

The Phenology and Growth Habits of Pines in Hawaii

Ronald M. Lanner



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Trees taken from their natural habitats and grown in another climate often develop in ways that cannot accurately be predicted. Foresters must understand this behavior if they are to make sound decisions in planting and managing these introduced species.

Over the years many pine species have been planted in Hawaii—both as ornamentals and as a potential source of locally grown softwoods. Even casual observers have noticed unusual behavior among some of these introduced species.

Pines in temperate regions undergo a regular annual growth cycle. They grow most actively in spring, stop growing in summer,¹ and remain dormant throughout fall and winter.

ical pines come from areas where a pronounced dry season imparts seasonability to the climate, although winter temperatures may be mild.

This paper reports on a study of how the coordinated seasonal cycle of growth and flowering has been influenced by the climatic conditions that pine species encounter in Hawaii. The study sought to define the unusual behavior among some species in terms of the interaction between the species and their new environment. In some cases, this goal was met. But much more research needs to be done before the effects of environmental conditions in Hawaii on introduced species are fully understood.

Climate of Hawaii

Three characteristics of the Hawaiian climate are of major importance to studies of plant response: (a) the comparatively slight change in daylength—a consequence of low altitude (19 to 22° N.); (b) mild temperatures except at high elevations—owing to the Islands' oceanic position within the tropics; and (c) generally high rainfall—owing to the orographic effects of mountains on moisture laden air brought in by the northeast tradewinds. Most of the sample data given below are from Blumenstock (1961).

The small variation in daylength is a striking feature (fig. 1). At 20° latitude the longest day is only 13.3 hours and the shortest 11 hours—a difference of only 2.3 hours.

Temperatures at low and middle elevations are not only mild but equable (table 1). Both mean temperatures and extremes show little variability. Thus at Hawaii Volcanoes National Park, on the island of Hawaii, the lowest temperature ever recorded in the coldest month (January) was 40°

F.; the lowest in the warmest month (September) was 51° F. The highest temperatures ever recorded for these months were 73° F. and 80° F., respectively. Records of the U.S. Weather Bureau show that the annual mean temperature for a typical year for Kulani Camp, Hawaii, was 55.3° F. And temperature extremes for a 5-year period there (1958-1962) ranged from 31 to 78° F. The highest temperature ever recorded in the entire State was 100° F., at Pahala, Island of Hawaii; the lowest, 18° F., near the summit of Mauna Kea, an extinct volcano that rises almost 14,000 feet above the sea.

Rainfall varies enormously. At low and middle elevations on the islands of Hawaii, Kauai, Maui, and Oahu, rainfall is heavy enough to support a rain-forest community on the windward (north and east) sides. But above the temperature inversion layer (usually present at 4,000-7,000 feet) and at leeward locations are some very dry areas. Rainfall in the State is somewhat seasonal in distribution, the winter months (October-April) being wetter than the summer months (May-September). This difference is less pronounced in high-rainfall areas, where rainfall may vary greatly from year to year.

¹The term "dormancy" is used in the sense proposed by Doorenbos (cited by Romberger 1963) as a "general term for all instances in which a tissue predisposed to elongate does not do so."

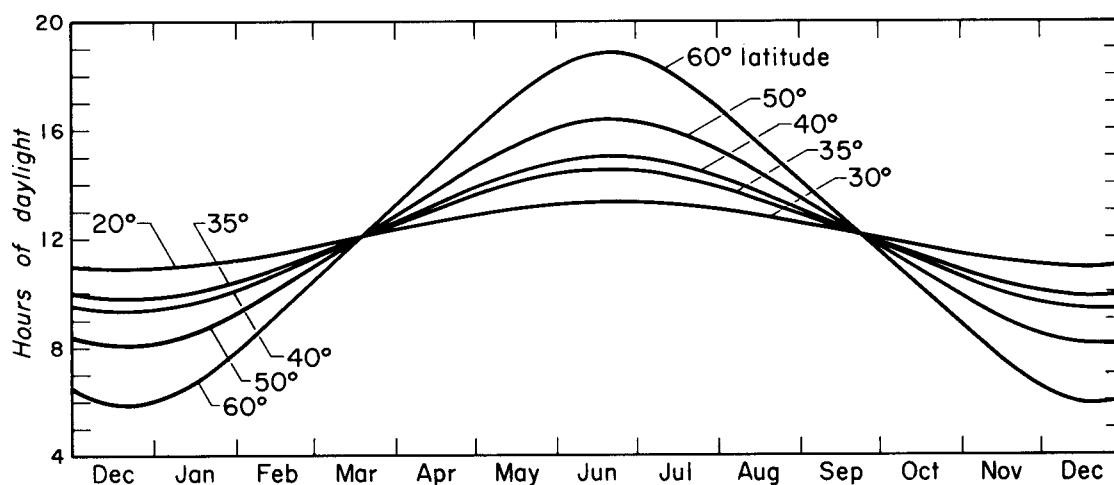


Figure 1.—Change in length of day at different latitudes. Civil twilight was excluded.

Table 1.—Temperature data for seven selected stations in Hawaii¹

Station	Elevation	Mean January temperature	Mean August temperature	Mean temperature range
	<i>Feet</i>	<i>Degrees F.</i>		
Hilo, Hawaii	40	71	76	5
Olaa, Hawaii	280	70	75	5
Mountain View, Hawaii	1,530	65	70	5
Hawaii Volcanoes National Park, Hawaii	3,971	58	64	6
Kulani Camp, Hawaii	5,190	53	58	5
Haleakala, Maui	7,030	52	58	6
Mauna Loa Observatory, Hawaii	11,150	39	47	8

¹Haleakala data from Britten (1962); all other data from Blumenstock (1961).

Methods

More than 200 observations were made of trees of 25 species (tables 2, 3). Sometimes only young trees were seen, so there was no opportunity to obtain flowering data. Because some trees or stands were difficult to reach, they were visited only once or at insufficient intervals to gather critical information.

Vegetative shoots were considered active if they showed evidence of elongation at the base of the

bud, or if the needles on the current shoot increment showed a distinct gradient in length. They are considered dormant if the buds were enclosed within scales and if the youngest needles were full-sized. Normally it can be inferred that pine shoots are elongating if pollen is being shed, but in Hawaii this is not always true. In some species male cones mature irregularly, and pollen may continue to fly for several months after shoots have become

Table 2.--Natural range and minimum probable displacement of species studied.

Common name ¹	Scientific name ¹	Natural range	Minimum probable displacement
			Degrees of latitude
Aleppo pine	<i>Pinus halepensis</i> Mill.	Mediterranean region	20
Caribbean pine	<i>P. caribaea</i> Morelet	West Indies and Central America	3
Chihuahua pine	<i>P. leiophylla</i> Schiede & Deppe	Mexico and South-western United States	0
Chir pine	<i>P. roxburghii</i> Sarg.	Himalaya Mountains	9
Coulter pine ²	<i>P. coulteri</i> D. Don	Central California to Baja California	14
Eastern white pine	<i>P. strobus</i> L.	Eastern United States and Canada	20
Jack pine	<i>P. banksiana</i> Lamb.	Northeastern United States and Canada	25
Japanese black pine	<i>P. thunbergiana</i> Franco	Japan, Korea	10
Jeffrey pine	<i>P. jeffreyi</i> Grev. & Balf.	Baja California to Oregon	15
Khasi pine	<i>P. insularis</i> Endl.	Southeast Asia, Philippines	2
Knobcone pine	<i>P. attenuata</i> Lemm.	Baja California to Oregon	15
Loblolly pine	<i>P. taeda</i> L.	Southeastern United States	10
Lodgepole pine ²	<i>P. contorta</i> Dougl.	Western North America	15
Longleaf pine	<i>P. palustris</i> Mill.	Southeastern United States	10
Maritime pine ²	<i>P. pinaster</i> Ait.	Mediterranean region	20
Masson pine ²	<i>P. massoniana</i> Lamb.	Southeastern China	3
Mexican weeping pine ²	<i>P. patula</i> Schiede & Deppe	Mexico	0
Mexican white pine	<i>P. ayacahuite</i> Ehrenb.	Mexico	0
Monterey pine ²	<i>P. radiata</i> D. Don	California	15
Montezuma pine	<i>P. montezumae</i> Lamb.	Mexico	0
Ponderosa pine	<i>P. ponderosa</i> Laws.	Western North America	15
Scotch pine ²	<i>P. sylvestris</i> L.	Europe and Asia	25
Shortleaf pine	<i>P. echinata</i> Mill.	Southeastern United States	10
Slash pine	<i>P. elliottii</i> Engelm.	Southeastern United States	9
West Indian pine	<i>P. occidentalis</i> Sw.	Haiti (known source)	0

¹Nomenclature here and elsewhere in this paper follows that given by Critchfield and Little (1966).

²Regenerates, naturally in Hawaii.

dormant. High humidity for prolonged periods may delay drying of male cones and hinders the normal shedding of pollen. Therefore it was usually necessary to examine vegetative and sexual shoots independently.

Reproductive structures were studied in greater detail following a classification based on that used at the Institute of Forest Genetics, Placerville, California (Cumming and Righter 1948). Male cones were classed on their progress toward anthe-

sis: (a) enclosed in buds, (b) not yet flying, (c) starting, (d) flying, (e) mostly shed, or (f) all shed; and female cones according to their stage of development: (a) buds large, (b) buds opening, (c) scales partly open, (d) scales fully open, (e) scales partly closed, (f) closed, or (g) conelet enlarging.

In collating the data for summarization, some interpolation has been necessary to reconstruct the annual cycles for selected species. But the observations were detailed enough to prevent serious error. Most of the observations were made in 1962-64, though a few data collected by R. G. Skolmen, of the Pacific Southwest Station in 1961, are included.

Table 3.--*Location of study trees*

Locale	Island	Elevation	Rainfall
		<i>Feet</i>	<i>Inches</i>
Hakalau	Hawaii	1,000	200
Haleakala Plot 1	Maui	6,500	50
Haleakala Plot 2 (Hosmer Grove)	Maui	6,800	104
Haleakala Plot 3	Maui	8,000	60
Hilo	Hawaii	50-400	150
Kamuela	Hawaii	2,600	29
Kamuela (Puu Ohu)	Hawaii	3,300	40
Keanakolu	Hawaii	5,300	110
Keawiwai	Hawaii	4,000	100
Keawiwai	Hawaii	6,000	50
Kokee	Kauai	3,000	100
Kulani Camp	Hawaii	5,200	98
Mauna Kea	Hawaii	9,000	26
Olinda Nursery	Maui	3,600	54
Pohakuloa	Hawaii	6,400	16
Poli Poli Spring	Maui	6,500	40
Puu Kihe	Hawaii	7,800	45
Puu Laau	Hawaii	7,500	20
Taro patch, Stainback Highway	Hawaii	3,600	150
Volcano	Hawaii	3,700	80
Waiakea Arboretum	Hawaii	800	200

Annual Growth Cycle

Major findings on the annual growth cycle of pines are summarized in table 4 and shown graphically in figure 2. The discussion that follows focuses on the species observed racist often.

