

TERMINAL BUD FORMATION IN LIMBER PINE

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ABSTRACT.— The progress of bud development was studied in limber pines growing in the mountains of northeastern Utah. Initiation of new bud scales began in mid-June, several weeks after elongation of the current shoot had begun. Needle primordia first appeared in September and continued to form through the winter, until all were present in May. This winter activity is believed to be fostered by surface temperatures on the terminal buds considerably higher than ambient air temperatures.

The annual shoot of limber pine (*Pinus flexilis* James), a five-needled species common in the Rocky Mountains, consists of a monocyclic spring shoot formed by the elongation of a winter bud. This is the most familiar shoot development pattern in northern pines and has been classified as the Resinosa pattern (Lanner 1976). But even among species of this habit, there is diversity in the developmental schedule of bud morphogenesis. For example, in some species formation of the new winter bud begins while the old one is still elongating, but in others bud formation is delayed until the cessation of current-season shoot growth. Further, the timing of short-shoot and needle morphogenesis is also subject to variation. In this report we describe the annual cycle of development of limber pine terminal buds to resolve the questions of when the short shoots and needles are formed, both in terms of calendar date and in regard to the growth stage of the spring shoot.

The trees studied grow at an elevation of 2130 m on a steep southeast slope in Logan Canyon, northeastern Utah. They vary from 12 to 27 cm DBH and 4 to 7 m in height. At each of 18 collection dates during 1978, 2 terminal buds of vigorous first-order branches in the upper crown were harvested from each of at least 2 of the 18 study trees. Buds were stored in formaldehyde-acetic acid-ethyl alcohol (FAA), dissected with standard micro-dissecting tools, and examined at 12-100x

with a Wild M-5 stereomicroscope. Two shoots had steel pins inserted at the base of the bud as a datum for observations of shoot elongation.

On each of the harvested buds we dissected at least two short-shoot budlets from the proximal (basal) end of the bud, and two from the distal (apical) end. We counted the budlet scales (future fascicle sheath scales) and needle primordia, if any. The study took place during a single calendar year, so we actually observed the late development and elongation of the 1978 spring shoot and the early development of the 1979 spring shoot. Ideally, a study of this kind should begin with early morphogenesis of a bud and end with the maturation of the resulting shoot.

RESULTS

One of the marked shoots started to elongate during the interval 20-30 May, and the other during the interval 30 May-5 June. These shoots completed their elongation growth prior to 8 July and 13 July, respectively. Final lengths of these shoots were 30.5 and 21.5 mm. Pollen was shed during the period 9-13 July.

Initiation of the primary bud scales (cataphylls) of the newly forming terminal bud began between 11 and 18 June. After cataphylls formed, meristems appeared in the axils of most of them. These axillary meristems became the apical meristems of the short-shoot

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budlets that would later become needle fascicles. Scales formed on these budlets are future fascicle sheath scales. Sheath scale initiation began in proximal budlets in early July, and in distal budlets in early August. Scale production continued in both types of budlets until about mid-January.

The earliest needle primordia started to appear in proximal budlets in late August and continued to appear over a period of three months. Needle primordia in distal budlets did not begin to form until about mid-November, but continued appearing up to early May, about 5.5 months later.

When bud scale initiation began, about two-thirds of the elongation growth of the marked shoots had been completed. Bud scale initiation probably continued throughout the remainder of the elongation period. Sheath scale initiation began in proximal budlets about the time shoot elongation was ceasing, and it began in distal budlets after the cessation of shoot growth. When needle primordia started to form, shoot growth had

been inactive for several weeks. The needle primordia formed in the spring developed prior to the onset of shoot elongation in late May.

When the first buds were harvested 22 January 1978, short-shoot budlets from proximal parts of the terminal bud contained 10–12 scales ($\bar{x} = 11.2$) and all had their full complement of 5 needle primordia. But budlets located at the distal end of those terminal buds tended to have fewer scales (8–11; $\bar{x} = 10.0$) and averaged only 1.7 needle primordia (Table 1). The difference in scale number was maintained even beyond 8 May, when, for the first time, all the distal budlets contained their full complement of 5 needle primordia (Table 1).

DISCUSSION AND CONCLUSIONS

The initiation of bud scales was first noted on 18 June, when the 1978 shoot had attained 68 percent of its final length, showing that bud morphogenesis began during the period

TABLE 1. Progress of sheath scale and needle initiation in proximal and distal short shoot budlets of first-order terminal buds of Limber Pine, and of shoot elongation.

