BUD MORPHOGENESIS OF *PINUS RADIATA* IN NEW ZEALAND

1: THE INITIATION AND EXTENSION OF THE LEADING SHOOT OF ONE CLONE AT TWO SITES

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ABSTRACT

This paper describes and analyses primordial initiation and development, and the subsequent elongation, of the leading shoot of a clone of **Pinus radiata** D. Don at two sites in New Zealand.

At Rotorua, initiation of the components of the annual shoot began between mid-September and mid-October and finished during August. Five clusters of branches developed, the first three of which bore seed cones. These clusters were initiated in December, at the end of January, and during March.

At Waimihia, located at a higher altitude than Rotorua, only three to four clusters of branches were initiated in the annual shoot, with at most two of those containing seed cones.

In Rotorua the new shoot began elongating in December, and by the time seasonal extension growth slowed (July) nearly half of the annual shoot extension had taken place. The remainder occurred the following spring.

INTRODUCTION

Pinus is a genus which, once out of the seedling stage, has pre-determined growth patterns. In a species with a simple annual shoot growth (e.g., *Pinus resinosa* Ait. — Lanner, 1976) the components of the new season's shoot are laid down during late summer and autumn as a series of primordia inside a bud in which they overwinter (Duff and Nolan, 1958; Owston, 1968; Sacher, 1954). In spring the bud extends to form a shoot, the length of which is to a large extent determined by the number of primordia initiated during the previous season (Lanner, 1970).

Such a growth pattern is called monocyclic* because only one "cycle" of growth (recognised by one cluster of branches marking the end of the cycle — Fig. 1a) is extended in a year. Monocyclic pine species show three sequential phases of development: (1) initiation of primordia for the next season's extension growth, (2)

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* The terminology used in this paper is after Doak (1935) and Debazac (1963) and is elaborated in the following paper in this Journal (Sweet and Bollmann, 1976).

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dormancy, and (3) extension of the primordia initiated the previous season. Frequently the third and first phases overlap in time to a greater or less extent (Sacher, 1954; Sucoff, 1971; Hanawa, 1972). The total period during which shoot development (phases 3 and 1) occurs varies of course between species and between environments (Lotan and Zahner, 1963; Sacher, 1954).

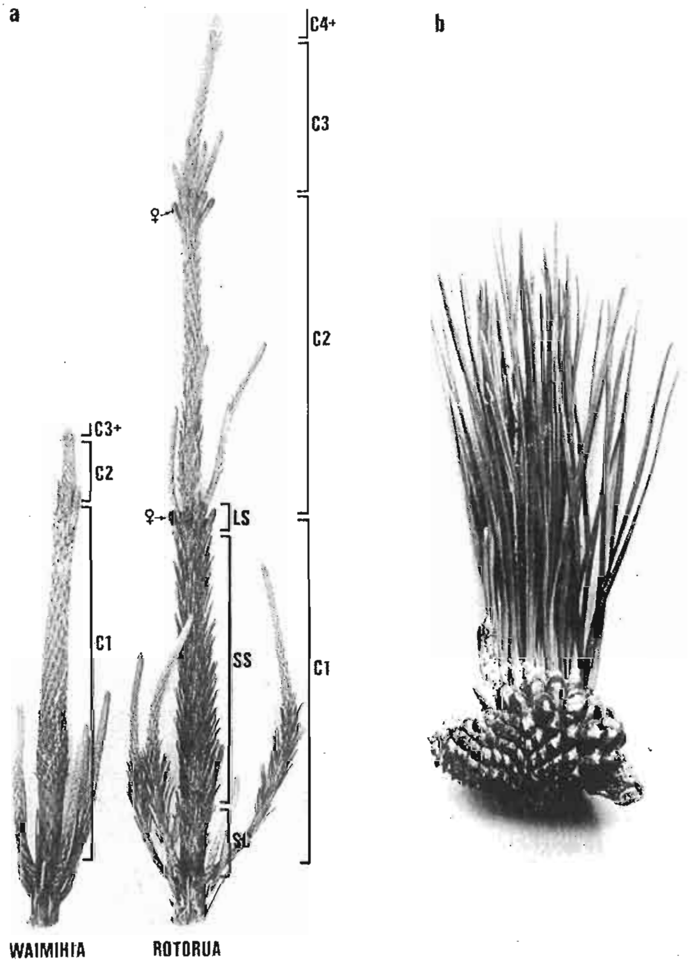

FIG. 1—Growth of **Pinus radiata**.

a. The leading shoot of Clone 7 at Waimihia and Rotorua in spring. C = cycle; SC = sterile cataphyll region; SS = short-shoot region; LS = long-shoot region; ♀ = receptive seed cone.

b. An aberrant seed cone found on Clone 7. It is not clear whether the needles and branch buds were initiated after damage to the already developed cone or whether they were formed in place of reproductive scales during early stages of cone development. The Figure illustrates the lack of fundamental differences between the reproductive and vegetative shoots in **Pinus** (**see** Doak, 1935).

In polycyclic species the single shoot growth cycle of a monocyclic species is repeated once or more than once in a single growing season (Debazac, 1963). In some polycyclic species (e.g., *Pinus echinata* Mill.; Tepper (1963)) cycles of growth may occur in which initiation is soon followed by shoot extension; but other growth cycles may be fully initiated, overwinter in a bud, and extend the following spring.

Polycyclic shoots vary from relatively simple, as in *Pinus contorta* Dougl., to complex as in *Pinus caribaea* Morelet (Lanner, 1976). In general, complex polycyclic growth is characteristic of warm temperate or tropical climates.