Findings for Selected Species

Mexican weeping pine.—At Olinda many spontaneous seedlings were found. Pollen-shedding was observed in December, January, February, March,

Table 4.--Summary of phenological data on annual growth cycle of pines in Hawaii¹

Species	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Aleppo pine			a									
Caribbean pine	a	da	a		a				a		d	
Chihuahua pine	d				a							
Chir pine			ma		a							
Coulter pine	dm				ma	am						
Eastern white pine	d	m				a						
Jack pine	mf ^{2/}	m ^{2/}				m ^{2/}						
Japanese black pine	mf ^{2/}		mad ^{2/}	maf	a	mf ^{2/}		md ^{2/}	d	mad ^{2/}	m ^{2/}	
Jeffrey pine	d				ma	am		d				
Khasi pine		a		a	a						ad	
Knobcone pine	ma				a				d			
Loblolly pine	dmaf		maf	a	a	a	m		ad		d	
Lodgepole pine				dmaf				mf				
Longleaf pine	d	a	a								d	
Maritime pine	dm	amf	madf	a	ma				m		d	d
Masson pine	dmfa	m			a				d			
Mexican weeping pine	fma	ma	maf	maf	maf				d		d	ma
Mexican white pine	d		a									d
Monterey pine	fam ^{3/}	fam ^{3/}	fam ^{3/}	fam ^{3/}	fam ^{3/}	af ^{3/}	fa ^{3/}	fam ^{3/}	a	a	fam ^{3/}	am ^{3/}
Montezuma pine	d		da									
Ponderosa pine	d					m					m	
Scotch pine	dm ^{2/}	m ^{2/}	da	fam		mf ^{2/}		m ^{2/}				
Shortleaf pine	da	a		m	fa						d	
Slash pine	d	m	amf		a				d			dm
West Indian pine	d		a									

¹a = vegetative shoots active

d = shoots dormant

f = female flowering

m = male flowering

²Flowering data (male) excluded from tabulation in text.³Flowering data (both sexes) excluded from tabulation in text.

April, and May. Pollen-receptive conelets were seen in January, March, and May.

Vegetative shoots became visibly active in December or January and grew until about September, several whorls of branches extending during this period. During the short dormant period many trees had, in their upper crowns, shoots that had elongated up to 3 feet without having extended their needles. These shoots appear similar to what I have termed "bare overwintering shoots" in knobcone pine (Lanner 1963), where they were associated with a bi-modal growth pattern. Similar shoots, though much shorter ones, have been described for jack pine (Rudolph 1964) and, in South Africa, for loblolly and Mexican weeping pines (Norskov-Lauritsen 1963).

Maritime pine.—One of the most commonly planted pines in Hawaii, maritime pine appeared to be quite normal in growth and form. It produces many cones, and the cones of both sexes are synchronized. Natural regeneration was noted at Olinda, Maui.

There were six reports of pollen-shedding for January and February, one for March, one for May, and one report for September. Conelets in the pollen-receptive stage were seen in February and March at Kulani Camp.

Dormant shoots were recorded in November, December, January, and March. The plantation with shoots dormant in March was considerably younger than the others. Except for the single case of pollen-shedding in September, maritime pine

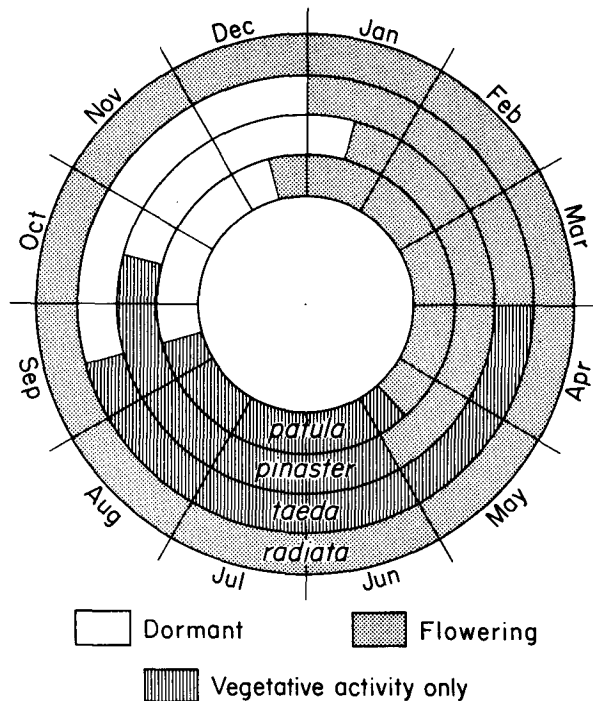


Figure 2.—Calendar of phenological events in four species of pine in Hawaii.

has been found to observe a regular seasonal cycle of growth and dormancy even where rainfall is about 100 inches annually (Kulani Camp).

Loblolly pine.—Periodic visits to a loblolly pine plantation at Olinda made it possible to view the same trees throughout an entire growth cycle. The trees were then in their fourth year (third year in plantation) and just starting to flower. Unfortunately, as with many of the trees reported upon in this paper, the seed source of this plantation is unknown, but phenologically the plantation was quite uniform.

Growth started in early January and both anthesis and the emergence of conelets occurred during this month. Shoot elongation continued, several whorls being produced, until September, when most trees became dormant. But in other trees the newly organized terminal bud elongated and became a lammas shoot or summer shoot (Shaw 1914). At the Waiakea Arboretum, where temperatures are milder and rainfall higher (Richmond 1963), the same vegetative cycle seemed to hold, but at Kamuela an isolated tree flowered heavily in July as well as in January. In a plantation above Kamuela (Puu Ohu), shedding male cones and pollen-receptive conelets were found in March.

Monterey pine.—Among a population of Monterey pines, most of the trees grow episodically, but some can grow continuously under suitable site conditions. This species is unusual in having no defined dormant season. Because of their bizarre appearance and their physiological and genetic significance, continuously growing trees are described elsewhere in this paper. Trees that grow episodically—and they are in the majority—do not all turn dormant at the same time of the year. Inspection of plantations of this species at any time of year will disclose shoots, vegetative buds, and male and female cones in several stages of development. And dormant and active shoots can be found side by side on a single tree. It appears that in Hawaii as in Australia (Jacobs 1937) the higher the order of a branch the more likely it is to form a resting bud.

Pollen-shedding was noted in January, February, March, April, May, August, November, and December, when there were male cones in earlier stages of development that probably shed pollen during the remaining months. Thus, pollen-shedding in Monterey pine may be considered a year-round affair.

Female cones at or near the receptive stage were observed in February, March, August, and November. Other cones probably reached this stage in April, July, October, and December. Conelets, like male cones, therefore can appear at any time. Within a period of several months, we saw branches on which five whorls of conelets were produced.

Synchrony of pollen-shedding and conelet receptivity was observed at Puu Kihe, Kulani Camp, and Pohakuloa. Natural regeneration has become established at Puu Kihe, where 809 pounds of cones yielded 9½ pounds of cleaned seed which germinated at the rate of 92 percent.²

Cyclic Pattern of Growth

The most significant finding in this study was that, except for Monterey pine, all species investigated in adequate detail showed a cyclic pattern of growth and dormancy. Most sites on which these trees were growing, and perhaps all of them, had climates mild enough to permit growth at any time. Yet the pines still showed the episodic growth pattern that characterizes their behavior at their places of origin.

² Personal correspondence with Masa Takaoka, Hawaii Forestry Division, March 18, 1964.

Romberger (1963) has pointed out that even in tropical woody plants episodic growth is the usual condition, with alternating periods of rapid elongation and little or no elongation. This condition is true even of the tropical evergreen species near Singapore, only 1° N. of the equator, and in a tropical rain forest environment where variations in climate are of far less amplitude than in Hawaii (Koriba 1958).

Equally significant was the near synchrony of the various species of pine—the regularity of dormant, flowering, and growing periods that permitted us to delineate seasons in Hawaii in terms of pine response. Thus we may say that, in general, pines stop growing in September and resume growing in December, January, or February.

Seasonality of Flowering

Flowering is also seasonal, though some of the data obscure this pattern. To discern seasonal pattern, it is first necessary to exclude Monterey pine because of its unique capability of flowering throughout the year. Pollen-shedding data for jack, Scotch, and Japanese black pines that were not undergoing an obvious grand period flush must also be excluded because of the effects of high humidity. Female flowering data for these three species are included in this analysis because the opening of female buds is probably far less affected by humid conditions than is the release of pollen. The seasonal distribution of pine flowering in Hawaii is as follows:

Month:	Species	
	With pollen-receptive female cones	Shedding pollen
	--- (number) ---	
January	5	6
February	1	5
March	4	5
April	6	5
May	2	2
June	2	1
July	0	1
August	1	1
September	0	1
October	0	0
November	0	1
December	0	2

Several other facts must be considered regarding seasonality of flowering. First it must be admitted that too few observations were made during the months of July, August, October, and December. Had more time been spent in the field

during those months, perhaps more flowering would have been seen. On the other hand, several observations of flowering late in the year are probably of little value in offsetting the strongly seasonal trend. For example, the records of pollen-shedding for June and for November refer to a single ponderosa pine at Hosmer Grove, Maui. There were no other data for this species, and this tree may be atypical. The July pollen-shedding record was for a single loblolly pine—this tree also flowered in January as have a large number of others of this species. The September record for maritime pine is another case in which one tree deviated from the behavior of many other trees of the same species.

There are precedents for flowering patterns that are other than strictly vernal. For example, Gregg pine (*P. greggii* Engelm.), a close relative to Mexican weeping pine, flowers regularly in June and November at Placerville, California.³ Hodgson (1963) reports that Mexican weeping pine has two distinct flowering seasons in Southern Rhodesia. The major flowering season for male and female cones is between July and November at this southern hemisphere location, but between January and March female flowering recurs.

Mirov (1962) reported that pollen is shed twice a year—during January-February and July-August—in plantations (elevation 4,900 ft.) of Merkus pine (*P. merkusii* Jungh. & De Vries) in Java. Near sea level, plantation records showed that pollen and conelets were produced year round. Chalmers (1962) reported that in Trinidad, Caribbean pine of British Honduras origin produces pollen in every month, but mostly during November-January. This latter period was the only time when he saw emerging conelets.