1978 Date	Proximal budlets		Needle primordium number \bar{x}	Distal budlets		Needle primordium number \bar{x}	Length of 1978 bud/shoot as percent of final length
	Scale number			Scale number			
	\bar{x}	range		\bar{x}	range		
1978 annual shoot							
22 January	11.2	10–12	5.0	10.0	8–11	1.7	31.5
21 March	10.0	9–12	5.0	9.6	9–10	2.5	31.5
12 April	10.3	9–12	5.0	9.5	9–10	3.3	31.5
8 May	10.0	9–11	5.0	10.6	10–11	5.0	31.5
20 May	9.5	8–11	5.0	9.5	9–10	5.0	31.5
4 June	10.0	10	5.0	9.5	9–10	5.0	45.0
11 June	13.0	13	5.0	11.0	11	5.0	55.5
1979 annual shoot							
11 June	0	0	0	0	0	0	55.5
18 June	0	0	0	0	0	0	68.0
2 July	0	0	0	0	0	0	95.0
13 July	2.0	2	0	0	0	0	100
23 July	4.5	3–6	0	0	0	0	100
2 August	5.0	5	0	0	0	0	100
16 August	6.0	6	0	0.75	0–2	0	100
26 August	6.0	5–7	0	2.3	2–3	0	100
15 September	8.0	8	5.0	7.3	6–9	0	100
5 October	8.3	8–9	3.0	7.3	6–9	0	100
15 November	8.8	8–10	2.2	7.0	6–8	0	100
9 December	8.0	8	5.0	8.0	8	1.8	100

of shoot elongation. In this regard limber pine resembles *P. strobus* L. and *P. lambertiana* Dougl. (Lanner 1976). It provides further evidence that shoot elongation does not inhibit the initiation of lateral structures on the shoot apical meristem. Bud morphogenesis in limber pine is delayed, however, in comparison to that of lodgepole pine (*P. contorta* Dougl.), one of its associates in this area (Van Den Berg and Lanner 1971). In lodgepole, initiation of the new bud and elongation of the shoot began almost simultaneously early in May.

A given stage of development—i.e., attaining a certain number of sheath scales or a certain number of needle primordia—is reached earlier in proximal than in distal short shoots. Thus, in the 1978 winter buds, the full complement of 5 needle primordia was present in proximal short shoots in January collections, but was not found in distal short shoots until May. This is another case of the developmental gradient in short-shoot maturation described in the more complex buds of lodgepole pine (Van Den Berg and Lanner 1971), the much larger buds of slash pine, *P. elliottii* Engelm. (Lanner 1978), and in eastern white pine (Owston 1969).

Perhaps the most unusual finding reported here is that morphogenetic activity continued in wintering limber pine buds. Buds collected early in 1978 showed periodic increases in needle primordium number in distal budlets. Buds collected late in 1978 showed consistent increases in needle primordium number in both proximal and distal budlets, and in sheath scale number in distal budlets (Table 1). Yet temperatures at a nearby temporary weather station at a comparable elevation fell as low as -21 C in January and -12 C in November and December (pers. comm., S. A. Loomis). In lodgepole pine studied just a few miles from this site, budlets overwintered with less than their full complements of sheath scales and needle primordia, but no changes were noted during the winter (Van Den Berg and Lanner 1971). Budlets of slash pine actively initiated scales and needle primordia during the winter months, but this was in the much milder climate of Florida (Lanner 1978).

Seed cone primordia have also been re-

ported as morphogenetically active during the winter. Duff and Nolan (1958) observed changes in ovulate strobili of red pine (*P. resinosa* Ait.) between October and January in the cold climate of Chalk River, Ontario. Gifford and Mirov (1960) also reported female strobilus development in ponderosa pine (*P. ponderosa* Laws.), but in the milder climate of the Sierra Nevada west slope.

Such meristematic activity may be permitted by surface temperatures considerably higher than those of the ambient atmosphere. For example, Tranquillini and Turner (1961) have reported maximum monthly temperatures of Swiss stone pine (*P. cembra* L.) needles 2.7 and 7.4 C higher than air temperatures during November and March, respectively, in the Austrian Alps. In March, needles reached a maximum of 18.4 C, though the mean air temperature for that month was only 0.3 C. At our study site, even in January, the coldest month of the year, air temperature on three occasions attained almost 6 C. Bud surface temperatures may have reached as high as 12 C or more, well above the apparent threshold for meristematic activity.

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