There is little published information on patterns of shoot initiation and extension for pine species native to areas with climates which are mild throughout the year. Lanner (1966), however, provides a general record of the growth and flowering of a number of pine species, including *Pinus radiata* D. Don, planted in Hawaii in an environment greatly different from that of their natural habitat. All species except *P. radiata* still showed a seasonal pattern of growth and dormancy in climatic conditions which were mild enough to permit growth at any time of the year. The unusual feature of *P. radiata* was the lack of a defined dormant season in the majority of the trees. The trees that did grow episodically did not all go dormant at the same time of year. The lack of a defined period of dormancy in *P. radiata* has also been reported from Italy (Eccher, 1968), Australia (Fielding, 1960; Pawsey, 1964; Cremer, 1973) and New Zealand (Jackson, Gifford and Chittenden, 1976).

Although there have been publications on seasonal patterns of stem extension growth of *P. radiata* (Jacobs, 1937; Fielding, 1960; Cremer, 1973), there has been little examination of seasonal patterns of primordial initiation in this species, despite the obvious importance of this to total stem growth (Lanner, 1970). Nor is much known of the extent to which differences in growth between clones, sites and years result from such differences in primordial initiation.

Part 1 of this paper reports the result of investigations into the morphogenesis of the terminal bud of the leading shoot of one clone of *P. radiata* at two sites in New Zealand. It establishes the general seasonal pattern of primordial initiation, and consequent development and growth of the shoot. Part 2 (in preparation) will report on primordial initiation and development in branch buds of seven clones at four different sites in New Zealand, to establish the extent of variation in growth and flowering potential between sites and clones.

MATERIALS AND METHODS

The material studied was from grafts of a single clone (No. 7) located at the Forest Research Institute, Rotorua. These grafts, planted 6 years prior to the study, were from scions taken originally from an ortet planted in 1885, and propagated repeatedly over the last 20 years. The ramets selected were some 5 m tall and uniform in both their pattern of growth and flowering behaviour over the past 3 years.

The fact that variability between ramets of a clone is so limited on any one site enables sampling to be reduced considerably relative to that which would be required from a seedling population. A preliminary study (Bollmann, 1974) indicated that an accurate picture of the seasonal growth pattern of a clone could be obtained by sampling one ramet from a population at frequent and regular intervals throughout the year; such a procedure was adopted for this study.

From 17 October 1973 until 23 October 1974 collections were made at weekly intervals during January and February (summer), and at two- to four-week intervals during the remainder of the period. At each collection, part of the leading shoot from a single tree was harvested. Counts and measurements were made of needles and branches already extended on the annual shoot. The terminal bud was cut in half longitudinally and fixed in FAA under vacuum. The two halves were then weighed and the heavier of the two was stored for subsequent microscopy. The remaining half of the bud was dissected and counts of cataphylls and primordia were made. Total numbers of bud components were estimated, based on counts of one-half adjusted proportionately by the fresh weight of both halves of the buds. Preliminary counts had shown such estimates to be accurate within 2%.

The bud material was dehydrated in a TBA series and the bud halves were embedded in polyester wax. Large material was sectioned on a sledge microtome at 8-10 μm, and smaller buds on a rotary microtome at 4-6 μm. The sections were stained in haematoxylin and orange –G (Heidenhain).

To provide some indication of the influence of site on shoot initiation, eight collections of the same clone were also made from a seed orchard in Waimihia Forest, 90 km south of Rotorua. This site has an altitude of 776 m, 406 m higher than that of Rotorua, and has temperatures 2 to 3°C lower at all times of the year.

RESULTS

The General Pattern

The seasonal pattern of initiation and subsequent extension growth of the annual shoot of Clone 7 at Rotorua is shown in Fig. 2a and 2b. The figures present data from 29 of the 33 trees, harvested at intervals during the 12 months of the experiment. In Fig. 2a changes with time are shown in the numbers of lateral components in the annual shoot, both extended and unextended from the bud. Figure 2b shows the length of the leading shoot elongating from the primordial initiation shown in Fig. 2a. In both Fig. 2a and 2b the shoot is shown divided into its growth cycles, i.e., sections of stem with sterile cataphylls at the base and a cluster of branches and/or seed cones at the top. From this it is readily possible to determine the initiation time of structures which elongate at a certain time of the year or, alternatively, the time at which any given primordia will extend.

Figure 2 illustrates a continuous pattern of initiation and extension throughout the year, with normally more than one complete cycle of growth unextended in the bud at any given time. The number of structures in the bud reaches its lowest value at the time of initiation of cycle 1.

Clearly, to understand the annual shoot growth pattern of a species with five cycles of growth in a year it is important to determine which is the cycle that corresponds with the annual shoot of a monocyclic species, and thus is the "starting cycle" of the annual shoot. As stated previously such a cycle is initiated after (or partially overlapping with) the rapid stem extension which occurs in spring. The cycle marked 1 in Fig. 2 is the first cycle to be initiated during the flush of spring extension growth (of cycles 4 and 5) and thus fills that position. Additionally, it normally bears seed cones — a necessary prerequisite to its being the starting cycle of the annual shoot.

One further attribute characterises it as a first cycle, and aids in its subsequent