In humid environments dates of anthesis can be misleading, because of lags in the opening of the pollen sacs. However, dates of flowering in Hawaii have been compared with dates for the various species in their native areas, or where such information was not readily available, in California (table 5). Of the 12 species seen flowering in Hawaii (excluding the jack, Japanese black, Monterey, and Scotch pines), in eight there is some degree of overlap, in two species flowering in Hawaii is no more than 2 months early, and in 2 species flowering in Hawaii is no more than 3 months early. So the Hawaiian environment

³ Personal correspondence with W. B. Critchfield, U.S. Forest Service, March 20, 1964.

usually deflects flowering periods either not at all or by only a few months; and when pines flower at the "wrong" time they are usually early. Magnitude of the deflection of flowering time and

latitudinal displacement of the species are not related. These results are consistent with Mirov's observation (1956) that pines are neither long-day nor short-day plants.

Cone Anomalies

Anomalies, or abnormalities, in the position and structure of the reproductive structures of *Pinus* have received attention from botanists and foresters for many years. Recent interest in tree im-

provement has shown the need for more detailed information on the entire process of flowering, and especially the physiological mechanisms underlying the initiation and development of cone pri-

Table 5.--*Pine flowering dates in Hawaii compared with other records*

Species	Hawaii flowering date	Flowering date outside Hawaii	Location	Reference
Chir ¹	March	Feb., March, April	India ^{2/}	Troup 1921
Coulter	January	April, May, June	California ^{2/}	Duffield 1953
Eastern white	February	May, June	Canada ^{2/}	Canada Dep. Forestry 1963
Knobcone	January	March, April	California ^{2/}	Duffield 1953
Loblolly ¹	Jan., March, July ^{3/}	Feb., March, April	North Carolina to Texas ^{2/}	Dorman and Barber 1956
Lodgepole ¹	April-May, July, August	April, May, June	California ^{2/}	Duffield 1953
		May, June, July	Alberta, Canada ^{2/}	Smithers 1962
Maritime ¹	Jan., Feb., March, May September ^{4/}	April	California	Duffield 1953
Masson	Jan., Feb.	April	California	Duffield 1953
Mexican weeping ¹	Jan., Feb., March, April, May, Dec.	March, April	California	Duffield 1953
Ponderosa ¹	June, Nov. ^{5/}	April, May, June	California ^{2/}	Duffield 1953
		May, June	Canada ^{2/}	Canada Dep. Forestry 1963
Shortleaf	April, May	March, April May	North Carolina to Texas ^{2/}	Dorman and Barber 1956
Slash ¹	Dec., Feb., March	Jan., Feb.	South Carolina to Texas ^{2/}	Dorman and Barber 1956

¹Indicates that flowering periods in Hawaii and elsewhere overlap.

²Trees growing within the natural range.

³Record for July based on single tree; others included numerous trees at each of two locations.

⁴Record for September based on single tree; others included several trees at three locations.

⁵Both records based on a single tree.



Figure 3.—Cone clusters of Japanese black pine, Puu Kihe, Hawaii.

mordia. This interest, in turn, has focused attention on anomalies because studies of the abnormal often shed light on the normal.

Normal Cone Development

Female cones are the ontogenetic equivalents of branches (long shoots). They originate from buds that occur in whorls just below the apex of a terminal bud, as do vegetative branches. After emerging from its cover of bud scales, the tiny conelet parts its scales, exposing to view the axis on which the scales are spirally arranged. At this point the conelet is said to be pollen-receptive, for this is when pollination takes place. After pollination the scales close and the conelet enlarges somewhat. Next spring the cone increases in size until it matures in late summer or fall.

Male cones are the ontogenetic equivalents of needle bundles (dwarf shoots). They emerge from small buds located below the zone of needle bundles on an elongating branch. They then elongate, and the pollen sacs along their axes split open, releasing the pollen. After pollen-shedding the male cones dry up and wither.

Types of Anomalies

Position Anomalies

In position anomalies, organs are found on parts of the tree where they do not usually occur.

Female cones in the needled zone is a condition known in German literature as Zapfensucht, or

"cone disease." The cones appear in positions normally occupied by needle bundles and are sometimes clustered in great numbers (Black 1961; Debazac 1963; Fielding 1960; Gal'pern 1956; Neubauer 1960). In Hawaii this condition was observed on a Maritime pine and a Masson pine, several times on Mexican weeping and lodgepole pines, and many times on Japanese black pine, where it is so common as to have become the "normal" mode of growth for this species—at least in the high elevation plantings on Haleakala and Mauna Kea (fig. 3).

Every cone in such a cluster occupies a position that would otherwise bear a fascicle of needles, and every cone that develops at a whorl occupies what would otherwise be the position of a branch. When both types of cones are produced in great profusion (fig. 4) an abnormal pagoda-like crown is formed.

In Japanese black pine the clustered cones may be found at the base of the needled tract, at the top of it, or within the tract of foliage. They may occur in dense masses, or be interspersed singly among needle bundles. Most of them fail to attain normal size because of severe crowding.

It is interesting that position anomalies are so much more common in Japanese black pine than in the other species in Hawaii. As Mergen (1963) has pointed out, many of the recent reports of sex transformation have pertained to this species. According to Black (1961), Jackson has reported



Figure 4. — *Japanese black pine* "pagodas" at Puu Kihe, Hawaii. Heavy coning prevents formation of a normal crown.



Figure 5. — Needles emerging from the portion of the stem bearing male cones. *Mexican weeping pine*, Kulani Camp, March 1964.



"cone disease" of this species in Britain, and Gal'pern (1956) in southern Russia.

Male cones mixed with needles is a condition common in Mexican weeping pine, where strobili may be found intermingled with needle bundles in predominantly needled zones, or needles in the zone of strobili (fig. 5).

Pseudo-terminal cones. — Female conelets in *Pinus* normally emerge from buds arranged in whorls below the apex of a terminal bud. There are, however, reports of "terminal cones" (Doak 1935, Fielding 1960), that is, cones actually borne at the tip of a shoot. Such a configuration renders the growth of the cone-bearing shoot determinate, in contrast to its normal indeterminate nature (Sinnott 1960). That is, the shoot can no longer extend its axis, for it is capped with a soon-to-be-dead structure instead of a living vegetative bud. Masters (1890, p. 309) attributed the apparently terminal position of cones to arrested development of the terminal bud and assumption of dominance by the cone.

At Olinda, Maui, N. H. Cheatham and I found three wildlings of Masson pine, each of which had its leader surmounted by what appeared to be a terminal cone in the pollen-receptive stage (fig. 6). Two of these were descaled and found not to be terminal at all. In each case the cone was a lateral appendage. The terminal bud was very small and still tightly enclosed within its scales. Apparently the terminal bud had not elongated after the cone emerged, and as a result of its superior vigor the cone had achieved dominance. The weak terminal bud would probably have remained inhibited and eventually aborted. These observations agree with those of Masters (1890).

A pseudo-terminal cone of Masson pine has been deposited in the herbarium of the Institute of Forest Genetics, Placerville, California.

Developmental Anomalies

The timing of development of reproductive organs is modified in developmental anomalies.

Late pollen-shed.—In several individuals of Mexican weeping pine, and in the single knob-cone pine available for study, there were male cones on the previous years' shoots that were just reaching anthesis. Presumably these were year-old



Figure 6. — Apparent terminal cone of Masson pine, Olinda, Maui, February 1964.

cones that had developed very slowly. This delay of one year in the maturation of male cones seems analogous to delay in needle maturation of Mexican weeping pine noted earlier in this paper and in knobcone pine (Lanner 1963).

Overlapping development of male cones.—Pollen-shed is normally a short-term affair. For example, Sarvas (1962) found that in most years pollen from Scotch pine was shed during a 5- to 10-day period. In Hawaii, however, male cones on the same branch may mature during a much longer period. Within a cluster of male cones all stages of development may be found, from tightly closed buds to totally shed-out male cones. Nor does maturation always proceed systematically upwards or downwards along the shoot (Fielding 1957). Instead, male cones in several stages may be intermingled along the shoot axis. The period of pollen-shedding is thus prolonged far beyond even the 19 days recorded for Monterey pine in Australia (Fielding 1957). This overlapping development of male cones has been commonly observed in Monterey, Scotch, Japanese black, and jack pines. It should not be confused with the delay in shedding from matured strobili though it is often associated with it.

Differential development within male cones.—On one tree each of ponderosa pine and loblolly pine, male cones have been found in which the

distal half was shedding or shed out while the proximal half was not yet ready to shed. In the ponderosa pine, too little material was available to establish the frequency of this pattern. But in the loblolly pine, which was flowering heavily, nearly all the male cones had developed in this way.

Structural Anomalies

In structural anomalies, the morphology of an organ is altered.

Bisexual cones of Japanese black pine have been found at the Hosmer Grove, Haleakala, and at Puu Kihe. The upper portion was female, the lower portion male in every case. Similar bisexual cones were found on Mexican weeping pine at Keanakolu and Puu Kihe, where they occurred within cone clusters in the male-cone zone.

Club-shaped male cones.—A slash pine at Kawaiki, Kauai, had male cones that were swollen to twice the normal diameter in the upper two-thirds of their length. Dissection revealed no sign of insect attack or other internal damage.

A recent tendency has been to view anomalies as evidence of physiological disturbances in introduced species (Zobel 1952; Black 1961). It is true that most reports of such anomalies deal with introduced species, but this may be due to the closer attention that these species receive.

Crown Form

A pine normally tends to produce a pyramidal crown until, at an advanced age, the leader loses dominance and the crown flattens. Any radical departure from the pyramidal shape that is not due to mechanical damage or pathological factors is considered abnormal for the purpose of this paper.

Larson (1962) has suggested a unifying concept of the influence of the crown on wood quality—mainly as to wood specific gravity and the annual ring. He points out that wood quality is influenced by environmental factors, not as independent agents, but as controllers or modifiers of growth within the crown. For example, latewood information is associated with the cessation of growth in the terminal shoot. If the environment is modified so that terminal growth is prolonged during the period of earlywood formation, then latewood formation will be delayed. In this case, the activity of the shoot is an intermediary between the environmental factor and the structure of the wood.

If the same environmental modification was used too late or too early to influence shoot growth suitably, it would not have the same effect on wood quality. Larson's concept is useful in solving some of the problems of pine growth in the tropics because it permits the observer to make inferences regarding wood quality based on simple phenological observations.

Influence on Annual Ring

In light of Larson's concept (1962) the annual ring is seen to be a manifestation of changing growth conditions in the crown. When shoot activity ceases and the tree becomes dormant, a band of latewood is laid down by the cambium. Thus, we would expect the pines that exhibit an annual growth cycle in Hawaii, including a period of dormancy, to produce truly annual rings. Except for the occurrence of false rings (and these are formed in pines in their natural habitats as

well) this generalization appears valid. Ring counts on trees of known age have disclosed annual rings in ponderosa, Jeffrey, Coulter, slash, and loblolly pines. And Skolmen (1963) has reported annual rings in maritime pine. Normal-looking rings were seen in a Scotch pine, but the age of this tree, a naturally seeded one, was not known independently. All of these pines go dormant in Hawaii.

