# MORPHOLOGY OF LONG-SHOOT DEVELOPMENT IN PINUS RADIATA

M. P. BOLLMAN

Forest Research Institute, New Zealand Forest Service,
Private Bag, Rotorua, New Zealand

(Received for publication 21 December 1981; revision 9 September 1983)

ABSTRACT

Long-shoot initiation in buds of **Pinus radiata** D. Don is first indicated when the growth rate of axillary primordia nearest the apex appears to exceed that of those located lower in the bud. A basipetally increasing number of primordia is affected by this accelerated growth. Primordia which will become branches form their own axillary primordia. Those which are to develop into seed cones increase the size of the apical dome as a result of a temporary halt of primordium scale initiation and, possibly, of continuing meristematic activity in the pith tissue immediately below the rib meristem. Long-shoot primordia which will remain vegetative grow at a faster rate than those which differentiate into seed cones. In any one bud, therefore, branch primordia are much larger and heavier than seed-cone primordia.

Researchers wishing to influence differentiation of long-shoot primordia in the bud will need to be selective in the choice of bud material and in the timing of possible treatments. Examination of the annual growth patterns of the shoot below the bud should enable them to do so more accurately.

## INTRODUCTION

Seed orchards today are faced with problems of insufficient initiation of reproductive structures reducing total seed production and especially its distribution among the clones (Sweet & Krugman 1977). Although seed-cone production has been increased in practice (Sweet & Krugman 1977) as well as experimentally (Sweet 1979), there is a particular requirement to increase seed production of the less productive clones (Sweet 1979). If this is ever to be achieved, a better understanding of the physiology and morphology of long-shoot differentiation is essential.

The broad picture of the growth pattern in *Pinus radiata* and the timing of long-shoot initiation, of leader and branch shoot, is already known (Bollmann & Sweet 1976, 1979). Long-shoot initiation in a bud is first indicated when the rate of growth of a number of axillary primordia closest to the apex appears to exceed that of primordia positioned lower in the bud, i.e., which were formed earlier. In some buds long-shoot primordia may be formed about mid December but there is much variability in the timing of their initiation, and long shoots may be formed any time during the second part of the growing season. The number of long-shoot primordia in a bud may vary from 10 to 15 per cluster, and several clusters may be formed in any one growing season.

Differentiation is considered to occur when morphological changes in long-shoot primordia lead to specialisation, i.e., to the formation of branches and seed cones. The time needed for long-shoot primordia to develop sufficiently for seed-cone primordia to be distinguished from vegetative primordia is 6 to 8 weeks. The earliest date that seed-cone primordia have been microscopically identified in buds (growing in a part of New Zealand with a comparatively mild climate) was mid January.

The objectives of this paper are (1) to provide more details on sequences of differentiation and its relationship to initiation and subsequent growth of long-shoot primordia, and (2) to establish some criteria which will enable researchers, who wish to influence differentiation of long-shoot primordia in buds, to be more selective in the choice of bud material to be used and in the timing of possible treatments. The paper describes the morphology of flowering* shoots of *P. radiata* and then examines long-shoot primordia in their buds as they develop and differentiate during the first growing season.

## MATERIALS AND TECHNIQUES

Shoots were obtained from "hedged" clonal material which was originally propagated from 8-year-old trees. The trees had been topped 2 years before the start of the investigation. For the purpose of this paper branches which developed as a result of "hedging" (topping) are termed shoots; vegetative laterals on these shoots are called "branches" or "branch primordia" when still in bud. The material used to examine the morphology of the flowering shoots during the 1978–79 growing season was from the Longmile area near Rotorua, that for the examination of long-shoot primordium differentiation in the bud was mainly from Cpt 1374 of Kaingaroa State Forest.

In spring 1978, eighty cone-bearing shoots were selected in the Longmile area, half of them with one cluster of cones (Type 1), the other half with two clusters of cones (Type 2). Within each type the shoots were carefully matched for the length of their growth cycles. Another 20 shoots (10 of each type) were selected similarly in spring 1979.

For 10 of each shoot type, the part representing the 1978–79 growing season was assessed in September, November, and December 1978 and in March 1979. The parts of the shoots below the first branch cluster and between Clusters 1 and 2 were measured and the numbers of stem units estimated. In addition, the sequences of initiation of cones and branches in Clusters 1 and 2 were determined for 20 shoots (10 of each type) in September and November 1978. This assesment was repeated in 1979 using 10 shoots (five of each type).

Estimates of stem unit numbers and determinations of sequences of initiation and differentiation of branches and seed cones were based on the 5/8 phyllotaxis of *P. radiata* (Bannister 1962). They were determined respectively by counting and numbering the points where the parastichies of the shoots intersect.

In December 1978 and in March 1979 the buds of 20 shoots were sampled (10 of each type in each month) to obtain numbers of long-shoot primordia and their dry weights.

---

* Throughout this paper the term "flower" is used as defined by Jackson & Sweet (1971) – "a determinate sporogenous shoot".

From shoots at Kaingaroa, terminal buds were harvested fortnightly between 9 January and 5 March. At each date six buds were selected as being potentially reproductive (i.e., probably containing reproductive primordia). Two of these were selected to represent advanced development, two as intermediate in this respect, and two were representative of less-developed buds. A final four buds were selected as likely to remain vegetative, two for histological examination and two for dry weights of their long-shoot primordia.

Long-shoot primordia from each bud were dissected under the stereo microscope after the buds had been put in FAA fixative under vacuum for 15 minutes and then kept in fresh fixative for at least 72 hours. Of the buds harvested from the Longmile (December and March) all long-shoot primordia were dissected out for dry weight determination. It was intended to use long-shoot primordia from the December harvest as well, but these were too small to handle. From the Kaingaroa buds two large and two small long-shoot primordia, as well as the apex of the main bud, were dissected.