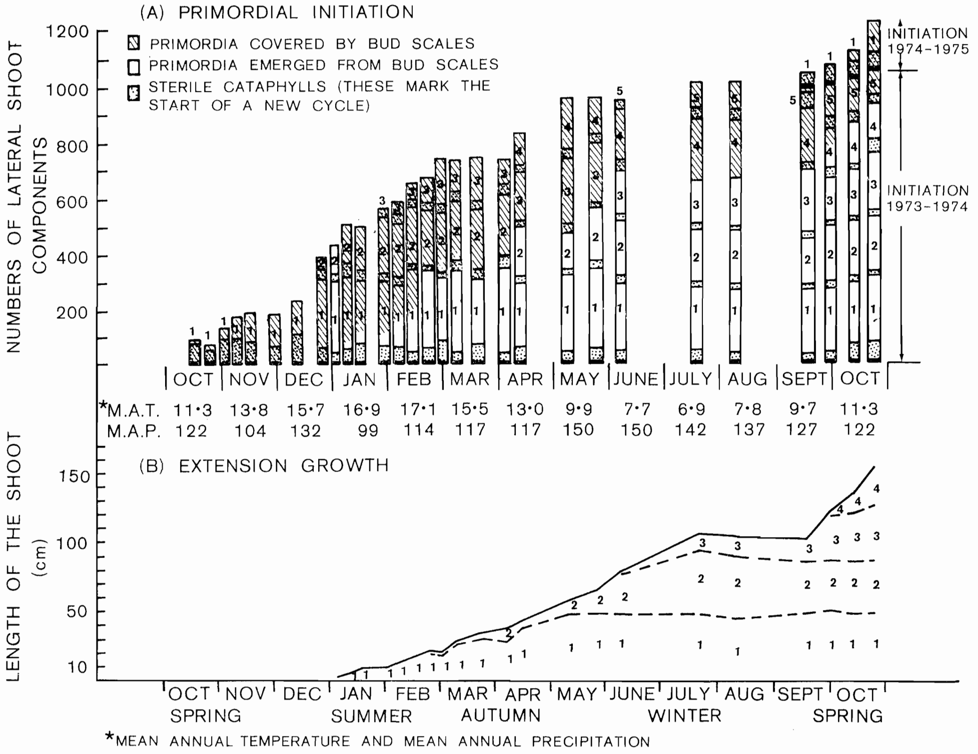

FIG. 2—Growth of the terminal bud of Clone 7 at Rotorua.

TABLE 1—Numbers of cataphylls initiated in 1973-74 by trees which produced 4 and 5 cycles during 1972-73*

By (date)	"5 cycle" trees	"4 cycle" trees
6 March	738	
13 March		923
20 March	743	
11 April	833	
24 April		984
8 May	957	
5 June	956	
19 June		1035
18 July	1003	
7 August	1016	
28 August		1070
16 September	1048	

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* Each value represents the total number of cataphylls on the leading shoot of one ramet, initiated between the start of the growing season and the time of harvest.

identification. In areas where there is a well-defined cold season there is a larger band of sterile cataphylls at the base of the first cycle than at the start of other cycles. This is characteristic and easily identifiable (Bannister, 1962). It is probable that the basal and more crowded cataphylls were laid down just before seasonal growth ceased (as happens in the shoot of a monocyclic species — Lanner and Van den Berg, 1975), and that the upper wider-spaced ones were initiated after the renewal of growth in spring. Cycles initiated after the first have been numbered consecutively for identification.

Because of the sequential harvesting pattern, it was possible to count the number of structures present in a given cycle on a large number of ramets, giving an indication of the repeatability of this factor and the adequacy of single ramet harvesting. Figure 2 illustrates clearly that there was little variability between ramets in this respect. Calculation of means and standard deviations for the numbers of primordia initiated in completed cycles on each ramet harvested gave values for cycle 1 of 304 ± 25 (22 ramets), for cycle 2 of 224 ± 21 (18 ramets), and for cycle 3 of 189 ± 26 (10 ramets). Table 2 provides comparable data for axillary primordia.

TABLE 2—Mean numbers of axillary primordia per cycle initiated at Rotorua and Waimihia

Cycle no.	ROTORUA (1) Number SD	n*	WAIMIHIA (2) Number SD	n*	DIFFERENCE (1) — (2)
1	248 ± 20	22	306 ± 39	8	— 58
2	192 ± 19	18	172 ± 12	5	+ 20
3	161 ± 30	10	160 ± 26	5	+ 1
4	170 ± 19	7	32	2	+138
5	85 ± 39	5	(no cycle formed)		+ 85
TOTAL†	856		670		+186

* The number of trees contributing to the sample. The rationale for these numbers is evident from Fig. 2.

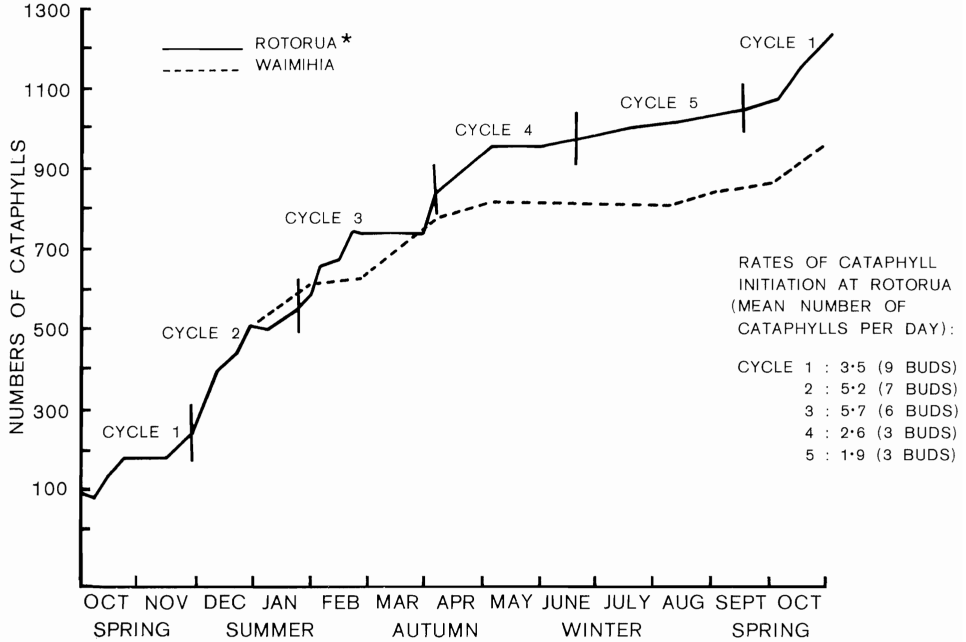
† To convert the total numbers of axillary primordia initiated to the total numbers of cataphylls initiated it is necessary to add 196 sterile cataphylls initiated at Rotorua, and 160 at Waimihia.