Japanese black pine appears to form a false ring about every other year on the average. The phenology of this species is not yet satisfactorily understood. Though it flushes in spring and becomes dormant in winter, its behavior during the growing season is erratic.

Monterey pine is difficult to interpret. Continuous-growing individuals of this species form practically no latewood, so ring counting is impossible. In other trees bearing no evidence of continuous growth, the latewood may or may not be well enough defined to demarcate rings. In some cases broad zones of latewood contrast but little in color with earlywood. The situation here is probably similar to that described by Oppenheimer in Aleppo pine under conditions of mild weather that permit recurrent growth flushes (Studhalter et al. 1963).

Morphology of the Shoot

Normalcy of crown form implies not only a certain phenological course of development and a specified anatomical organization of the woody tissue but a well-defined pattern of shoot morphology as well (Debazac 1963; Doak 1935). A new vegetative branch that has just elongated and become dormant is organized in a particular fashion. At the base is a series of closely-knit scars. They show the points of attachment of the bud scales that enclosed the branch when it was an unextended bud. Further along the branch is a needle-less zone, or sterile-scale zone. Beyond this zone is the needled portion of the branch, which is surmounted by a whorl of lateral buds and a terminal bud. When these buds extend, the same pattern will be repeated on the branches they produce—bud-scale scars, sterile-scale zone, needled zone. On so-called "multinodal" shoots there are intermediate branch whorls, but just above the whorls is the usual sterile-scale zone. Bud-scale scars are found only at the base of the first shoot increment (Jacobs 1937).

If normal growth of pines is understood from the three points of view—phenological, anatomical, and morphological—it is possible to gain some insight into the nature of abnormal forms.

Branchless Pines or Foxtails

Numerous reports of branchless or nearly branchless trees among pines planted in tropical and sub-tropical areas, chiefly Africa and Latin America (table 6), have cropped up in recent years. Such trees are called foxtails—a term coined by Lloyd (1914). Except for the reports by Lloyd and by Kummerow (1962) there have been no serious efforts to describe such trees, so it is necessary to describe here in some detail a typical foxtail of Monterey pine.

Monterey Pine

Morphological Features

This Monterey pine foxtail was planted at Kulani Camp, Hawaii, in August 1958 and cut in March 1964. It was then 22 feet tall, and had several whorls of branches or branch scars between the base and 3.5 feet above ground (figs. 7, 12).

The shoot.—The terminal shoot had no branch scars or lateral buds over its entire 18.5-foot unbranched length. The only sterile-scale zone was

just above the branch whorl at the base of the foxtail. Thus, most of the shoot consisted entirely of the elongated internodes⁴ between dwarf shoots. The foxtail bore about 3,200 needle fascicles between the basal sterile-scale zone and a point several inches below the tip. The shoot tapered very gradually as it was only 3 inches in diameter at the stump.

Along a 4-foot section of the trunk starting 2 feet above the ground, nearly all of the needle fascicles had proliferated (fig. 8), giving that portion of the stem the bearded appearance remarked upon by Lloyd (1914) and Kummerow (1962). Most of the branches arising in this way were only a few inches long, but occasionally branches up to 3 feet long have been encountered. In one case such a branch was found bearing male cones.

⁴Internode" is used in the strict botanical sense to refer to the portion of a stem between the points of attachment of successive lateral appendages, not the space between branch whorls. In this case it is the portion of the shoot between successive needle bundles.

Table 6.--Reports of branchless pines or long leaders.

Species	Location	Length of branchless stem (feet)	Reference
Canary Island pine (<i>P. canariensis</i> C. Smith)	Kenya, Nyasaland, Tanganyika	--	Anonymous 1962
Caribbean pine	Argentina	--	Golfari 1963 ^{1/}
	British Honduras	up to 10	Anonymous 1962
	Kenya, Tanganyika	--	Anonymous 1962
	Northern Rhodesia	up to 35	Anonymous 1962
	Trinidad and Tobago	20	Streets 1962
	Transvaal, Zululand	up to 50	Poynton 1957
	Hawaii	12	ff. this paper
Chihuahua pine	Kenya	--	Anonymous 1962
Chir pine	Kenya, Nyasaland	--	Anonymous 1962
Khasi pine	Kenya, Northern Rhodesia, Tanganyika	--	Anonymous 1962
	Nyasaland	--	Anonymous 1962
	Hawaii	9	ff. this paper
Longleaf pine	British Honduras	--	Anonymous 1963
	Hawaii	42	Skolmen 1963 ^{1/}
	New Zealand, Southern Rhodesia	--	Streets 1962
Masson pine	Kenya	--	Anonymous 1962
Merkus pine (<i>P. merkusii</i>)	Northern Rhodesia Vietnam ^{2/}	-- ^{3/} 10	Anonymous 1962 Gaussen 1960 ^{1/}
Mexican pinyon (<i>P. cembroides</i> Zucc.)	Arizona ^{2/} Nyasaland	4 --	Phillips 1911 ^{1/} Anonymous 1962
Mexican weeping pine			
Michoacan pine (<i>P. michoacana</i> Martinez)	Northern Rhodesia	--	Anonymous 1962
Monterey pine	Australia Brazil California ^{2/} Colombia, Peru Hawaii Kenya New Zealand Nyasaland, Tanganyika California ^{2/}	up to 17 -- -- up to 22 up to 19 up to 20 up to 20 -- 15.8	Fielding 1960 ^{1/} Golfari 1963 Lloyd 1914 ^{1/} Kummerow 1962 ^{1/} ff. this paper Anonymous 1962 Streets 1962 Anonymous 1962 Institute of Forest Genetics 1933 ^{1/}
	California ^{2/} Austra- lia and New Zealand	12	Scott 1960
Montezuma pine	Northern Rhodesia Tanganyika	-- up to 8	Anonymous 1962 Anonymous 1962
Pseudostrobus pine (<i>P. pseudostrobus</i> Lindl.)	Nyasaland	--	Anonymous 1962
Slash pine	Fiji, Kenya, Mauritius, Nyasaland, Tanganyika	--	Anonymous 1962
	Florida ^{2/} (var. densa Little and Dorman)	--	Little and Dorman 1954 ^{1/}
Tropical pine (<i>P. tropicalis</i> Morelet)	Isle of Pines ^{2/}	^{3/} 10	Little and Dorman 1954 ^{1/}
West Indian pine	Kenya	--	Anonymous 1962

¹Appropriately illustrated.²Trees were growing within natural range.³Estimated from photograph.



Figure 7.—Monterey pine foxtail at Kulani Camp, Hawaii. The tree, 5½ years after planting, was 22 ft. tall, with 18½ ft. of unbranched leader.

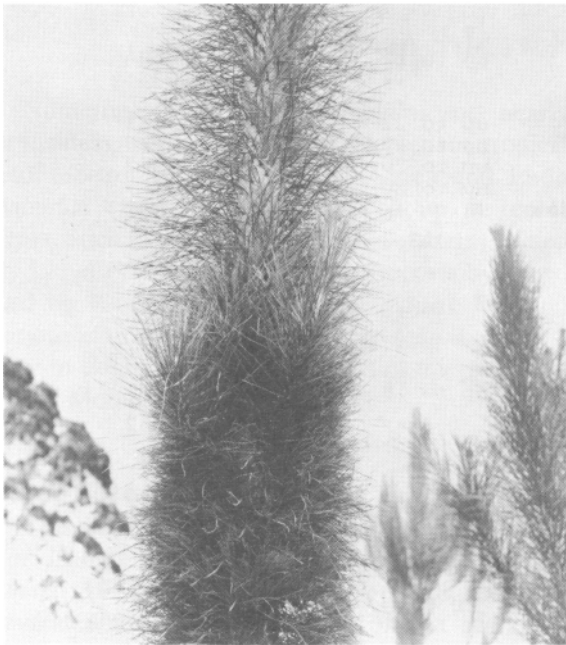


Figure 8. — Proliferated dwarf shoots on a Monterey pine foxtail give it a characteristic appearance.

The spacing of needle fascicles along the foxtail was regular. In normal annual shoot increments of pines (Bannister 1962; Debazac 1963), grapevines (Gard 1900), eucalypts (Carr and Carr 1959), *Ribes* (Haskell and Wills 1963), and several other genera (Busgen and Munch 1929), the distance between nodes varies systematically. At the base of the shoot, internodes are short, in the middle they are longer, and at the distal end they again shorten. But if the distances between lines of phyllotaxy intersecting a hypothetical orthostichy on the woody portion of a foxtail are plotted, the result is a nearly straight line (fig. 9).

The branches.—All but the uppermost whorl included fine wire-like branches that were probably already present when the seedling was planted or that elongated soon after. The uppermost whorl had the only strong branches on the tree, but the longest of these was only 5 feet long. Each branch of the upper whorl had at its base a zone of sterile scales, then a short portion along which the dwarf shoots had proliferated, and finally a needled portion. Some branches were further ramified, but several were unbranched in the manner of the foxtail itself.

The terminal bud.—In contrast to the conventional pine bud the terminal bud of a foxtail consisted only of primary leaves subtending needle fascicles. The needles decrease in length as the summit is approached. Despite the lack of sterile bud scales the terminal bud was brown due to the

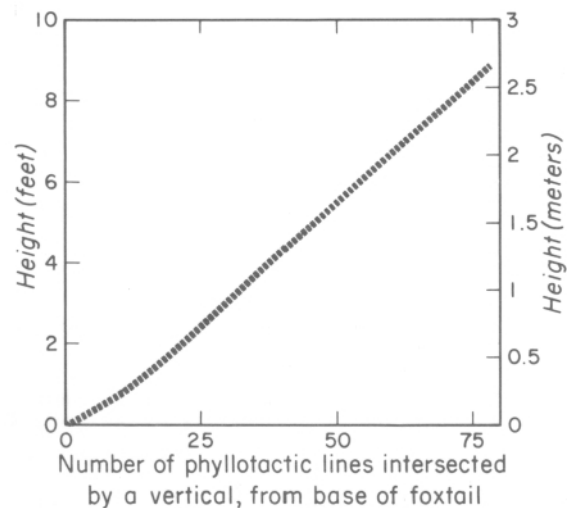


Figure 9.—Cumulative distance, by lines of phyllotaxy, along the woody portion of a Monterey pine foxtail. Starting point is 3 ft. above highest branch whorl.

overlapping primary leaves (fig. 10). The foxtail bud is analogous to the central portion of a conventional pine bud during the period of shoot elongation, but it looks the same all year round. It has no grand period flush so there is never a long, bare, limber shoot at the top of the leader.