Primordia to be weighed were classified and then soaked in 50% alcohol for 1 hour and oven dried at 70°C for 72 hours. Those to be sectioned were dehydrated in a TBA series, infiltrated with polyester wax, and sectioned on a rotary microtome at 6–8 $\mu$m. For easy identification of meristematic tissues the sections were stained for DNA (Fuelgen) and for DNA/RNA (Azure-B) according to Riding (1971). Subsequently the primordia were microscopically classified and assessed.

Dome diameters were measured from the base of the smallest primordium scale on the left of the dome to a similar position on the right, and dome heights were obtained by measuring from the dome apex perpendicular to the imaginary line connecting these two points (Fig. 1). Cell counts were made using three longitudinal sections from each primordium, one median and the two adjacent. The counts were made, using a microscope eyepiece grid, in the region of the pith tissue just below the rib meristem. The cells counted were those with large round nuclei, those with small but densely stained nuclei (which are often of a squashed appearance and are not centrally placed within the cells), and those of "structural" cells. These latter are large cells, often filled with densely staining tannins and other substances, which may have a strengthening role in the tissue (Fig. 2).

## RESULTS

### Morphology of the Flowering Shoot

In *P. radiata* flowering shoots may form from one to eight female strobili per cluster annually (Bannister 1962; Bollmann & Sweet 1976). In our seed orchards branches with one or two clusters of seed cones are predominant. The part of the annual shoot below the first cluster and that between Clusters 1 and 2 may vary in length and in number of shoot components they contain. Generally, in shoots which produce one cluster of cones per year, the first annual growth cycle is longer and contains more shoot components than Cycle 1 of shoots which have two clusters of seed cones. Flowering shoots of the latter type often have a slightly shorter first cycle than second cycle, with about the same number of components (Table 1).

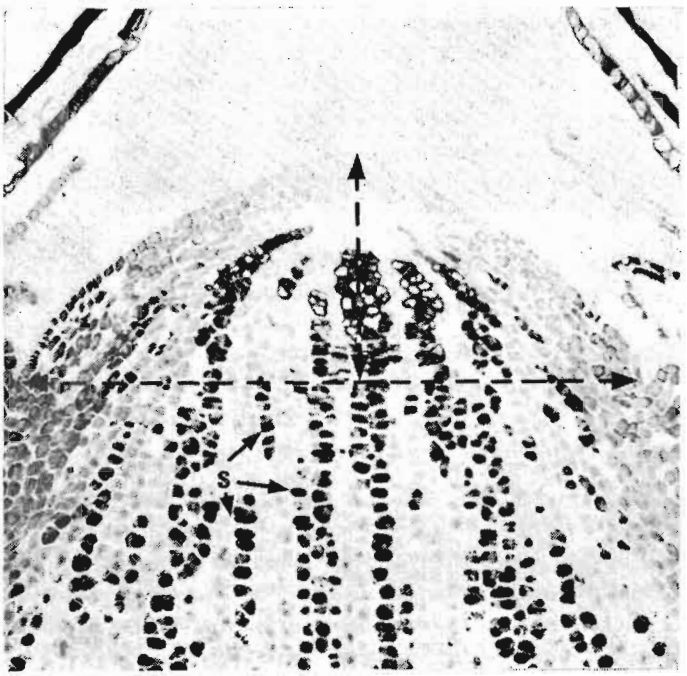


FIG. 1—The dome of a branch primordium (×80) showing where some measurements were made.

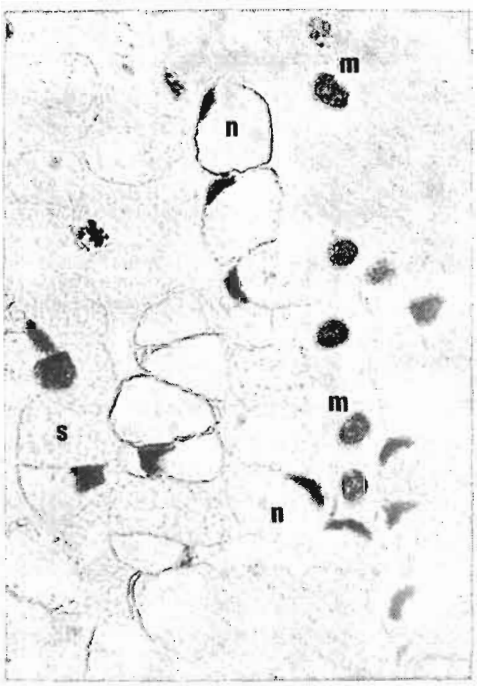


FIG. 2—Cell types in young pith tissue (×320): m = meristematic cells are small and have large, round nuclei; n = larger more mature cells with "squashed" nuclei, not centrally placed; s = structural cells, large and filled with tannins and other substances (**see also** Fig. 1).

TABLE 1—Mean lengths and mean numbers of shoot components below and between clusters of long shoots in two types of flowering shoots

| Shoot type | Shoot length | | | | Number of components | | | |
|---|---|---|---|---|---|---|---|---|
| | Cycle | Mean length (cm) | ± SE | No. of shoots examined | Cycle | Mean number | ± SE | No. of shoots examined |
| Type 1 – one cluster of cones | 1 | 76.6 | ± 3.3 | 31 | 1 | 320.9 | ± 12.5 | 34 |
| | 2 | 37.1 | ± 2.6 | 34 | 2 | 169.2 | ± 4.1 | 34 |
| | 1+2 | 113.7 | | | 1+2 | 490.1 | | |
| Type 2 – two clusters of cones | 1 | 41.2 | ± 3.0 | 40 | 1 | 203.6 | ± 9.6 | 39 |
| | 2 | 49.3 | ± 2.9 | 40 | 2 | 200.3 | ± 7.2 | 39 |
| | 1+2 | 90.5 | | | 1+2 | 403.9 | | |

