISTER, M. H. 1962: Some variation in the growth patterns of *Pinus radiata* in N.Z. **N.Z. J. Sci.** 5: 342-7.
- BOLLMANN, M. P. and SWEET, G. B. 1976: Bud morphogenesis of *Pinus radiata* in N.Z. I. The initiation and extension of the leading shoot of one clone at two sites. **N.Z. J. For. Sci.** 6(3): 376-92.
- SWEET, G. B. 1973: Shedding of Reproductive Structures in Forest Trees. In "Shedding of Plant Parts" T. T. Kozlowski (ed.). Academic Press, New York and London.
- 1977: What you always wanted to know about site — but didn't like to ask! **N.Z. For. Serv., For. Res. Inst., Genetics and Tree Improvement Rep.** 127 (unpubl.).