The needles.—The needles of foxtails attain lengths much greater than is encountered in this species' natural range in California. According to Forde (1964) needles of Monterey pine population samples ranged from 7 to 18 cm. in length. Sample means varied from 11 to 15 cm. A typical foxtail from Kulani, however, had needles ranging in length from 14.5 to 23 cm., and the mean length of 100 needles was 20.0 cm. These were in fascicles of 3, 4, and 5. On the limbs of the foxtail-bearing trees, needles are of normal size; especially if these branches are themselves branched. The short branches arising through proliferation of dwarf shoots also carry needles of normal dimensions.

Wood anatomy.—Several foxtails were cut and their wood examined. The sections examined ranged from 2 to 5 inches in diameter and were at least 5 years old—yet not a single definite ring was visible (fig. 11).

The wood specimen shown in figure 11 was studied with a stereomicroscope at 100x. The smoothed transverse section was projected by a camera lucida on squared paper, and the number of tracheids in a radial file that occupied successive squares were counted. A total of 1,727 tracheids were counted along a composite radius extending from just outside the pith to the cambium. Viewed in the camera lucida, there were 6 to 9 tracheids along the side of each square. Taking the tracheids along each square as a single sample, mean tracheid diameter varied from 29 to 43 micra. The standard deviation of 218 samples was 0.36; the coefficient of variation was 0.045.

These extremely low values attest to the striking uniformity of tracheid diameter within foxtail wood formed during 5½ years. None of the tracheids seen had the tangential flattening of typical latewood cells, nor was there any discernible rhythm in tracheid diameter.

It is true that within the "juvenile core" of some pines the latewood zone is very narrow (Larson 1962), but in Monterey pine grown in California the annual rings are distinctly visible all the way to the pith (fig. 12). So the lack of latewood bands in the foxtails cannot be attributed to juvenile core characteristics. Actually, the wood of the ju-

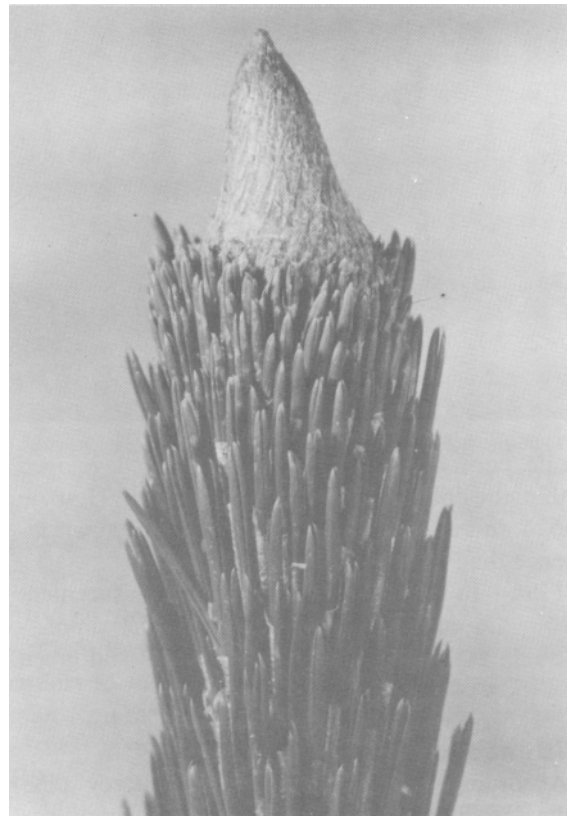


Figure 10.—*Tip of a Monterey pine foxtail showing the continuous series of scales subtending needle fascicles, and the absence of sterile bud scales. This tip was photographed in March, but appears the same all through the year while growth is continuous.*

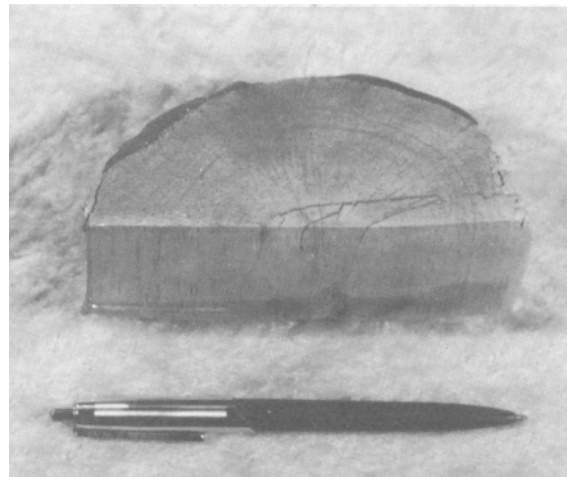
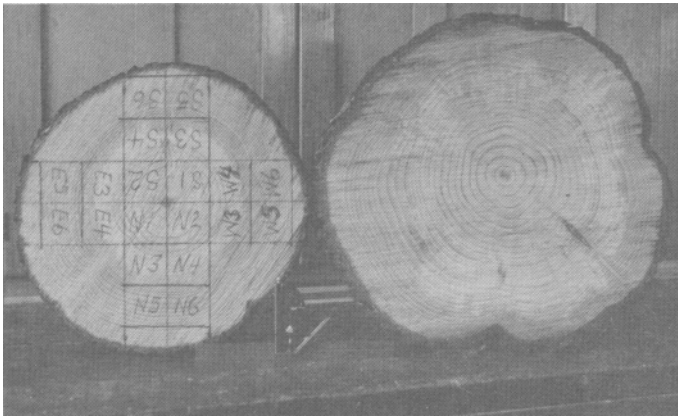
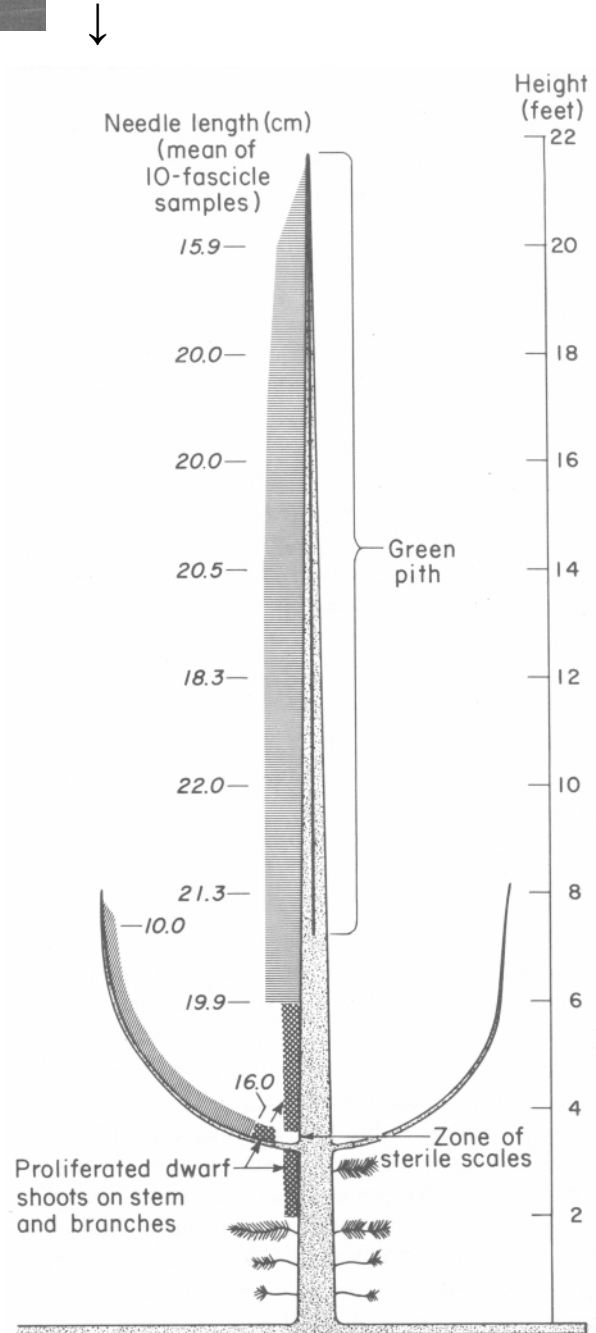


Figure 11.—*An example of foxtail wood.*



←
Figure 12. — *Monterey pine* from its native California habitat.

Figure 13.—Diagrammatic representation of a *Monterey pine* foxtail.



venile core is merely wood that has developed within the influence of an active crown (Larson 1962) and is a less extreme example of crown influence than is foxtail wood.

Pith.—In several foxtails the pith was succulent within the entire needled portion of the shoot—as much as 16 feet down from the tip—and green over most of this length (fig. 13).

Evidence of Continuous Growth

According to Shreve (1924) *Monterey pine* elongates slightly during the winter even in its native habitat. But this is not continuous growth as defined by Romberger (1963) and as understood here.

The evidence for continuous growth is all indirect, but in light of its consistency it is compelling nevertheless. In discussing implications of episodic growth, Romberger (1963, p. 76) reported that:

"If growth is to be continuous, development of primordia must be controlled so that scales are not formed or do not accumulate. In addition meristematic activity must persist in the subapical region. Continuous growth requires a delicate balance between initiation and development of primordia and elongation of internodes."

This passage describes precisely the conditions in a foxtail. During the period when foxtails are growing, no bud scales are produced, nor are sterile scales or lateral long shoots. The absence of these is evidence that a foxtail is branchless because *branch primordia have not been formed*. These structures have not been formed because the tree is in a "morphogenetical steady state," so to speak, and produces primary leaves subtending dwarf shoot primordia and only dwarf shoot primordia for a period far in excess of a normal season's growth. How long this condition can persist is not known, but some foxtails at Kulani Camp have

almost certainly not produced any axillary structures, except dwarf shoots for 6 years. It should be evident that foxtails satisfy Romberger's first criterion in not forming or accumulating scales.

Does meristematic activity persist? There are several reasons for believing it does. The appearance of the shoot tip is suggestive (fig. 10). Throughout the year, needles of all sizes and stages of development may be found. The shoot tip itself is made up of tightly packed needles still within their unbroken sheaths. Below these are needles penetrating the sheaths and needles free of their sheaths and gradually increasing in size until an abnormal length is attained. The progressive increase in needle size, culminating in proliferation of the interfoliar bud, also suggests continuous growth.

The significance of succulent and green pith is not entirely clear. According to Esau (1953) mature pith is normally devoid of chlorophyll.

Coordination of Growth Activities

The extension of shoots, formation of early and latewood, initiation of primordia, emergence of cones, elongation of needles—each of these events takes place at a particular time relative to the occurrence of the others. They normally occur in specific relation to the calendar—there is a time of year (season) for these activities. The pattern in Monterey pine foxtails is obscured by their bizarre appearance, but nevertheless, these trees are in a certain stage of growth. And the several activities in these foxtails are in synchrony with each other if not with the calendar.