Initiation of Cataphylls

Initiation of the first cycle at Rotorua in 1973 began before 17 October; in 1974 it began between 16 and 27 September. In the 12 months during which Clone 7 was studied intensively, initiation of cataphylls continued throughout the summer into winter with only two notable interruptions. One occurred in November during the initiation of cycle 1, and another pause of about 6 weeks occurred near the completion of the third cycle (Fig. 2 and 3). Both pauses followed a period of exceptionally dry conditions during the preceding month (New Zealand Meteorological Service, 1973; 1974). Initiation rates for each cycle at Rotorua, expressed as the mean number of cataphylls initiated per day, are given in Fig. 3. The rate was highest during January and February when cycles 2 and 3 were laid down. The rates during autumn and winter when cycles 4 and 5 were initiated, were markedly lower.

The first collection from Waimihia was made early in January, at which time

500 cataphylls had been produced, all of the first cycle. This compared with 509 cataphylls (of which 188 belonged to the second cycle of initiation) in the Rotorua bud collected at about the same time. Overall, cataphyll initiation at the two sites was comparable until the end of the third cycle. After that time initiation largely ceased at Waimihia, while it continued at Rotorua (Fig. 3).



*(DIVISIONS BETWEEN CYCLES ARE MARKED FOR ROTORUA ONLY)

FIG. 3—Initiation of cataphylls.

In the 1970-71 growing season the buds of all the 33 ramets in the study had initiated and extended 5 cycles of shoot growth and, in the following year only 4 cycles were laid down. During 1972-73 (the growing season prior to that of the experiment) 29 out of the 36 trees had again produced 5 cycles of growth, but the remaining trees had produced only 4 cycles. In the year of harvest these "4-cycle trees" grew somewhat differently from the others in terms of early seasonal primordial initiation and extension growth, and for this reason they have been excluded from Fig. 2. Table 1 illustrates that the number of cataphylls initiated by the "4-cycle trees" at the time they were harvested was always greater than that initiated by the "5-cycle trees" at the nearest subsequent harvest. This implies that cataphyll initiation is affected by factors other than the current environment of the tree.

Initiation of Axillary Primordia

After a number of cataphylls are laid down by the apical meristem, swellings develop in the axils of cataphylls below the fourth from the apex (as seen in microscopic section — Fig. 4a). The cataphylls subtending these young primordia already have differentiated vascular tissue connecting with that of the axis of the bud.

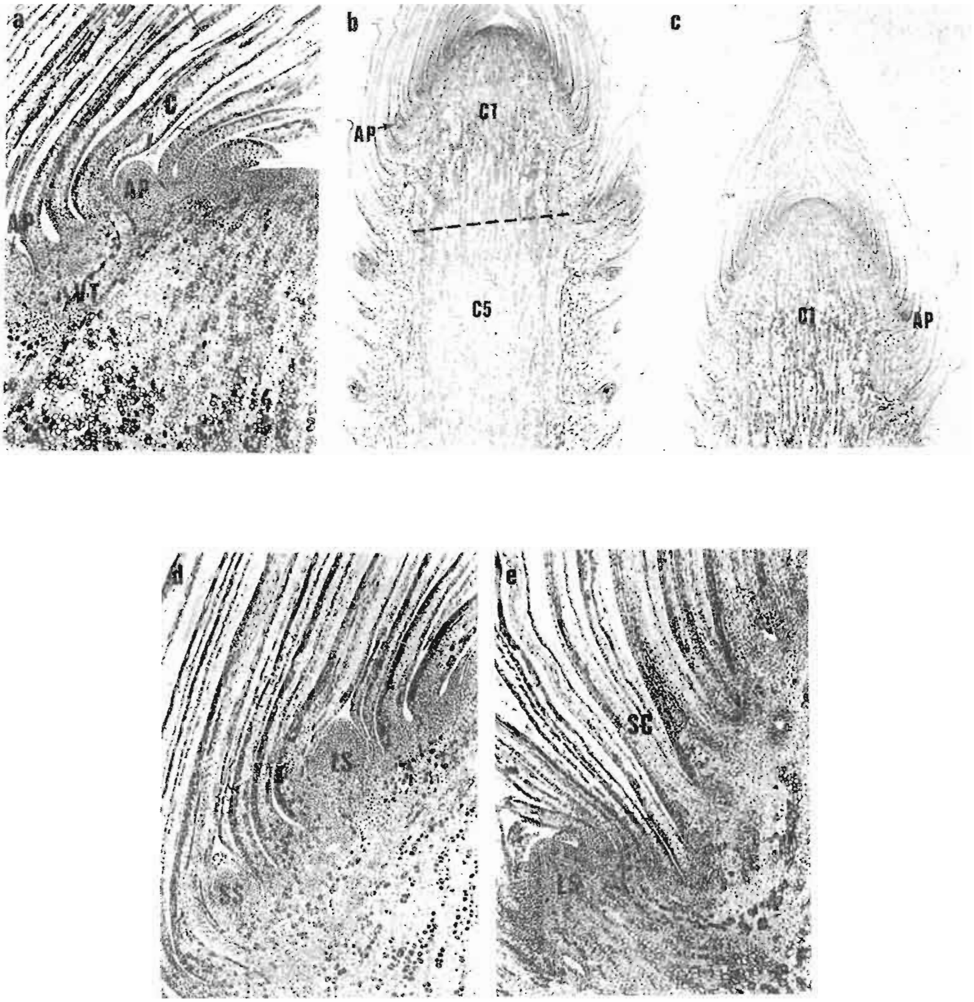


FIG. 4—Early development of axillary primordia.

a. (32×). Part of the terminal bud near the apex showing cataphylls (C) and newly initiated axillary primordia (AP). The cataphyll subtending the last formed axillary primordium has differentiated vascular tissue (VT).

b. (6×). The terminal bud on 7 November 1973. Part of cycle 5 (C5) of the previous season's initiation is still protected by cataphylls while cycle 1 has initiated a number of cataphylls and axillary primordia (AP).

c. (6×). The terminal bud on 15 November 1973. The bud now contains only cycle 1 and more axillary primordia are being initiated (AP).

d. (32×). Newly initiated long-shoot primordia (LS) are larger than short-shoot primordia (SS), initiated earlier.

e. (32×). A number of sterile cataphylls (SC) always occur above developing long shoots (LS).

