Some Shoot and Cone Characteristics of Taiwan Red Pine¹

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TAIWAN RED PINE³ (Pinus taiwanensis Hayata) is endemic to the island of Taiwan, or Formosa (Li, 1963). It is one of the so-called uninodal pines — that is, its winter bud elongates to form an unbranched axis bearing lateral long shoot buds only near the distal end. However, it is remarkably prone to lammas growth or summer shoots (premature elongation of a newly formed dormant bud) and to several other anomalous forms of behavior. Some of these strongly affect tree form; others are economically unimportant but serve to illustrate further the morphological plasticity within the genus Pinus. The observations reported here were made in early March 1969, in natural stands, plantations, nurseries, and a seed orchard.

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VEGETATIVE SHOOT CHARACTERISTICS

Lammas Growth

Lammas growth is a common feature of Taiwan pine leaders. Unlike the lammas shoots of northern species (Rudolph, 1964; Shaw, 1914), those of Taiwan pine usually become fully elongated and are morphologically indistinguishable from shoots that result from winter bud elongation. In this respect they more closely resemble the summer shoots of pitch pine (Pinus rigida Mill.) and shortleaf pine (P. echinata Mill.) described by Tepper (1963). In Taiwan pine, however, we saw no axis that had borne more than one lammas increment during a single season. The lammas shoot is frequently longer than the shoot originating from

the winter bud. At Chu Yuan Shan seed orchard, for example, a grafted bud produced a 20-cm-long shoot in the spring of 1968 and a 45-cm-long lammas shoot shortly afterward. Lammas shoots up to 1.6 meters long have been measured in watered nursery beds at Chu Yuan Shan.

Prolepsis

When lammas growth occurs in lateral branches, it is often termed "prolepsis" (Rudolph, 1964). Proleptic growth is very common in Taiwan pine and results in one or more fully developed lateral shoots assuming dominance over the leading shoot. These laterals bear fully developed new buds which produce further vigorous growth in the spring. The seriously forked trees that result are often worthless as timber producers. Such forking has been observed even in trees starting their second year of growth. It often occurs repeatedly.

In some cases the leader bud fails to elongate during the following spring, apparently because of inhibition by the vigorous proleptic shoot. This results in a crooked stem, with the lateral assuming dominance.

Bud Suppression

When spring growth commences, elongation may proceed more rapidly (or begin earlier) in laterals than in the leading shoot. Sometimes this results in only a partial elongation of the terminal bud of the leader, and both its needles and cones may remain "frozen" in their current developmental stage. One such terminal bud at Ama Shan had needles 1 to 2 cm long, and purple conelets that still appeared receptive almost a year after elongation had been arrested.

Forking of Buds

Forked buds occur very frequently. A tree at Ta Yu Ling had its 1966 leader forked within the foliated zone, indicating dichotomy or bifurcation of the bud. Two trees near Lishan had a total of five bifurcations and two trifurcations in the actively elongating 1969 shoots. Such

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³ Referred to hereafter in this paper as Taiwan pine.

buds are extremely rare in pines. The only example in the literature known to the authors is in Monterey pine, *P. radiata* D. Don (Fielding, 1960). One of us (Lanner) has seen one example each in Swiss mountain pine (*P. mugo* Turra) and Scotch pine (*P. sylvestris* L.), both of which, like Taiwan pine, are in the subsection *Sylvestres* (Critchfield and Little, 1966).

Foxtails

Foxtails are branchless leaders resulting from continuous primordium initiation by the shoot apex, accompanied by continuous elongation in the subapical zone. They occur in many pine species planted in tropical and subtropical areas (Lanner, 1966). At Ta Yu Ling a foxtail was found that differed from those described by Lanner (1966) in having needles of distinctive length on each of three successive annual increments of the leader, and three well-defined annual rings. The stem, however, had no bare sterile-scale zones and no lateral appendages bearing structures other than needle fascicles. Fascicles were not proliferated.

At the Chu Yuan Shan nursery, foxtailing was common in a watered bed of seedlings. These seedlings had had dormant terminal buds a year earlier. One of them had elongated 2.7 meters in 12 months, an astonishingly rapid rate of growth for a pine shoot, and far in excess of other foxtails reported in the literature (Lanner, 1966; Slee and Nikles, 1968).

False Foxtails

These are branchless forms that exhibit true annual growth but lack lateral branches. At Ama Shan we found a stem bearing four annual increments. Each of these had a leafless base, but, unlike false foxtails described elsewhere (Lanner, 1966), there was no trace of aborted lateral buds. Such buds may have atrophied in an early developmental stage, or perhaps none ever developed.

ANOMALOUS REPRODUCTIVE STRUCTURES

Mixed Cone Clusters

Clusters of female cones in the foliated zone of pine shoots have often been reported (see Lanner, 1966), but at Chu Yuan Shan and at Fu Yuan such clusters were found to contain male cones interspersed among the females. Although the shoots bearing these cones had elongated a year earlier, the male cones were only approaching anthesis. Normally, anthesis occurs simultaneously with the elongation of the shoots bearing the male cones. A majority of the female cones were entering the pollen-receptive stage, but a few had done so the previous year. Therefore, most of the female cones were also a year late in developing.

Cone-bearing Lammas Shoot

At Kuan Wu was a tree whose 1968 leader developed normally and bore a female cone. Soon afterward, a vigorous lammas shoot elongated which also bore a female cone in the normal position near its distal end. The lammas shoot cone was similar in size and shape to normal cones entering their final year of growth, but was still purple.

DISCUSSION

In recent years it has become increasingly clear that conventional patterns of pine growth and development may be violated in many ways. This is especially true in the tropics and subtropics where exotic northern species express characteristics seldom encountered in their natural areas. But in Taiwan pine many growth peculiarities occur even in natural stands.

Detailed studies of growth, development, and morphology have not been made for most of the tropical and subtropical pines. More information is needed in order to properly analyze some of the peculiarities described above. Because of its unusual morphological and developmental instability, Taiwan pine appears to be a potentially valuable species for study.

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