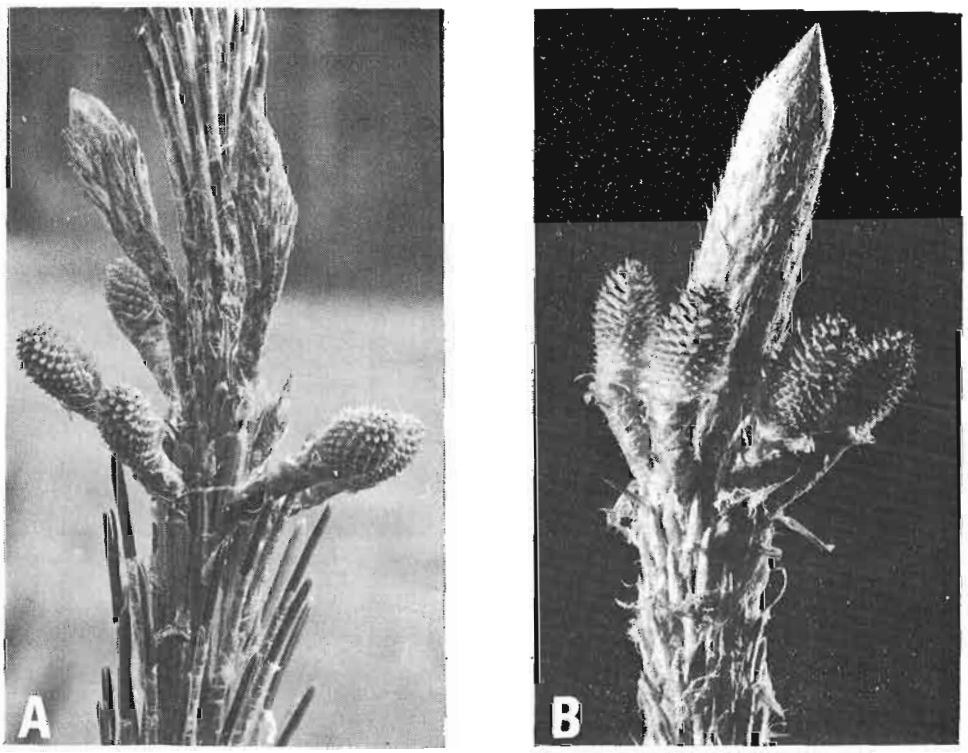


FIG. 3—A: Seed cones are located below the branches. B: Sometimes no branches are formed, only seed cones are present.

As a rule, seed cones grow with branches in clusters (Fig. 3A), although there are instances when seed cone clusters can be seen to grow alone (Fig. 3B).

Within clusters, seed cones are located below branches, which means that they were initiated (in the form of undifferentiated axillary primordia) first. This was verified, using a method described in the previous section, with shoots harvested in spring 1978 and 1979. The result of the assessment is graphically illustrated in Fig. 4. The long-shoot region of the flowering shoot can be divided into two zones, one containing predominantly reproductive (female) structures, the other vegetative ones. However, there is not always a clear boundary between the long-shoot region and the adjacent short shoots nor between the seed cone and branch zones within the long-shoot region. Dormant, undifferentiated, long-shoot buds are often found on the borderline. Occasionally, one or two needle fascicle buds may also be present among the long shoots.

In spring (of the second season since long shoots were formed in the bud) a cluster of long shoots includes about 30% seed cones (Fig. 4). In shoots with two clusters of cones, proportionally more seed cones may be present in the second cluster

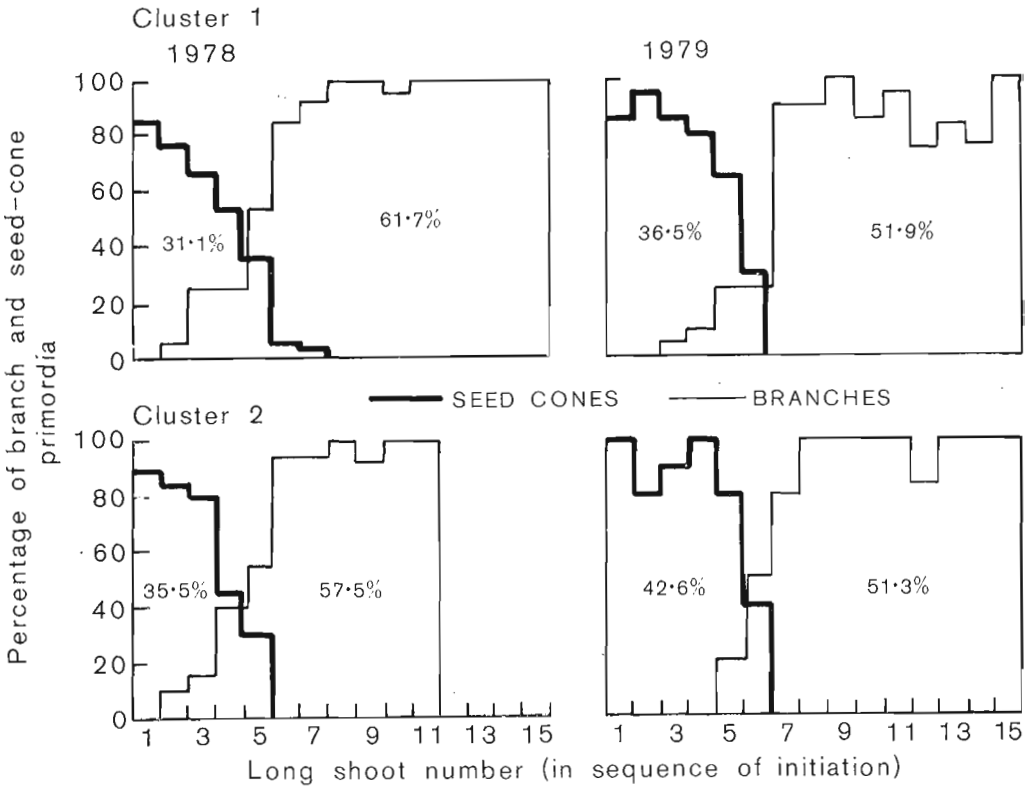


FIG. 4—Long-shoot primordium differentiation in relation to the order in which they were initiated during the preceding season. Because some long-shoot primordia remain undifferentiated, figures do not add to 100%.

than in the first (Table 2) because fewer branches were formed initially or fewer primordia remained undifferentiated when the shoot was formed in the bud.