The earliest harvest at which first-cycle axillary primordia were found was comparable at the two sites. At Rotorua there were 19 primordia present on 17 October 1973, and 64 primordia on 10 October 1974; at Waimihia there were 15 primordia on 22 October 1974.

Soon after initiation axillary primordia start to form their own cataphylls, here referred to as axillary bud cataphylls to distinguish them from the main bud cataphylls. As viewed in median section no further differentiation into needle fascicle, pollen cone, seed cone, or branch is evident until five axillary bud cataphylls can be seen on one of the sides of the bud.

Axillary primordia may be short-shoot or long-shoot primordia, the former occurring within a cycle, and the latter at the end of a cycle. Short-shoot primordia, although normally developing into needle fascicles, may be modified to form pollen cones; long-shoot primordia may develop into branches or be modified to form seed cones.

The development of those axillary primordia which will form long shoots can be detected at an early stage. Even at the time they form their first cataphylls, long-shoot primordia are larger than the adjacent short-shoot primordia (Fig. 4c). The position of the long shoots is also detectable by the presence above them of sterile cataphylls (Fig. 4e). These belong to the next cycle.

In Rotorua Clone 7 initiated four to five cycles a year, containing in total some 850 axillary structures. At Waimihia only three to four cycles were produced, totalling about 670 axillary structures. Comparative numbers of axillary structures per cycle from the two sites are presented in Table 2.

The reduction in the number of cycles at Waimihia was in part compensated for by the increased number of axillary structures in the first cycle.

The Initiation of Needles

The axillary bud cataphylls which develop on short-shoot primordia serve to protect the needles which are to be initiated (Fig. 5a, b). Once five of these cataphylls can be identified on one side of the primordium in median section, the meristem of the primordium prepares for needle initiation by increasing cell numbers in the flank meristem, thus widening the base of the dome. Near the apex the rib meristem appears to be very narrow as the dome divides to form separate needle meristems (Fig. 5c). At an early stage the initiated needle (in section) has the general shape of a cataphyll (Fig. 5d) but is larger, probably because most, if not all, of the flank meristem has been incorporated in its base. By the time the developing needle is about 0.5 mm long vascular tissue begins to extend into it (Fig. 5e). The needles progressively increase in length until they emerge from the protective scales. The apex is still present in its reduced form (Fig. 5f).

The short-shoot primordia needed considerable time to develop and to form needles. The first primordia of cycle 1 which were initiated in October did not begin needle development until 17 March, some 5 months later (Table 3).

Needle development, however, may occur more rapidly than this. A period of 3 months from primordial initiation to needle emergence was recorded for another clone in an earlier year (Bollmann, 1974). It is possible that the dry weather in October 1973 and January-February 1974 (New Zealand Meteorological Service, 1973; 1974) may have affected the rate of needle formation and development in this clone.