Figure 14 shows the nature of this internal coordination. The curve is the S-shaped height-growth curve obtained by measuring a normal shoot periodically during the growing season and plotting its total height at each time. Such a curve exemplifies normal episodic growth. Stages I, II, and III represent the slow start of elongation, the grand period of height growth, and the onset of dormancy. In the accompanying chart three growth activities are correlated in time with these stages of shoot growth. The cited data pertain to other species of *Pinus*; no such studies having been made of Monterey pine.⁵ If we hypothesize that

⁵The timing of needle primordium initiation in *P. resinosa* differs from that of *P. ponderosa* and *P. lambertiana* (Duff and Nolan 1958). Until comparative studies in the genus clarify the variation in the morphogenetic sequence, it seems useful to retain the generalized model used here.

the apical meristem of a foxtail remains in the late stage II condition, the continued production of dwarf shoots, the laying down of earlywood, and the sustained growth of the needles can be put into a meaningful context. Under this hypothesis, the growth rate of a foxtail could be expected to be rather steady without a typical grand period flush: this condition is indicated by the dashed line tangent to the S-shaped curve. Field observations of foxtails at Kulani during every month of the year were consistent with this expectation. A consequence of the steady growth rate of foxtails was the absence of stem kinks caused by leader flop (Jacobs 1938), and the temporary collapse of long, limber, top-heavy leaders. Sinuous curves were common but these were probably due to wind pressure.

Environmental Factors

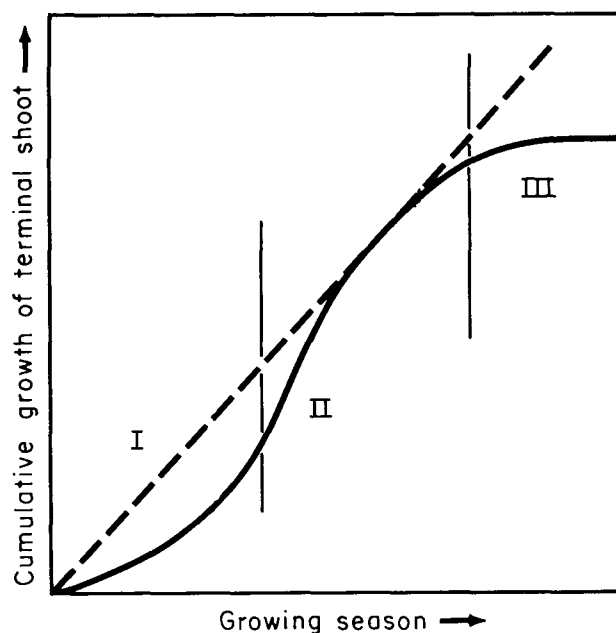
Only two reports in the literature give enough details to make it certain that they concern foxtails. Kummerow (1962) described Monterey pine foxtails planted in the Andes of Colombia and Peru.

Lloyd (1914) reported on a Monterey pine foxtail growing in a yard at Carmel, California.

The Colombian and Peruvian plantations reported on by Kummerow were 5–8° from the equator and the Chilean seed source was at 33° S. latitude. Although he included the possibilities of mutation or injury by insects or pathogens, Kummerow thought photoperiod was responsible for the development of foxtails. The Chilean plantation is in a strongly seasonal climate, with a marked dry season; the Colombian and Peruvian plantations grew in areas of relatively little seasonal change. Thus he reasoned that photoperiod rather than seasonal change would act as a growth control factor.

The foxtails described by Lloyd grew close to a cesspool. Several other trees with proliferating dwarf shoots grew near springs. Lloyd suggested that abundance of water and possibly nitrogen was responsible for the proliferation of dwarf shoots and the branchless stem. Lloyd was uncertain whether branchlessness was due to abortion of buds or failure to initiate branch primordia. Neither Lloyd nor Kummerow attributed foxtails to continuous growth. Lloyd's report of foxtailing at about 36° N. under conditions of abundant soil moisture appears to conflict with Kummerow's interpretation.

Foxtailing can be readily understood if it is rec-



	Stage of Terminal Shoot Activity		
	I	II	III
Primordia being initiated at apex: <i>P. ponderosa</i> and <i>P. lambertiana</i> (Sacher 1954)	Sterile scales	Dwarf shoots	Lateral long shoots and bud scales
Type of wood formed (Larson 1962)	Earlywood	Earlywood	Latewood
Stage of needle activity: <i>P. resinosa</i> (Kienholz 1934)	Not yet elongating	Growth starting, rapidly reaching a peak	Growth slowing

Figure 14.—Generalized model showing relationship of growth activities in pines and the annual growth cycle.

ognized as the result of continuous growth. Of special importance is the fact that foxtailing occurs only in some trees, and that it probably does not persist in any of them for the life of the tree. Thus, the factors that permit continuous growth are not permanent but transient. In the locations where Monterey pine foxtails have been studied, photoperiod of course follows the same pattern every year. Temperatures vary but little from year to year, and are seldom low enough to stop growth for more than a few hours at a time. Rainfall, however, can vary considerably both within and between years, at any location.

The role of abundant rainfall in sustaining continuous growth is made apparent by comparing growth and rainfall data for two Monterey pine

plantations in which foxtailing has been observed. These plantations were established within 3 months of each other—the Kulani stand in August, and the Olinda stand in November 1958.

The Olinda Plantation.—The Olinda stand was inspected and measured about 3 years after planting by N. H. Cheatham, of the Hawaii Forestry Division, Kahului, Maui. At that time at least 18 percent of the stand (spacing plot 33) was noted as unbranched above stump height and at least 11 feet tall. During this period of foxtailing mean monthly rainfall was 4.36 inches; the longest drought was a 7-month period when mean monthly rainfall was 1.77 inches. For the purpose of this report "drought" months are those in which rainfall was less than 4 inches (table 7).

When I inspected this plantation in January 1964, I found that all of the original 29 foxtails had branched. During this period of branching, mean monthly rainfall (for 27 months) had declined to 3.53 inches. But there had been an 8-month drought during which monthly rainfall averaged only 0.85 inches. For the 62 months elapsed since planting mean monthly rainfall was 3.99 inches.

The Kulani Plantation.—In January 1964 this stand contained about 20 percent foxtails. In the 65 months after planting, the most severe drought was a 3-month period when monthly rainfall averaged 1.33 inches—far less severe than either of the Olinda droughts. Monthly rainfall for the entire period averaged 7.82 inches, almost twice that at Olinda (table 8).

This comparison supports the hypothesis that an

Table 7.--Rainfall at Olinda, Maui, during the early years of a Monterey pine plantation in which foxtails were common in October 1961 but absent in January 1964.

Month	1958	1959	1960	1961	1962	1963
	<i>Inches</i>					
January	--	17.87	1.08	5.83	2.03	7.13
February	--	8.55	15.50	9.13	2.70	2.62
March	--	1.16	5.23	.09	4.01	4.92
April	--	5.90	3.12	10.58	.05	9.85
May	--	2.53	3.17	3.18	1.51	9.12
June	--	.06	1.56	1.67	.17	2.55
July	--	1.73	1.22	1.42	.30	2.89
August	--	2.87	.72	1.65	.87	3.03
September	--	2.23	1.79	.75	1.23	5.08
October	--	.39	.81	5.11	.24	3.48
November	3.60	11.16	4.91	8.20	2.41	4.52
December	7.31	9.99	3.78	2.32	6.53	2.54
Total	10.91	64.44	42.89	49.93	22.05	57.73
	Period of foxtailing			,Period of branching		

Table 8.--Rainfall at Kulani Camp, Hawaii, during the early years of a stand in which foxtails were still common at the end of the period.

Month	1958	1959	1960	1961	1962	1963
	<i>Inches</i>					
January	--	17.57	15.10	1.46	1.00	3.13
February	--	14.95	11.37	17.14	3.59	2.01
March	--	5.57	9.48	6.62	7.54	17.07
April	--	8.11	15.11	5.43	3.29	41.35
May	--	6.47	6.75	4.15	5.06	13.07
June	--	1.33	3.24	2.17	^{1/} .32	7.07
July	--	5.56	2.48	4.13	^{1/} 2.09	12.83
August	16.55	11.35	9.04	4.47	^{1/} 1.58	4.35
September	3.44	4.16	5.66	3.95	5.48	5.04
October	8.02	3.26	3.65	14.44	3.35	3.42
November	10.91	14.42	16.05	17.80	3.74	5.37
December	2.41	13.70	2.56	20.95	5.07	.50
Total	41.33	106.45	100.49	102.71	42.11	115.21

¹Drought.

abundance of rainfall permitted certain trees to grow continuously. Such growth was arrested by drought which induced the formation of a terminal bud complete with long-shoot primordia. In terms of the scheme in figure 14, while rainfall was abundant, the foxtail leader remained in stage II; moisture stress induced the shoot to enter stage III.

Further support to the hypothesis is lent by measurements of tree 29 at Olinda. Assuming a steady rate of growth between the times this tree was measured in 1961 and 1964 it appears that its single whorl of branches emerged about May 1963. Allowing several months for the elongation of previously formed internodes between formation and unfolding of the lateral long shoots, it seems likely that the long-shoot primordia were formed in response to the drought of April–November 1962.

The importance of abundant moisture in permitting continuous growth is also suggested by Scott's (1960) comment that very long leaders ". . . 12 feet or more, with no side branches" were common among Monterey pines planted in warm parts of California and irrigated. Earlier, Chamberlain (1935) had written that near Jalapa, Mexico (Tabasco State) trees growing in forests "wet throughout the year" had no well-defined annual rings. But individuals of the same species just a few miles away, where there were alternating wet and dry seasons, showed clear growth rings.

Monterey pine is notorious for its great genetic variability (Fielding 1953, 1960; Syrach Larsen 1956) despite its restricted natural range. Fielding (1960) has demonstrated genetic variation in the number of whorls per annual shoot increment. He has shown that while most trees produce several whorls per year some produce only one whorl per year. Perhaps the so-called "uninodal" trees are the ones that produce foxtails. Such a tree would have fewer opportunities to make lateral branch primordia instead of short-shoot primordia. Environmental conditions (droughts) necessary to bring about this changeover would have to occur more often than in the case of multinodal trees in order to favor branching. In the strongly multinodal trees the opportunity to respond to a drought would occur more often and would be more likely to coincide with one.