Table 2, however, shows that in real terms (numbers per cluster) in spring numbers of strobili may be comparable in both clusters of such shoots, as well as in Cluster 1 of both types of shoot.

TABLE 2—Mean numbers of long shoots per cluster in "one cluster" and "two cluster" flowering shoots

| Time of assessment | Shoots | Shoot type* | | |
|---|---|---|---|---|
| | | 1 | 2 | |
| | | Cluster 1 | Cluster 1 | Cluster 2 |
| September and November 1978 | Branches | 6.2 ± 0.20 | 6.2 ± 0.41 | 5.4 ± 0.30 |
| | Cones | 3.4 ±0.37 | 3.0 ± 0.27 | 3.1 ± 0.27 |
| | Total long shoots | 10.3 ± 0.63 | 10.5 ± 0.41 | 9.4 ± 0.24 |
| March 1979 | Branches | 6.2 ± 0.53 | 5.1 ± 0.69 | 6.7 ± 0.60 |
| | Cones | 2.1 ± 0.58 | 3.1 ± 0.55 | 1.9 + 0.50 |
| | Total† | 8.3 ± 0.56 | 8.2 ± 0.62 | 7.9 ± 0.55 |
| September and November 1979 | Branches | 5.7 ± 0.33 | 6.5 ± 0.54 | 5.9 ± 0.41 |
| | Cones | 4.5 ± 0.40 | 4.3 ± 0.54 | 4.9 ± 0.23 |
| | Total long shoots | 11.5 ± 0.35 | 12.6 ± 0.58 | 11.4 ± 0.58 |

* Type 1 = one cluster of cones
Type 2 = two clusters of cones
† Does not include long shoots which remained undeveloped.

Within flowering clusters, branches vary considerably in length (Fig. 5). Those growing on the boundary between the reproductive and vegetative zones usually remain small. In the vegetative zone of the long-shoot region the branches formed last (as axillary primordia in the bud) tend subsequently to elongate more than those initiated earlier. When shoots with one and with two clusters of clones at a given time were compared (Fig. 5), mean branch length in the first cluster of the former type was in between that of Clusters 1 and 2 of the latter.

## Morphology of Long-shoot Differentiation in the Bud

Branch and seed-cone primordia in the buds are identified by their position within the long-shoot region, their size and shape, and their morphology.

Seed-cone primordia are wedged between the bases of the much larger branch primordia (Fig. 6). In cross-section seed-cone primordia are consequently of a triangular shape, whereas branch primordia are more oval. Branch primordium buds are morpho-

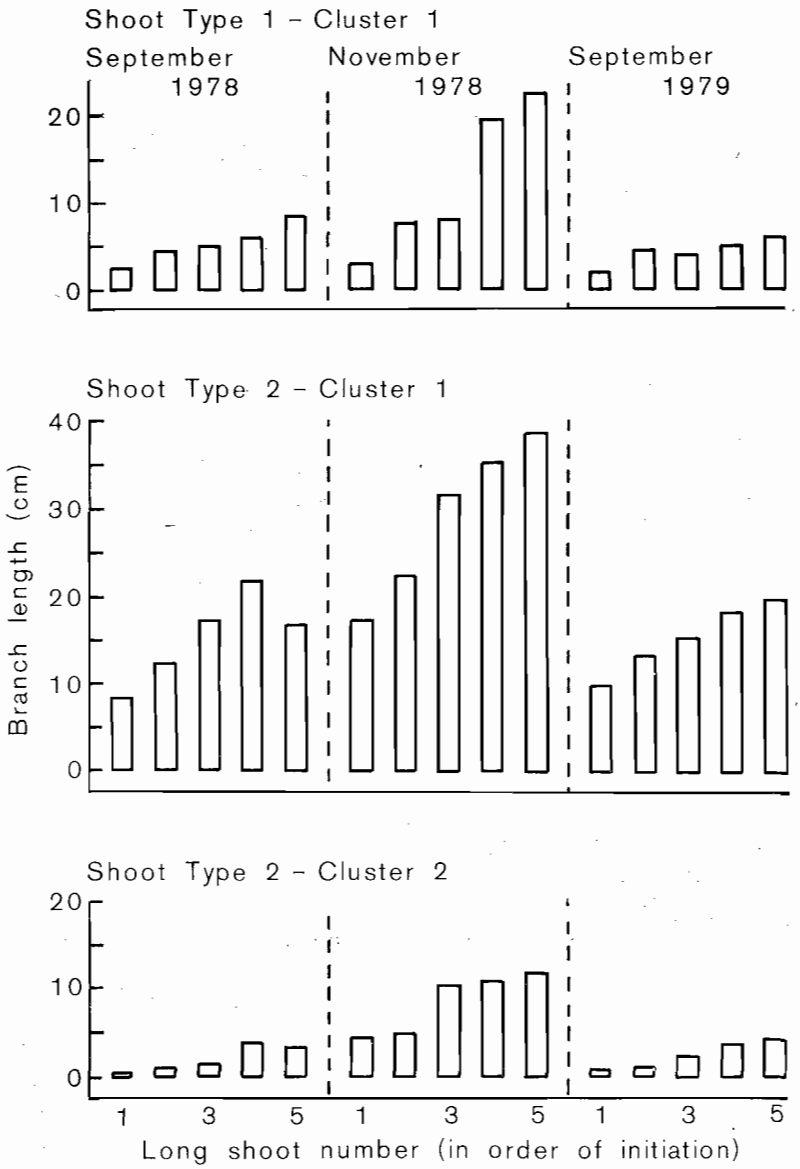


FIG. 5—Mean branch length in September 1978 and 1979 and November 1978 in relation to the order in which branches were initiated during the preceding season.

logically similar to the bud in which they develop; they also form axillary primordia. Seed-cone primordia in *P. radiata,* as in other pines (Mergen & Koerting 1957; Hong & Lee 1970; Owens & Molder 1975, 1977), have a greatly enlarged apical dome resulting in a bulbous shape at the base of which, at a later stage, a number of modified scales or bract scales are formed (Fig. 7F).