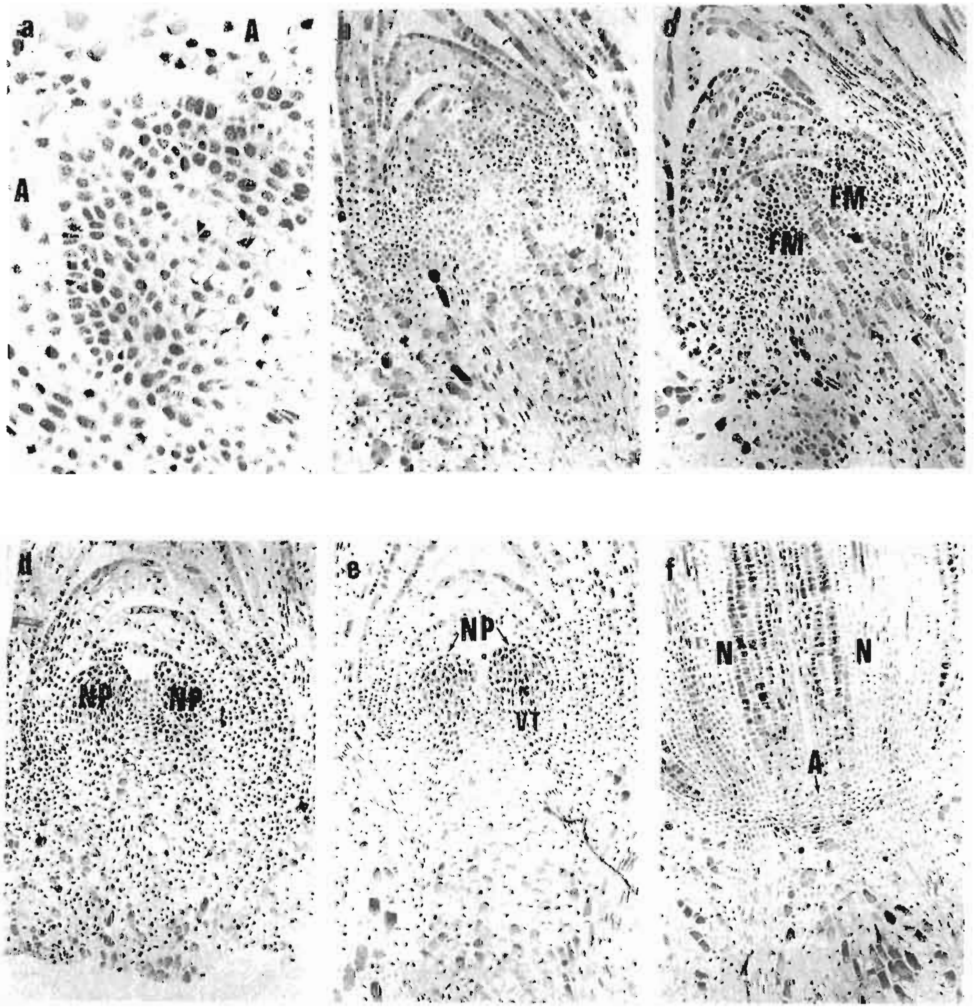


FIG. 5—Initiation of needles.

a. (252×). Short shoot at an early stage of development showing newly initiated bud cataphylls (A).

b. (80×). Short shoot before needle initiation.

c. (80×). Short shoot showing increased numbers of cells in the flank meristem (FM), a first indication that needles are about to be initiated.

d. (80×). Short shoot with newly initiated needle primordia (NP). The cells of the flank meristem of the short shoot form the base of the needle primordia.

e. (80×). The needles develop and their vascular tissue (VT) begins to be differentiated.

f. (80×). Needle fascicle with needles (N) emerging from the short shoot bud. Note the remains of the apex (A) of the original short shoot.

TABLE 3—Needle development

Cycle no.	Approx. date of initiation of: (i) Short shoots	(ii) Needles	Time lapse in days (i) to (ii)	Approx. date needle emergence	Time lapse between needle initiation and needle emergence
1	17 Oct	17 Mar	151	22 May	66
2	26 Dec	11 Apr	106	5 Jun	55
3	6 Feb	5 Jun	88	7 Aug	63
4	11 Apr	18 Jul	98	9 Sep	53
5	End Jun	16 Sep	83	31 Oct	45

Seed Cone Determination

Seed cones are regarded as modified branches (Doak, 1935) (Fig. 1b), and they cannot be distinguished anatomically from branch primordia at early stages of development (Eggler, 1961; Hong and Lee, 1970; Lanner, 1970; Owston, 1969). Long-shoot primordia in general, however, are readily distinguishable from short-shoot primordia on the basis of their initial growth rate. Knowledge of the approximate time of seed cone initiation simply requires observation of the time when the first long shoots are initiated (often most easily detectable by the presence of the sterile cataphylls at the start of the next cycle above).

It needs stressing, however, that the initiation of primordia which may develop into seed cones is only a first step. The critical subsequent steps which determine whether development, if if proceeds, does so towards seed cone or branch have been called determination (Romberger, 1967).

The initiation of long-shoot primordia (and therefore possible seed cone primordia) in the first, second, and third cycles occurred respectively in mid December, at the end of January, and during March. As in all axillary primordia, the early development of long-shoot primordia consists of the initiation of a number of axillary cataphylls which will protect the cone or branch bud when it emerges from the terminal bud. The earliest time at which positive identification of a seed cone (as distinct from a branch) could be made was at a stage just after the fifth axillary bud cataphyll on one side (as seen in median section) had been formed (Fig. 6a). The initiation of two large even-sized swellings on the flank meristem could be seen at that time (Fig. 6b). These primordia differ from those in a vegetative development sequence in that the normal acropetal size development is absent. It is uncertain whether these even-sized swellings represent the first bract scales of the developing cone or the last cataphylls which will protect it, but the lack of an acropetal sequence on the flank of a developing long-shoot primordium is an indication that development is sexual rather than vegetative.

At the time when the bud shown in Fig. 6a was harvested, long-shoot primordia of various sizes were present in the cluster terminating the cycle. The seed cone was one of the smaller of these: the base of its apical dome measured 462 μm as compared