At Kulani Camp after almost 6 years in plantation many trees were still unbranched. The other trees showed the full range of branching habit from foxtails that had just put on the first whorl since seedling days to trees averaging more than two

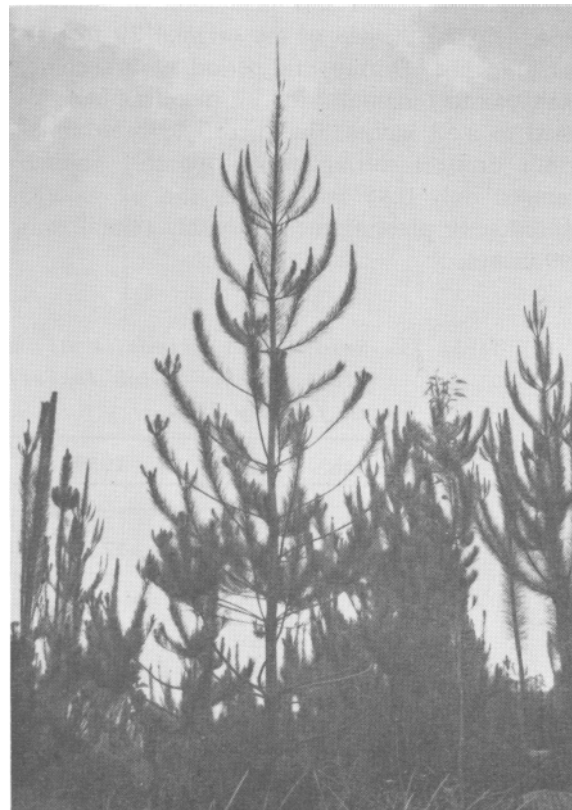


Figure 15.—*Strongly multinodal Monterey pine at Kulani Camp, Hawaii.*

whorls per year (fig. 15). Unfortunately, little time was devoted to the study of these more nearly normal trees. The presence of branches shows that the leaders of these trees do not grow continuously in the sense that the foxtails do, but some of the limbs may grow continuously for several years before producing branches of the second order (fig. 15). During this period the branch tips are similar to the tip shown in figure 13. An increment core from the base of such a tree was similar to those from foxtails in lacking latewood. Perhaps the formation of latewood is inhibited by continuous growth anywhere in the crown. Further study is needed to clarify this point.

Silvicultural Considerations

Should foxtails be regarded as desirable forms or as poor ones? At present this question cannot be answered, as evidenced by confusion in the minds of foresters of many countries (Anonymous 1962). The few small plantations of Monterey pine in Hawaii have not been subjected to silvicultural treatment or study. Present planting plans in Hawaii do not indicate any great enlargement of

the acreage of pines so this is not a matter of importance there. But the likelihood that Monterey pine will be planted in other areas of the world under similar environmental conditions lends interest to this question.

It is true that spectacular lengths of clear stem can be obtained. But these may be associated with larger and steeper-angled branches if it is the so-called "uninodal" trees that tend to form foxtails (Fielding 1960). The fact that only earlywood is produced during the foxtail period would seem to argue against retaining such trees in the stand. Height measurements at Olinda showed that 3 years after planting the average height of the entire stand of 158 trees was 12.4 feet while the average height of the 29 foxtails in that stand was 12.3 feet, an insignificant difference. Breast-height diameter averaged 2.0 inches for the entire stand and 1.9 inches for the current foxtails, again an insignificant difference. Stem crooks are common among foxtails, but as explained above, they may not be serious. Perhaps further crooks result from heavy branching above a long foxtail that has ceased continuous growth. The silviculturist would have to make his own determination under his own local conditions if he were managing plantations in which foxtailing is rampant.

Most of the Monterey pines seen in these studies were less than 10 years old. And it was in the younger stands that foxtails were most apparent. Without exception the foxtails had whorls of branches on the lower portion of the trunk in positions that indicate those branches were either

present when the trees were planted or elongated shortly afterwards. No signs of foxtailing were seen in Monterey pines in the nursery. Therefore selection for or against continuous growth cannot be accomplished in the nursery unless the seedlings are permitted to remain at least 2 years.

Foxtails of Other Species

Foxtails were also found in a small plantation of Khasi pines at the Waiakea Arboretum. These trees were examined in April 1964, about 4 years after planting (Richmond 1963). Several showed evidence of continuous leader growth and others had continuously growing laterals.

The buds of these trees are similar in appearance to those of Monterey pine foxtails and the shoot is similar in structure (fig. 16) but lacks proliferated dwarf shoots.

At Olinda, Maui, several foxtails were observed in a plantation of 7-year-old Caribbean pine of Honduran origin. A review of published photographs leads me to conclude that foxtails develop on Merkus pine in Vietnam (Gaussen 1960) and on Caribbean pine in Argentina (Golfari 1963).

The term "foxtail" has been used indiscriminately in the British Commonwealth (Anonymous 1962). This practice is also true of several zoomorphic terms in New Zealand and what is called "furry fishing rod" in Kenya. I suggest that the term foxtail be used only for trees in which long-sustained continuous growth has prevented branches from forming.

"False Foxtails"

Some branchless trees do not develop from morphogenetically continuous growth, but rather through the abortion of lateral branch buds. To distinguish these trees, I suggest calling them "false foxtails." By applying some of the same morphological, anatomical, and phenological criteria that aided in understanding foxtails, the nature of false foxtails has also been resolved.

The following description is a composite of several slash and longleaf pines growing on a variety of sites in Hawaii.

Morphology

Shoot.—The terminal shoot bears the alternating series of bud scale scars, sterile scales, and dwarf shoots found on a normal stem. At the base

of each sterile-scale zone is usually a whorl of lateral buds that are much reduced in size and still dormant if not aborted (fig. 17). In the Waiakea Arboretum, 10 lateral buds were recovered from three whorls of a branchless 4-year-old slash pine. Eight of these were merely empty shells consisting of bud scales whose contents had withered; the other two were still alive but dormant and small.

Terminal bud is normal in all respects. During the winter it is enclosed in sterile bud scales and in spring it undergoes a typical grand-period flush.

Needles.—In several cases needles from false foxtails have been measured and found to fall within the range of normal length for the species.

Wood anatomy.—Increment cores have been taken from a false foxtail of longleaf pine of

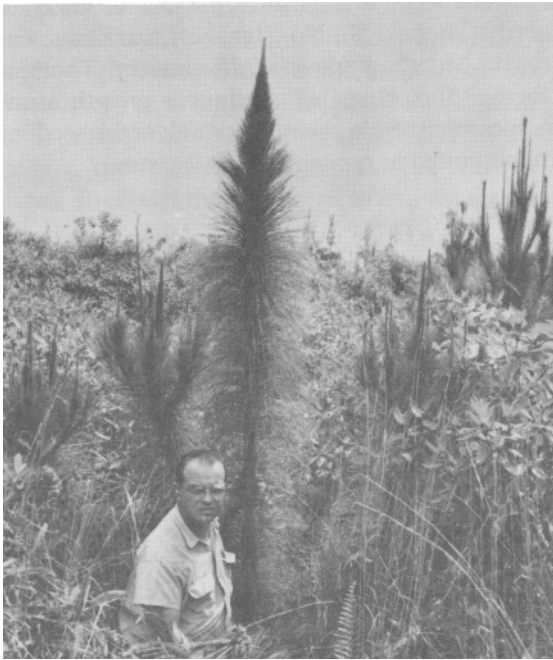
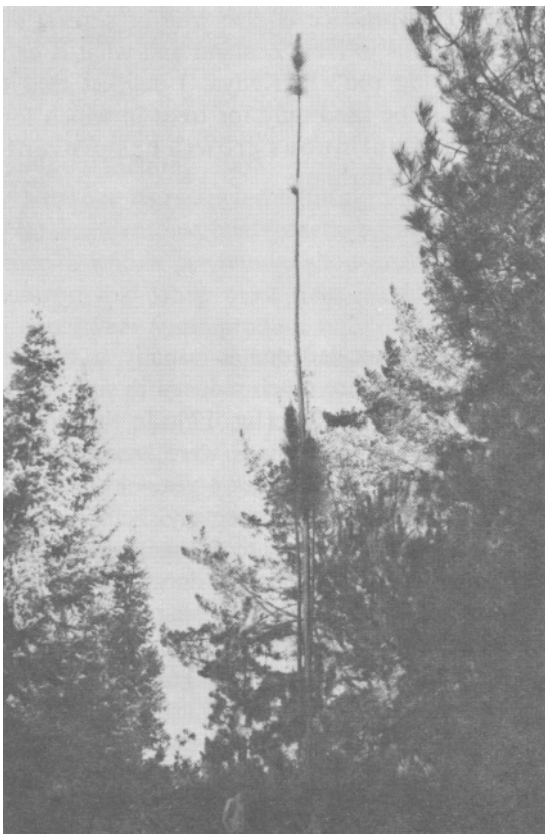


Figure 16.—Foxtail of Khasi pine (*P. insularis*) at Waiakea Arboretum, April 1964.



Figure 17.—A false foxtail of *Pinus palustris* at Waiakea Arboretum, November 8, 1963. The exposed portion of the stem is covered with sterile scales which have never borne needle fascicles. At the base of this zone is a whorl of aborted buds and branches, one of which is visible in silhouette on the right side.



←

Figure 18.—False foxtail of *P. palustris*, Keanakolu, Hawaii.

known age. The number of distinct latewood bands corresponded closely with the age of the tree, suggesting truly annual growth.

Cyclic or episodic growth.—The differences between the two types of branchless trees are indicated by the presence of bud scales, sterile-scale zones, lateral buds on the stem, zonation of the wood, normal needle length, and phenological data on the species in which false foxtails have been observed.

False foxtails result not from the absence of lateral buds, but from failure of the buds to elongate. They grow cyclically, not continuously.

Causes

Despite the failure of lateral buds to elongate, the branchless leaders themselves are entirely normal in their morphology and development. Diameter growth is retarded, but this is to be expected because the only foliage available to carry on photosynthesis is that borne on the leader. The needles live for only a few years so as the tree grows the amount of foliage diminishes in relation to the surface area of cambium it must support. Even though diameter growth becomes progressively less, it is remarkable that these trees can live as long as they do—up to 30 years in the case of the longleaf pine at Keanakolu (fig. 18).

Examination of published photographs shows that some of the branchless trees reported in the literature are false foxtails. These include Mexican

pinyon (Phillips 1911) and South Florida slash pine (Little and Dorman 1954). In the southeastern United States, there are occasional longleaf, slash, and loblolly pines in which the lateral branches have failed to develop.⁶ These and other branchless southern pines grown abroad (Anonymous 1962; Poynton 1957; Streets 1962) also are probably false foxtails, as this group of pines seems especially prone to this growth habit. The tropical pine illustrated in the bulletin by Little and Dorman (1954, p. 25) is probably a false foxtail judging from the appearance of its terminal bud. And most of the "foxtails" mentioned in the Forestry Newsletter (Anonymous 1962) are probably false foxtails too, as most of them are reported from regions with a pronounced dry season that would not permit continuous growth.

False foxtails therefore result from the wholesale inhibition, dormancy, or abortion of lateral buds. The growth habit is most obvious in trees where this happens year after year, but there may be trees that "miss" a whorl only occasionally. Such trees might be of interest to tree breeders and would also seem to be helpful in the study of bud inhibition and suppression. The presence of dormant buds in the whorls of pines is of course well-known (Stone and Stone 1943). And perhaps the false foxtail results merely from an intensification of whatever factors cause them.

⁶ Personal correspondence with Keith W. Dorman, U.S. Forest Service, July 1, 1963.