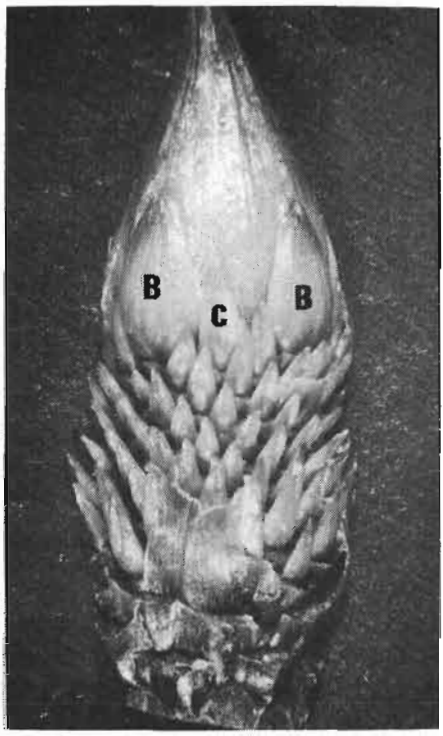


FIG. 6—A bud, harvested on 7 March and from which some of the scales were removed, showing positions and differences in size of branch (B) and seed-cone (C) primordia.

From the time that long-shoot primordia (as axillary primordia) are initiated, until differentiation begins, the young lateral apices initiate a number of cataphylls – five to six as seen in medium longitudinal section (Bollmann & Sweet 1976). In more advanced seed-cone primordia, the initially formed five to six scales can be observed at the base of the developing cone (Fig. 7F). In advanced branch primordia they form part of the sterile cataphylls located below those cataphylls which subtend axillary primordia. As these initial primordium scales are formed the dome gradually enlarges both in diameter and in height (Table 3).

Close to, and during differentiation, the domes of all primordia enlarged in diameter. The apical dome of primordia which develop into seed cones increased 1.8 times in width and 1.6 times in height. By March, when seed-cone primordia could be recognised clearly under the stereo microscope (i.e., when the domes had attained their typical shape (Fig. 7F)), dome widths had tripled and dome heights doubled since differentiation began (Table 3).

On 7 February branch primordium apical domes were 1.4 times as wide as the domes of undifferentiated primordia and by March had increased further. Dome heights did not increase and remained comparable with those of undifferentiated primordia (Table 3). Dome heights may decrease when the branch primordia develop further and the formation of axillary primordia is resumed.