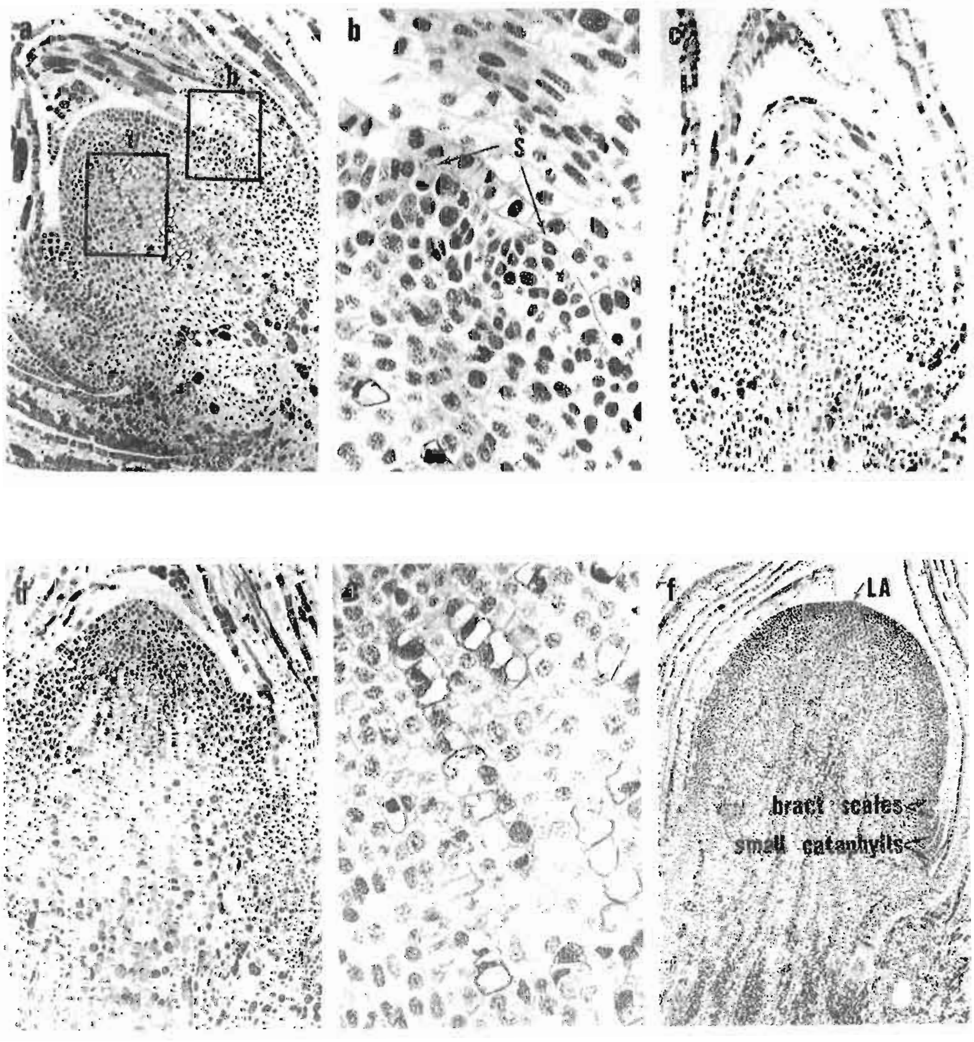


FIG. 6—Early development of seed cones.

a. (80×). Long shoot at the time of seed cone determination.

b. (320×). Close up, 6a. Two swellings (S) on the flank meristem lack the acropetal size development shown by axillary bud cataphylls indicating that further development may be sexual rather than vegetative.

c. (80×). A short shoot located below the seed cone in 6a.

d. (80×). A long shoot located above the seed cone in 6a. Acropetal size development on the flanks of the meristem indicates that it is a branch bud.

e. (320×). Rib meristem of the seed cone in 6a showing periclinal cell division increasing the diameter of the cone.

f. (32×). Developing seed cone of the second cycle on 8 May, 100 days after initiation and 60 days after determination. The remains of the original long-shoot apex (LA) are still recognisable.

with 585 μm for the next larger primordium (branch) and 218 μm for the next smaller one (Fig. 6c). This smaller primordium in turn was considerably larger than the short-shoot primordium located closest to the long shoots. Compared with a branch primordium at the same stage of development (Fig. 6d) the seed cone primordium showed more frequent divisions in the rib meristem and a wider peripheral zone, in preparation for bract scale development (Fig. 6f).

At the start of bract scale development, the apex of the developing cone may still be recognised (Fig. 6f). Soon after this, however, the apical meristem loses its function.

Examination of median microscopic sections of developing seed cones which have already attained their typical shape show that the last two scales at the base of the cone are quite small (Fig. 6f). They may have developed from the even-sized swellings discussed earlier in this section. Again, they are characteristic of cone as distinct from branch development.

The time interval between initiation of a long-shoot primordium and the first recognition of the swellings on its flank meristem (Fig. 6b) indicating that seed cone determination had taken place, was almost exactly 6 weeks for all three cone-bearing clusters of Clone 7 (Table 4).

Table 4 also indicates that a length : width ratio of about 1.0 may be necessary for the apex of the developing cone before its surface area is sufficiently increased to accommodate bract scales. At that stage the mean length : width ratio of the apical dome of developing branches in the same cluster was 0.58. Lill (1976) has described in detail the further development of the seed cone of *P. radiata* from the Rotorua area. Subsequent development during winter will therefore not be discussed here.

Pollen cones are initiated in spring when the first short shoots are being formed. They are not initiated by the terminal bud of the leading shoot but are found on first or second order branches, usually in the lower part of the crown. Thus, they will be discussed in Part 2 of this paper which reports on branch bud development.

Shoot Elongation

Figures 2b and 7 show the timing of shoot extension. The first cycle started to elongate during the first week of January. The second cycle showed growth of a few centimetres on 13 February and by 20 March it had elongated only a little further. At that stage the components of cycle 2 were still tightly protected by cataphylls, and the rate of primordial initiation was also limited (Fig. 2a). Only after 8 May did cycle 2 again begin to elongate appreciably. Three weeks later the shoot of cycle 3 had extended to about one-third of its final length before a reduction in temperature (Fig. 2) apparently slowed further extension. By then 48% of the season's growth had taken place.

Extension growth resumed on 16 September with further elongation of the third cycle. At the same time cycle 4 began to elongate. It was 29 cm long when the series of collections of the shoot of Clone 7 had to stop. However, in order to determine the approximate time when extension of the last cycle ceased, the two last cycles initiated in the previous season had also been harvested when the first collections were made. From these it was shown that cycles 4 and 5 ceased elongation at the end of October and in mid-December, respectively (Table 5).

TABLE 4—Early seed cone identification

Cyle	DATES Initiation of long shoots	Harvest of buds	Time lapse (days)	DEVELOPMENT Numbers* of normal axill. bud cataphylls	Numbers* of distinct bract scales present	SIZE OF DOME Length (μm)	Width (μm)	L : W ratio
1	20 Dec	31 Jan†	42	5	0	639	911	0.70
		21 Feb	63	5	2	1020	1102	0.93
2	25 Jan	6 Mar†	40	6	0	367	639	0.57
		20 Mar	54	6	0	258	435	0.59
		6 Apr	71	6	0	422	635	0.65
		11 Apr	76	6	4	1342	1279	1.05
3	27 Feb	11 Apr†	43	5	0	367	503	0.73
		8 May	70	6	0	588	734	0.75
		5 Jun	98	5	2	1092	905	1.21

* As counted in a median section — see, e.g., Fig. 6f.