Literature Cited

- Anonymous.
1962. **"Foxtail" in young pine trees.** Forest Newsletter, Great Britain Dep. Tech. Co-op. (London) Append. D, 9 pp.
- Bannister, M. H.
1962. **Some variations in the growth pattern of *Pinus radiata* in New Zealand.** New Zeal. J. Sci. 5(3): 342-370, illus.
- Black, T. M.
1961. **Abnormalities of the reproductive system of *Pinus contorta* Loudon.** Ann. Bot. 25(97): 21-28, illus.
- Blumenstock, David I.
1961. **Climates of the states. Hawaii.** Climatography of the U.S. No. 60-51. U.S. Dep. Commerce, Weather Bur., 20 pp., illus.
- Britten, E. J.
1962. **Hawaii as a natural laboratory for research on climate and plant response.** Pacific Sci. 16(2): 160-169, illus.
- Büsgen, M., and Münch, E.
1929. **The structure and life of forest trees.** Engl. transl. by T. Thomson. 486 pp., illus. New York: John Wiley & Sons, Inc.
- Canada Department of Forestry
1963. **Native trees of Canada.** Bull. 61, 291 pp., illus. Ottawa.
- Carr, D. J., and Carr, Stella G. M.
1959. **Developmental morphology of the floral organs of *Eucalyptus*. 1. The inflorescence.** Austral. J. Bot. 7(2): 109-141, illus.
- Chalmers, W. S.
1962. **The breeding of pine (*Pinus caribaea* Mor.) and teak (*Tectona grandis* L.) in Trinidad—some early observations.** Caribbean Forestry 23(2): 100-111, illus.
- Chamberlain, C. J.
1935. **Gymnosperms, structure and evolution.** 484 pp., illus. Chicago: Univ. Chicago Press.
- Critchfield, William B., and Little, Elbert L., Jr.
1966. **Geographic distribution of the pines of the world.** U.S. Dept. Agr. Misc. Publ. 991, 97 pp., illus.
- Cumming, W. C., and Righter, F. I.
1948. **Methods used to control pollination of pines in the Sierra Nevada of California.** U.S. Dep. Agr. Circ. 792, 18 pp., illus.
- Debazac, E. F.
1963. **Morphologie et sexualité chez les pins.** Rev. Forestiere Franc. 15(3): 293-303, illus.
- Doak, C. C.
1935. **Evolution of foliar types, dwarf shoots, and cone scales of *Pinus*.** Ill. Biol. Monogr. 13, 106 pp., illus.
- Dorman, K. W., and Barber, J. C.
1956. **Time of flowering and seed ripening in southern pines.** U.S. Forest Serv. Southeast. Forest Exp. Sta. Paper 72, 15 pp., illus.
- Duff, G. H., and Nolan, Norah J.
1958. **Growth and morphogenesis in the Canadian forest species. M. The time scale of morphogenesis at the stem apex of *Pinus resinosa*** Ait. Canad. J. Bot. 36: 687-706, illus.
- Duffield, J. W.
1953. **Pine pollen collection dates—annual and geographic variation.** U.S. Forest Serv. Calif. Forest & Range Exp. Sta. Res. Note 85, 9 pp., illus.
- Esau, Katherine.
1965. **Plant anatomy.** Ed. 2, 767 pp., illus. New York: John Wiley & Sons, Inc.
- Fielding, J. M.
1953. **Variations in Monterey pine.** Australia Forestry & Timber Bur. Bull. 31, 43 pp., illus.
- _____.
1957. **Notes on the dispersal of pollen by Monterey pine.** Austral. Forestry 21(1): 17-22.
- _____.
1960. **Branching and flowering characteristics of Monterey pine.** Australia Forestry & Timber Bur. Bull. 37, 59 pp., illus.
- Forde, Margot B.
1964. **Variation in natural populations of *Pinus radiata* in California. Part 2. Needle characters.** New Zeal. J. Bot. 2(3): 237-257, illus.
- Gal'pern, G. D.
1956. **Sexual variability in certain species of pine.** Glav. Bot. Sad AN SSSR Bull. 24: 58-63. OTS Transl. 61-11427, 9 pp., illus.
- Gard, M. R.
1900. **Sur les variations de la structure anatomique considérée dans la série des entre-noeuds d'un rameau d'un an.** Soc. Linn. Bordeaux Act. Compt. Rend. 55: 117-122.
- Gaussen, H.
1960. **Les gymnospermes actuelles et fossiles. Fasc. VI, chap. XI, Generalites, genre *Pinus*.** Trav. Lab. Forestiere Toulouse. T. II, sec. I, vol. I, part II, 272 pp., illus.
- Golfari, Lamberto.
1963. **Climatic requirements of tropical and subtropical conifers. The behavior of certain exotic pines, mainly in Latin America.** Unasylva 17(1): 33-42, illus.
- Haskell, Gordon, and Wills, Anthony.
1963. **Ideograms for exploring the taxonomy, evolution and genetics of plants.** Nature 198 (4885): 1072-1074, illus.
- Hodgson, L. M.
1963. **Initiating a breeding programme with *Pinus patula* in Southern Rhodesia.** FAO World Consult. on Forestry Gen., Stockholm, 7 pp.
- Institute of Forest Genetics, U.S. Forest Service.
1933. **Science seeks new trees for the forests of the future.** Placerville, Calif., 23 pp., illus.
- Jacobs, M. R.
1937. **The detection of annual stages of growth in the crown of *Pinus radiata*.** Comm. Forestry Bur. Bull. 19, 16 pp., illus.

- Jacobs, M. R.
1938. **Notes of factors influencing the straightness of the internodes of *Pinus radiata*.** Austral. Forestry 3(2): 78-84, illus.
- Kienholz, R.
1934. **Leader, needle, cambial, and root growth of certain conifers and their interrelations.** Bot. Gaz. 96: 73-92, illus.
- Koriba, Kwan.
1958. **On the periodicity of free-growth in the tropics, with reference to the mode of branching, the leaf-fall, and the formation of the resting bud.** Gardens' Bull. Singapore 17(1): 11-81, illus.
- Kummerow, J.
1962. **Über Wachstumsanomalien bei *Pinus radiata* unter tropischen Bedingungen.** Bericht. Deutschen Botanischen Gesellschaft 75(2): 37-40, illus.
- Lanner, Ronald M.
1963. **Growth and cone production of knobcone pine under interrupted nights.** U.S. Forest Serv. Pacific SW. Forest & Range Exp. Sta. Res. Note PSW-38, 16 pp., illus.
- Larson, Philip R.
1962. **A biological approach to wood quality.** TAPPI 45(6): 443-448.
- Little, Elbert L., and Dorman, Keith W.
1954. **Slash pine (*Pinus elliotii*), including south Florida slash pine. Nomenclature and description.** U.S. Forest Serv. Southeast. Forest Exp. Sta. Paper 36, 82 pp., illus.
- Lloyd, Francis E.
1914. **Morphological instability, especially in *Pinus radiata*.** Bot. Gaz. 57: 314-319, illus.
- Masters, Maxwell T.
1890. **Review of some points in the comparative morphology, anatomy, and life-history of the coniferae.** J. Linn. Soc. (London) 27: 226-332, illus.
- Mergen, Francois.
1963. **Sex transformation in pine hybrids.** Forest Sci. 9(3): 258-262, illus.
- Mirov, N. T.
1962. **Phenology of tropical pines.** J. Arnold Arboretum 43: 218-219.
1956. **Photoperiod and flowering of pines.** Forest Sci. 2(4): 328-332, illus.
- Neubauer, H. F.
1960. **Über eine Zapfenkolonie bei *Pinus merkusii*.** Willdenowia 2(4): 598-601, illus.
- Norskov-Lauritsen, G.
1963. **Notes on the growth habits of the main pine species of the eastern Transvaal region.** Forestry in S. Afr. 3: 67-82, illus.
- Phillips, E. J.
1911. **Conifers without normal whorls.** Plant World 14: 66-69, illus.
- Poynton, R. J.
1957. **Notes on exotic forest trees in South Africa.** Ed. 2. Dep. Forestry Bull. 38, 135 pp.
- Richmond, George B.
1963. **Species trials at the Waiakea Arboretum, Hilo, Hawaii.** U.S. Forest Serv. Pacific SW. Forest & Range Exp. Sta. Res. Paper PSW-4, 22 pp., illus.
- Romberger, J. A.
1963. **Meristems, growth, and development in woody plants.** U.S. Dep. Agr. Tech. Bull. 1293, 214 pp., illus.
- Rudolph, T. D.
1964. **Lammas growth and prolepsis in jack pine in the Lake States.** Forest Sci. Monogr. 6, 70 pp. illus.
- Sacher, J. A.
1954. **Structure and seasonal activity of the shoot apices of *Pinus lambertiana* and *Pinus ponderosa*.** Amer. J. Bot. 41: 749-759, illus.
- Sarvas, Risto.
1962. **Investigations on the flowering and seed crop of *Pinus silvestris*.** Comm. Inst. Forest. , Fenn 53.4, 198 pp., illus.
- Scott, C. W.
1960. ***Pinus radiata*.** FAO Forestry and Forest Prod. Study 14, 328 pp., illus.
- Shaw, George Russell.
1914. **The genus *Pinus*.** Publ. Arnold Arboretum 5, 96 pp., illus.
- Shreve, Forrest.
1924. **The growth record in trees and massive organs of plants.** Carnegie Inst. Wash. Publ. 350: 89-116, illus.
- Sinnott, E. W.
1960. **Plant morphogenesis.** 550 pp., illus. New York: McGraw-Hill Book Co.
- Skolmen, R. G.
1963. **Wood density and growth of some conifers introduced to Hawaii.** U.S. Forest Serv. Pacific SW. Forest & Range Exp. Sta. Res. Paper PSW-12, 20 pp., illus.
- Smithers, L. A.
1962. **Lodgepole pine in Alberta.** Canad. Dep. Forestry Bull. 127, 153 pp., illus.
- Stone, Earl L., Jr., and Stone, Margaret H.
1943. **Dormant buds in certain species of *Pinus*.** Amer. J. Bot. 30: 346-351, illus.
- Streets, R. J.
1962. **Exotic forest trees in the British Commonwealth.** 765 pp., illus. Oxford: Oxford Univ. Press.
- Studhalter, R. A., Glock, Waldo S., and Agerter, Sharlene R.
1963. **Tree growth.** Bot. Rev. 29(3): 245-365.
- Syrach Larsen, C.
1956. **Genetics in silviculture.** 224 pp., illus. Edinburgh: Oliver and Boyd.
- Troup, R. S.
1921. **The silviculture of Indian frees.** 3 vols., 1, 195 pp., illus. Oxford: Oxford Univ. Press.
- Zobel, Bruce J.
1952. **Abnormal cone formation in pines.** Texas J. Sci. 4: 517-520, illus.