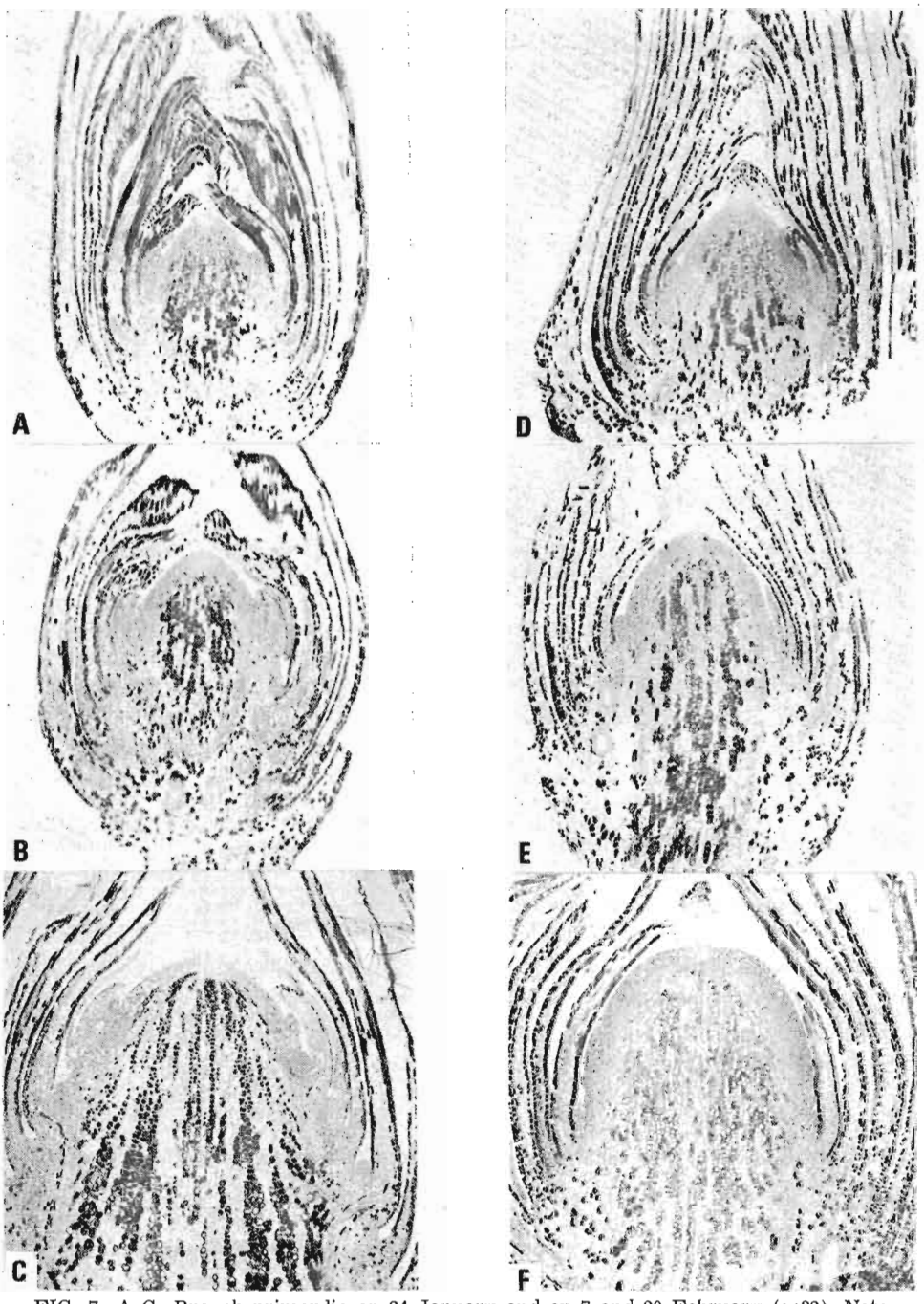


FIG. 7—A–C: Branch primordia on 24 January and on 7 and 20 February (×32). Note increased numbers of primordium scales.

D–F: Seed-cone primordia on 7, 20, and 27 February (×32). Note that the number of primordium scales at the base of the primordia is constant at about five or six.

TABLE 3—Dome size ($\mu$m) of long-shoot apices prior to and during differentiation

| Variable | Date | Undifferentiated* | Potential† seed cones | Branches | Seed cones |
|---|---|---|---|---|---|
| Diameter‡ | Jan 9 | 299 ± 19 | | | |
| | 24 | 305 ± 21 | 522 ± 24 | | |
| | Feb 7 | 379 ± 20 | 533 ± 30 | 536 ± 28 | |
| | 20 | | 505 ± 25 | 682 ± 27 | 920 ± 31 |
| | 27 | | 644 ± 30 | 684 ± 19 | 939 ± 120 |
| | Mar 5 | | | 605 ± 37 | 1056 ± 177 |
| Height‡ | Jan 9 | 156 ± 8 | | | |
| | 24 | 149 ± 12 | 242 ±18 | | |
| | Feb 7 | 222 ± 13 | 292 ± 32 | 201 ± 12 | |
| | 20 | | 304 ± 84 | 249 ± 15 | 627 ± 249 |
| | 27 | | 311 ± 24 | 222 ± 11 | 659 ± 101 |
| | Mar 5 | | | 240 ± 9 | 755 ± 161 |

* Primordia with one to five scales attached, as seen in median longitudinal section.
† Primordia which are on the verge of differentiating (see Fig. 6D–F).
‡ See Fig. 1A.

Cell counts in young pith tissue (just below the rib meristem) showed that seed-cone primordium tissue had proportionally more meristematic cells than similar tissue of undifferentiated and branch primordia. In terms of mean numbers per count, more meristematic cells were counted in seed-cone primordia than in branch primordia, but mean numbers of meristematic cells were comparable with those in undifferentiated primordia (Table 4). The mean numbers of total cells per count were: undifferentiated 98.8 ± 1.8, seed cone 75.4 ± 2.5, and branch primordia 84.1 ± 2.0.

Dry weights of branch primordia increased as they rapidly developed and elongated (Fig. 8). The seed-cone primordia initially increased fourfold in dry weight in 2 weeks after 21 February but then they remained at about the same weight, possibly for the remainder of the growing season. In March seed-cone primordia were much lighter than branch primordia (Table 5). Mean dry weight of seed-cone primordia (first cluster), dissected from buds of shoots which produced two clusters of cones during the previous year, was 6.11 ± 1.13 mg; those from "one cluster shoots" weighed 5.34 ± 0.47 mg. Long shoots from buds of predominantly vegetative material weighed only 3.21 ± 0.84 mg. However, differences between the two flowering shoot types are possibly not significant because of the high variability in primordium weight in buds of the former type.

When long-shoot primordia dissected from buds collected during the second half of the growing season had been identified, examined, and classified, the time that differentiation might be expected to occur could be determined reasonably well. Counts from dissections suggested that on 9 January the primordia were still undifferentiated but that some of the more advanced ones could have been close to differentiation. By 24 January a small proportion of primordia were already identified as being possibly

TABLE 4—Mean numbers and proportion of meristematic cells in the young pith tissue* of long-shoot primordium apices

| Date | Undifferentiated | | Seed cones | Branches |
|---|---|---|---|---|
| | Less advanced | Advanced† | | |
| Jan 9 | 36 | 23 | | |
| 24 | 45 | 43 | | |
| Feb 7 | 37 | 40 | | 42 |
| 20 | 37 | 36 | 45 | 37 |
| 27 | | 39 | 51 | 31 |
| Mar 5 | | 39 | 59 | 33 |
| Mean number of meristematic cells per count‡ ± SE | 38 ± 1.8 | 36 ± 1.7 | 38 ± 2.5 | 27 ± 1.4 |
| Weighted mean proportion (as % of total cells) | 38.5 | 38.9 | 50.2 | 32.4 |
| Number of counts‡ | 99 | 114 | 72 | 168 |

* Located just below the rib meristem.
† Advanced primordia included possible branch and seed-cone primordia.
‡ See Materials and Techniques. Three to four counts per primordium.

TABLE 5—Mean dry weights (mg) of the first cluster of long-shoot primordia in buds of three shoot types at differentiation time (March)

| Primordia | Shoot type* | | |
|---|---|---|---|
| | 1 | 2 | V |
| Branches | 29 ± 9.7 | 35 ± 8.6 | 9 ± 4.5 |
| Identified seed cones | 5 ± 1.1 | 7 ± 1.5 | 2 ± 0.5 |
| Potential seed cones | 4 ± 0.9 | 5 ± 1.0 | 3 ± 1.2 |
| Total long shoots | 18 ± 6.3 | 20 ± 4.8 | 5 ± 2.2 |

* 1 = shoots with one cluster of seed cones
2 = shoots with two clusters of seed cones
V = shoots with predominantly vegetative laterals

vegetative (branches). Differentiation into seed-cone primordia, however, only started after 7 February. No undifferentiated primordia (in Cluster 1) were found after 20 February (Table 6). It seems that generally the primordia which will remain vegetative (i.e., which will become branches) are determined before those which will differentiate into seed cones.

