THE TERMINOLOGY OF PINE SHOOT GROWTH

G. B. SWEET and M. P. BOLLMANN
Forest Research Institute, Rotorua, New Zealand

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ABSTRACT

In the interests of obtaining a terminology of pine shoot growth which is applicable to all species in the genus, it is proposed that the terms spring shoot and summer shoot should be dropped from the literature; and that usage of the term free growth should be restricted. The term predetermined growth is preferable to that of fixed growth.

The terminology of pine shoot growth dates back to Shaw (1914) and Doak (1935). It was based on Northern Hemisphere cold-temperate species and was adequate to describe their growth patterns. In more recent years the original terminology has been amended slightly: Bannister (1962), for example, pointed out that it was incorrect to use Shaw's terms "uninodal" and "multinodal" to describe stem growth patterns; and Van Den Berg and Lanner (1971) brought to the attention and acceptance of biologists unfamiliar with the French literature the substitute terms "monocyclic" and "polycyclic", coined by Debazac (1968). They also revived Doak's term "stem unit" to describe "an internode, together with the node and nodal appendages at its distal extremity".

These factors have all helped to rationalise the descriptions of shoot growth, now being presented in the literature for an increasing number of the hundred or so species of Pinus widely distributed in the world's natural and planted forests. But as species with increasingly complex shoot growth patterns are investigated, it has become clear that there are still deficiencies in existing terminology. During our recent study of shoot growth in Pinus radiata (see paper by Bollmann and Sweet in this issue) we came to accept that current usage of the terms "spring shoot and summer shoot" and "free growth and fixed growth" is both inappropriate and confusing when applied to some species in the genus.

The term "summer shoot" was used by Shaw (1914) for the second flush of growth that often follows elongation of a vigorous first flush in shoots of pine species growing in cold-temperate latitudes. The main flush of extension growth in the spring was termed a "spring shoot"; and the second flush which, if it occurred, followed in summer was termed a "summer shoot". This converted the season's growth from monocyclic to dicyclic. It was alternatively called a "lammas shoot". Such terminology was adequate for simple shoot growth patterns in a cold temperate climate. Problems arose, however, when it was used to describe growth in species with more complicated growth patterns in more equable climates. Tepper (1963), describing a species (Pinus echinata) with...
more than one "summer shoot", was forced to extend the definition. He classified as a "summer shoot" any shoot which elongated during the same season that it was initiated. Only if it overwintered before elongation did it become a winter bud and produce a "spring shoot". Lanner (1976) has broadly accepted that definition, although in practice he appears to have replaced the word "overwintered" by "rested". To contrast with a resting bud he uses the term "temporary non-resting" bud.

Tepper's usage, of course, implies the existence of definitive seasons and Lanner's usage requires, at the least, some clear distinction between a "resting" and a "temporary non-resting" bud. Yet such distinctions simply cannot be made for some species of Pinus. Some tropical species and some temperate species growing under equable climates do not have a clear period of bud rest, or if they do, it does not necessarily equate with winter (Lanner, 1966; 1976). The difference between a "resting" and a "temporary non-resting" bud is also difficult to define. Species such as Pinus radiata in New Zealand, while having a brief period of winter rest, at least in some parts of the country, may nevertheless produce four or five cycles of growth a year (Bollmann and Sweet, 1976 — Fig. 1). Two or three of these cycles, in Tepper's (1963) and Lanner's (1976) terminology, should be called "summer shoots", and thus have "temporary non-resting" buds. Non-seedling Pinus radiata in Rotorua, New Zealand, always has an apical bud and, apart from one brief period, this never contains less than one complete cycle of unextended initials. That is, for every cycle there is a time period between the initiation of stem units and their extension. The duration of this does differ from cycle to cycle but not, in our view, sufficiently to warrant defining the bud at some stages as "resting" and at others as being in a "temporary non-resting" condition.

Periods of temporary bud rest, when neither primordial initiation nor extension of stem units take place, have been observed on occasion during moisture stress. The timing of such periods is probably not repeatable from year to year and is certainly not always constant from clone to clone in the same year. Because of this variation in the cause of bud rest, its difficulty of definition, and its lack of consistency, it seems to us inappropriate to base a terminology on it.

As used by Shaw (1914) the term "summer shoot" has an implication of elongation in summer. Yet again, for Pinus radiata in New Zealand, the term is a misleading one, for the "summer shoots" elongate not only in summer, but also during the autumn and much of the winter (Bollmann and Sweet, ibid, Fig. 1). A similar situation applies to P. caribaea var. hondurensis whose entire annual shoot growth, occurring fairly evenly throughout the year, is called by Lanner (1976) "summer shoot" growth.

We see such terminology as not only confusing, but also unnecessary. At least in P. radiata it has been possible to determine the cycle of annual shoot growth which corresponds in seasonal terms to the single cycle of a monocyclic species (Bollmann and Sweet, ibid). Provided such identification can be made, the cycles of the annual shoot can simply be numbered consecutively from that cycle with no possibility of confusion, enabling an easy comparison to be made between species. And a simple illustration (as in Bollmann and Sweet Fig. 1) will indicate the number of cycles present in the bud at any given time. It may be difficult in some tropical species of pine to find such a point, but if so we contend that in these cases it would make more sense to number the cycles
from an arbitrarily chosen time of year, rather than refer to them indiscriminately as "summer shoots", as is being done under prevailing terminology. It is important that terminology used in Pinus should be applicable to all, and not just some, species in the genus.

The term "free growth" was taken up by Pollard and Logan (1974) from an original usage by Jablanczy (1971). They use it to describe a situation in which the extent of annual shoot growth is not restricted by a limited complement of preformed primordia, as it may be in the case of predetermined growth. In conifers an obvious usage is for describing the shoot growth of first-year seedlings of the Pinaceae, but it could also be used to describe, for example, some aspects of adult shoot growth in a number of species of the Cupressaceae. We find the term useful, but we are concerned that in recent usage (Lanner, 1976) the term has been extended to describe not only seedling growth, but also all "summer shoot" growth in non-seedlings. As an illustration of the latter, Lanner's paper compares the "free growth summer shoot habit" (of Pinus elliottii) with the "fixed growth spring shoot habit". This second type of usage concerns us on several counts. Firstly, we see no need to replace the well-established term "predetermined growth" with that of fixed growth (which implies an absence of variation). Secondly we are critical, in terms of our previous objection, of the whole concept of spring and summer shoots; and thirdly, we are concerned because of the considerable difference in growth pattern between a seedling and a "summer shoot" of Pinus. In a young seedling undergoing free growth, primordia elongate as they are initiated; but it appears that a number of adult pines that display "summer shoot" growth patterns maintain a large number of initiated, but unextended, primordia in the terminal bud.

In such shoots, stem extension may occur from the base of a bud at the same time as initiation of new primordia occurs at the apex; but so long as an entire cycle of growth (or even a large number of stem units) exists in the bud between the primordia initiating and those being extended, the situation is very different from that in a seedling. The difference is so great that we do not believe the same term should be used to describe both types of growth. We see no need for a term to differentiate the type of growth in "summer shoots" from that in "winter shoots", for reasons we have already given. We consider that in essence they represent the same type of growth, and that whether or not a winter or a period of rest separates their initiation from their elongation is immaterial.

Thus in summary we believe (1) that the terms "summer shoot" and "spring shoot" should be dropped from the literature on pine shoot growth; and (2) that the term "free growth" should be restricted to defining differences in growth habit between, say, a mature pine and a seedling pine, or a mature pine and a mature cypress. We see no place for the phrase "fixed growth": predetermined growth is a preferable term.

REFERENCES