† Date at which non-acropetal development on flanks (Fig. 6b) was first detected.

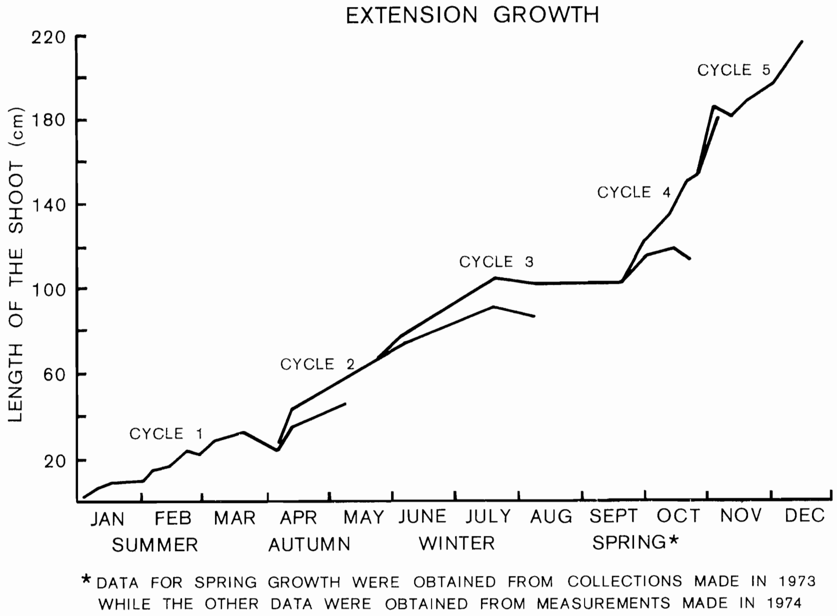


FIG. 7—Extension growth.

Rates of elongation as well as mean cycle length are given in Table 5.

In an earlier section it was indicated that in the first two or three cycles (a) 4-cycle ramets initiated more primordia than 5-cycle ramets, and (b) more primordia were initiated at Waimihia than at Rotorua. Shoot extension data indicate that an increased number of primordia in a cycle led to increased extension growth.

TABLE 5—Shoot elongation

Cycle	DATES Start	Finish	Days	Mean length (cm)	Standard deviation	(n)*	Elongation per day (cm)
1	26 Dec	8 May	133	47	± 2	9	0.35
2	20 Mar	18 Jul	120	38	± 4	6	0.32
3	22 May	23 Oct	154	40		1	0.30
4	16 Sep	31 Oct	45	46		3	1.02
5	24 Oct	12 Dec	39	27		3	0.69

* The number of trees contributing to the values for each cycle mean.

DISCUSSION

In considering the information presented in this paper it is necessary to be aware that there is considerable clonal variation in shoot growth patterns of *P. radiata*. Clone 7 selected for this study represents one extreme of this variation being a clone which, on favourable sites, produces many cycles in the annual shoot. While the typical *P. radiata* is thoroughly polycyclic, clones do exist which, at least on some sites and in some years, may produce only one cycle in the annual shoot.

One of the major reasons for growing *P. radiata* so widely in temperate and warm-temperate regions of the world is its high growth rate. The data in this paper suggest that in large part this attribute results from the capacity of the species to make full use of a long growing season. This attribute presumably is characteristic of a polycyclic species generally, but Lanner's data from Hawaii (Lanner, 1966) suggest that *P. radiata* may have some exceptional capability in this respect. Otherwise, the growth of *P. radiata* does not differ in major detail from that of some of the other polycyclic pine species described (Tepper, 1963; Lanner, 1976). It has, however, one of the more complex patterns of pine shoot growth so far reported and as such its detailed description may be valuable to those studying the growth of other species in temperate or tropical areas.

In the comparison reported here between Rotorua and Waimihia, Clone 7 initiated two extra cycles of growth under the more favourable conditions at Rotorua, resulting in some 20% more primordia and a 40% increase in shoot length. Or, looked at in the reverse way, it ceased growth sufficiently early in the autumn at Waimihia to avoid winter frost damage. Such opportunism is rare in conifers generally, and there is often a strong tendency for the length of the growing season of any provenance of a species to be tightly (and conservatively) tied to that of its seed source. Such species, when used as exotics, frequently either fail to cease growth before damaging winter frosts or, alternatively, are unable to take advantage of a growing season milder than that of their seed source.

Little is known of the physiology of primordial initiation in conifers, but the subject is clearly an important one. In *P. radiata* this study has indicated that the variation in growth on different sites may in large part be a reflection of the numbers of primordia initiated; further studies have been designed to examine the role of specific climatic variables in influencing primordial initiation. The very restricted growth in New Zealand of pines from interior United States, however, suggests that primordial initiation in turn is strongly controlled by endogenous factors, and it is important that a knowledge of these be obtained also.

One reason for carrying out the study reported here was to obtain information on the timing of initiation and determination of seed cones. Ebell (1972) has demonstrated the importance of applying treatments designed to increase yields of cones in seed orchards prior to, or at the time of seed cone determination. The data presented here indicate, for a limited clone sample and a limited geographic area, the approximate times of seed cone determination for each growth cycle. (These data, which show little variability, will be extended in the second part of this paper). Of course, cone yields vary between clones and between sites. The more cycles of growth a tree initiates during a growing season, the more opportunity there is for seed cone determination to occur. This was demonstrated by the shoots of Clone 7 collected from the Waimihia seed orchard which had only one to two cone clusters on the leading shoot as compared with three clusters on the shoots growing in Rotorua. The location of seed orchards on sites favourable for cycle formation is therefore important for seed cone production.

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