Numbers of branch primordia, present in the buds after differentiation had occurred, compared very well with numbers of branches which were produced by the same shoot during the previous season. The correlation coefficient (obtained from 17 shoots which were assessed in March) was +0.9615 ($p = 0.001$). Numbers of seed cones formed

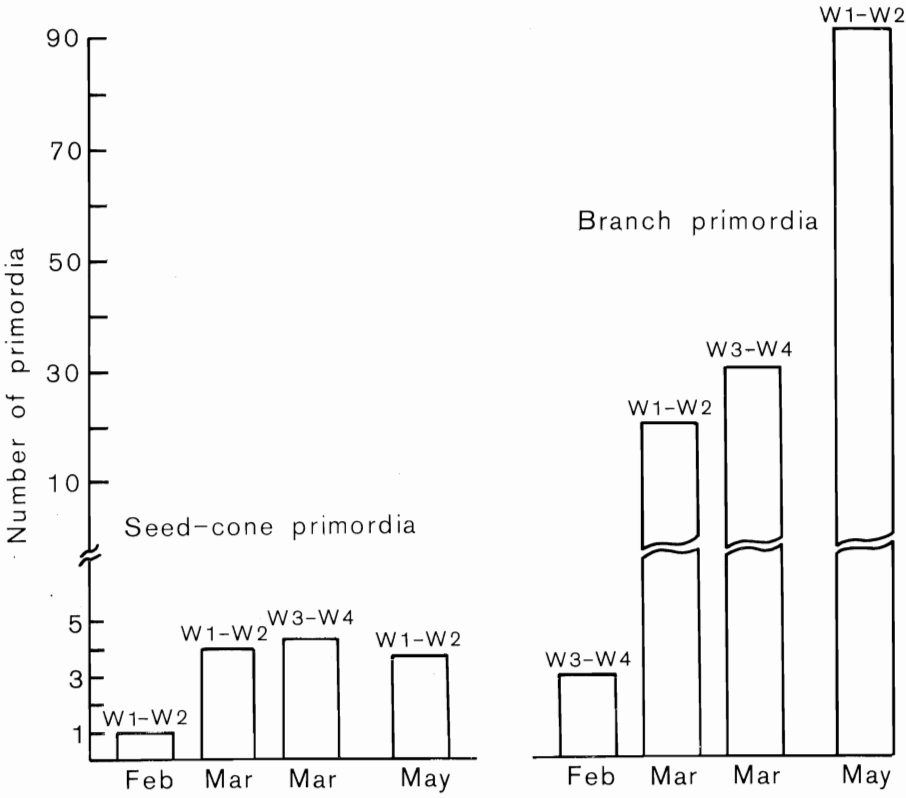


FIG. 8—Mean dry weights (mg) of reproductive and vegetative primordia.

TABLE 6—Progress in long-shoot differentiation - proportion of four categories of long-shoot primordia present in buds on seven dates between January and April

| Date | Location* | Undifferentiated | | Branches | Seed cones | Total No. of primordia | No. of buds sampled |
|---|---|---|---|---|---|---|---|
| | | Less advanced (%) | Advanced† (%) | (%) | (%) | | |
| Jan 9 | K | 81 | 19 | | | 16 | 4 |
| 24 | K | 63 | 26 | 11 | | 19 | 6 |
| Feb 7 | K | 50 | 32 | 18 | | 22 | 8 |
| 20 | K | 12 | 17 | 50 | 21 | 24 | 8 |
| 27 | K | | 20 | 56 | 24 | 25 | 8 |
| Mar 5 | K | | 29 | 50 | 21 | 14 | 4 |
| 20 | L | | 19 | 53 | 28 | 167 | 18 |

* K = Kaingaroa; L = Longmile.
† Advanced primordia include possible branch and seed-cone primordia.

during 2 years in flowering shoots of the "two cluster" type were correlated at r = + 0.8219 (p = 0.01), but when eight shoots which form one cluster of seed cones annually were included in the calculation the correlation was not significant (r = + 0.3952).

## DISCUSSION

Axillary primordia which are present in buds of *P. radiata* differ in size. In November those at the base of the buds are largest, gradually decreasing towards the apex. In January, however, most buds will have near the apex a number of primordia which, although formed last, are much larger than those located below (Fig. 6) and 5 to 6 weeks later the number of such primordia may have increased to 15 (Bollmann & Sweet 1976, 1979). In the following spring, when the buds have grown into shoots, the group of primordia of which those near the base of the growth cycle were largest (short-shoot primordia), have developed into needle fascicles. Those nearer the apex may still be in bud (Fig. 3B). The largest of the long-shoot primordia, nearest the bud apex, have become branches which have grown acropetally since formation (Fig. 5). They constitute the vegetative zone of the long-shoot region of the flowering shoots. The smaller long-shoot primordia below the vegetative zone develop into female strobili and, usually, small branches. These form the predominantly reproductive zone of the long-shoot region of flowering shoots (Fig. 3A).

From the data on which the above description of bud development of flowering shoots is based, a number of conclusions may be drawn.

Primordia which are to become seed cones develop more slowly and take longer to differentiate than branch primordia because, as axillary primordia, they are formed earlier (they grow below branch primordia – Fig. 4) and differentiate later (Table 6). Consequently, in any one bud, seed-cone primordia are smaller (Fig. 6) and lighter than branch primordia (Table 5).

Increases in dome diameters occur prior to and during differentiation and affect all categories of long-shoot primordia (Table 3). Dome diameters may therefore merely reflect general cambial activity which is at its peak at that time (February – Jackson *et al.* 1976). Dome heights, on the other hand, increased markedly in those primordia which were to differentiate into seed cones and only marginally in those which developed into branches (Table 3). Since changes in dome heights are a measure of primordium scale initiation in relation to primordium elongation (the dome is that part of the apex which is not occupied by scales) one may conclude that differentiation into reproductive primordia is preceded by a halt or slowing down of primordium scale initiation.

The characteristically voluminous domes of seed-cone primordia (Fig. 7F) may have resulted, in part, from continuing cell divisions in the ground meristem of the young pith tissue and from the enlargement of non-meristematic cells (Table 4, Fig. 2).

Perhaps the most important aspect of early long-shoot development is the accelerated growth of a basipetally increasing number of axillary primordia near the apex in the time between long-shoot formation and differentiation. This growth must be in response to a stimulant, possibly biochemical (Ross *et al.* in prep.), which affects primordia basipetally over a short period after initiation. Given also that branches develop from

primordia closest to the bud apex (Fig. 8), it follows that branches developed from axillary primordia which were affected most and seed cones from those affected less. It seems reasonable to suggest that, in research aimed at manipulating long-shoot differentiation (e.g., increasing seed-cone production), the treatments of the buds should be closer to long-shoot formation and not at the time of differentiation as has been done in the past (Sweet 1979; Ross *et al.* in prep.).

From previous studies of bud morphogenesis in *P. radiata* it is clear that there is a degree of variability between shoots in the times that long shoots form and develop (Bollmann & Sweet 1976, 1979). A careful selection of shoots must therefore be made if treatments, intended to "catch" long-shoot formation in the buds, are to be successful. It is difficult to determine what is happening in individual buds in the field, but examination of the annual growth patterns of the shoot below the bud may give an indication of the approximate time long shoots are formed and seed cones differentiate. For example, if the part of the annual shoot below the first cluster of branches (Growth Cycle 1) is shorter than the second cycle, and considering the regression of primordium numbers on shoot length (Bollmann & Sweet 1979), long-shoot formation in the bud will probably be relatively early. Comparison of the mean length of the first cluster of branches (Fig. 5) and the dry weight of the first cluster of long-shoot primordia in the bud of the two types of shoots (Table 5) seems to support this. Also, shoots of this type will consequently form two clusters of seed cones (Table 1).

There remains the question whether conclusions drawn from the examination of the shoot below a bud (which represents bud development during the preceding season) give an indication of what will happen in the bud at the present. Unfortunately, direct comparisons of stem unit numbers in shoots and buds were not made because of the time-consuming nature of bud scale counts. However, the highly significant correlations between numbers of branch primordia in the buds of both shoot types in March with branch numbers present in the first cluster, is one of the reasons why a shoot : bud comparison may be possible. Another reason is that the correlation involving seed-cone numbers in the shoot and seed-cone primordium numbers in the bud (March), although significant in shoots considered to form long shoots early in the season, was not significant in buds of shoots of the type supposed to form long shoots and differentiate seed cones relatively late (because not all potential seed-cone primordia had differentiated by March). Finally, in the buds of shoots suggesting late long-shoot formation, primordium dry weights were indeed relatively low in March.

ACKNOWLEDGMENTS

The encouragement and guidance received from Dr G. B. Sweet of this Institute is appreciated. The author also thanks the following for reviewing the original manuscript: Dr R. T. Riding of the University of New Brunswick, Canada; Dr D. A. Rook of this Institute, and Dr M. V. Slee of the Australian National University, Australia.

REFERENCES

BANNISTER, M. H. 1962: Some variations in the growth pattern of **Pinus radiata** in New Zealand. **New Zealand Journal of Science 5:** 342–70.

BOLLMANN, M. P.; SWEET, G. B. 1976: Bud morphogenesis of **Pinus radiata** in New Zealand. I: The initiation and extension of the leading shoot of one clone at two sites. **New Zealand Journal of Forestry Science 6:** 376–92.

——— 1979: Bud morphogenesis of **Pinus radiata** in New Zealand. II: The seasonal shoot growth pattern of seven clones at four sites. **New Zealand Journal of Forestry Science 9:** 153–65.

HONG, SUNG OK; LEE, BO SIK 1970: Initiation and developments in buds of **Pinus rigida**. **Institute of Forest Genetics (Korea) Research Report No. 8.**

JACKSON, D. I.; SWEET, G. B. 1971: Flower initiation in temperate woody plants. **Horticultural Abstracts 42(1):** 9–24.

JACKSON, D. S.; GIFFORD, H. H.; CHITTENDEN, J. 1976: Environmental variables influencing the increments of **Pinus radiata**: (2) Effect of seasonal drought and diameter increment. **New Zealand Journal of Forestry Science 5:** 265–86.

MERGEN, F.; KOERTING, L. E. 1957: Initiation and development of flower primordia in slash pine. **Forest Science 3(2):** 145–55.

OWENS, J. N.; MOLDER, M. 1975: Development of long shoot terminal buds of **Pinus contorta** ssp. **contorta**. Pp. 86–104 **in** "Management of Lodgepole Pine Ecosystems", Vol. 1, Proceedings. Pullman WA, United States.

——— 1977: Development of terminal buds of white pine (**Pinus monticola**). **Canadian Journal of Botany 55(10):** 1308–21.

RIDING, R. T. 1971: Cytohistological changes at the seedling shoot apex of **Pinus radiata**. Ph.D. Thesis, University of California, Davis, California.

ROSS, S. D.; BOLLMANN, M. P.; PHARIS, R. P.; SWEET, G. B.: Gibberellin A4/7 and the promotion of flowering in **Pinus radiata**: Effects on partitioning of photo-assimilates within the bud during primordia differentiation (in prep.)

SWEET, G. B. 1979: A physiological study of seed cone production in **Pinus radiata**. **New Zealand Journal of Forestry Science 9**: 20–33.

SWEET, G. B.; KRUGMAN, S. L. 1977: Flowering and seed production problems – and a new concept of seed orchards. Paper presented at Third World Consultation on Forest Tree Breeding, Canberra.