

# ANNUAL GROWTH STAGES FOR HEIGHT AND DIAMETER IN *PINUS RADIATA*

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## ABSTRACT

An asynchronism is evident in *Pinus radiata* D. Don between the seasonal discontinuities for height and stem diameter growth respectively. For stem diameter growth, a clear discontinuity which consistently arises in midwinter is visible in the outer boundary of latewood in a growth ring. For height growth, however, the discontinuity is often less clear, but where it is externally visible it typically arises in summer. Where substantial "autumn" height growth occurs, the asynchronism can generate a major discordance between annual growth stages for height and diameter growth; this can cause confusion in stem analysis and potentially biases estimates of stem volume increments. The extent of the discordance can be influenced by moisture regime, soil fertility, temperature, latitude, genotype, ontogenetic stage, shoot vigour, and tree size.

**Keywords:** growth rhythm; phenology; stem analysis; *Pinus radiata*.

## INTRODUCTION

Detection of annual growth stages, for both height and diameter, is central to stem analysis which is often used to study rates of stem volume growth. To define annual growth stages, *post hoc*, one needs to identify visible discontinuities in both height and diameter growth. In *Pinus radiata*, however, this process and the interpretation of measurements therefrom, can be difficult. The species can grow throughout the year (Cremer 1973; Jackson *et al.* 1976; Bollmann *et al.* 1986), and visible demarcations of annual stages of height growth are often unclear. A further, much less understood, complication is an evident seasonal asynchronism in the discontinuities for height and diameter growth respectively. This latter feature, which can be very confusing, is the main topic of this paper. My interpretation is that, whereas the discontinuities occur in midwinter for diameter growth, the externally visible discontinuities for height growth in *P. radiata* occur in summer. While this asynchronism is not peculiar to *P. radiata*, it is of only academic interest in many other pines which show negligible shoot extension between summer and midwinter.

The nature of growth discontinuities is outlined separately for diameter and height, with special emphasis on the timing. Also considered is how the nature of growth discontinuities

in shoot extension can be affected by climate, latitude, mineral nutrition, genotype, vigour of shoot, ontogenetic stage, and tree size.

## NATURE OF DISCONTINUITIES

### Diameter Growth

The seasonal discontinuity is usually unmistakable, as the sharp boundary between the outerwood of one growth ring and the innerwood of the next one. Evidence reviewed by Jenkins *et al.* (1977) points very strongly to this discontinuity occurring around midwinter, on sites where diameter growth never actually ceases. Under those conditions the visible discontinuity is associated with a pronounced minimum in measurable diameter growth. Where winters are cold enough to halt diameter growth for a significant period, that period will typically straddle the winter solstice and the exact timing of the visible discontinuity becomes academic.

The one convincing explanation for this switch from latewood to earlywood is a photoperiodic response, actuated by the change from shortening days to lengthening days after the winter solstice.

### Height Growth

For shoot extension growth, especially on the leader, the situation is far less straightforward. Not only is an externally visible discontinuity often hard to locate, but also it can be strongly influenced by climate, soil fertility, genotype, ontogenetic stage, and even chance developmental factors. Moreover, where a visible sign of discontinuity occurs it may not be associated with a very pronounced minimum in the measurable height growth. The morphological features that are associated with annual growth stages on the leader have been described by Bannister (1962), who has provided an excellent frame of reference. In a more recent paper Sweet & Bollmann (1976) reviewed the terminology used to describe phenomena of shoot extension in *Pinus*. Their emphasis was on achieving a terminology that was general to species that grow in widely differing environments.

The typical visible discontinuity is a zone of compressed parastichies at the base of a zone of bare cataphylls (with no fascicles in their axils) which occur immediately above a branch cluster. This branch cluster will usually be the largest among those on the annual shoot, and of course it will be the only one if the shoot is monocyclic (or "uninodal"), which can occur even on the leader in *P. radiata*. In *P. radiata* such a cluster almost never contains cones, so cone production in *P. radiata* is necessarily associated with polyacyclism.

There may be no obvious zone of compressed parastichies in any of the shoot cycles of an annual growth stage, which often happens in some seed orchard clones. However, one can usually examine the branches (Jacobs 1937) to identify annual growth stages on the leader. The discontinuities (namely, zones of compressed parastichies) are typically clearer on the branches, which can also be far more accessible for identifying a growth stage than the leader unless a tree is felled. Additional clues on the bole itself can be used (Bannister 1962); for instance, the lowermost cluster of cones in an annual growth stage usually belongs in the branch cluster at the top of the first shoot cycle of that stage. However, the value of branches for this purpose can be reduced or destroyed by their suppression, death, or even loss.

The compressed parastichies usually occur at the base of the shoot cycle (so-called “internode” between branch clusters) immediately above the zone (which may comprise only one or several shoot cycles) involved in the main flush of elongation that is completed in spring. These compressed parastichies are evidently associated with relatively slow shoot elongation, marking the start of a period when the zone of sealed bud at the apex steadily lengthens, through more primordia being initiated and partly developing than are involved in shoot elongation—although the cataphylls in the compressed-parastichy zone are actually initiated in early spring (Bollmann & Sweet 1976). On post-juvenile trees the tips of the leader and main branches typically appear to be comparatively dormant during December and January (cf. Cremer 1973, Fig. 1A; Tennent 1986), although the situation can vary from tree to tree (R.W. Jackson unpubl.).

During autumn the behaviour of the leader can vary widely according to site conditions. On sites that permit vigorous growth, significant shoot elongation can occur between midsummer and midwinter. This elongation, which I term “autumn elongation” or “autumn growth” (termed a “basal flush” by Cremer 1973), can exceed 1 m. Thus, while the zone of sealed bud will steadily lengthen during this period, the base of the bud may elongate. Sometimes this autumn elongation involves just part of a shoot cycle, or the entire first shoot cycle, or can extend into even part of a third cycle (*see* Jackson *et al.* 1976, Fig. 6, Unit 21) within the compound “multinodal bud” structure. When more than one cycle is thus involved the lateral long-shoot (branch) buds typically elongate along with the leading bud axis. Most interestingly, however, the female conelet buds borne on an elongating zone of stem do *not* elongate and become receptive before the pollination season which occurs some time after the winter solstice (cf. Burdon 1977).

Fascicle elongation prior to midwinter on the zone of autumn elongation typically occurs in slow acropetal succession (Cremer 1973), but is highly variable. On some trees it is minimal, on others it can be essentially complete.

Shoot elongation in the spring typically involves the entire length of sealed bud, except for a small zone at the tip which is in the early stages of primordial differentiation. There tends to be relatively a much greater overlap in time of the elongation of consecutive shoot cycles in the compound bud structure than occurs with the autumn elongation (Cremer 1973). Occasionally a zone of compressed parastichies can occur in mid-shoot cycle; more common seems to be a change in mid-cycle to longer needles (Cremer 1973, Plate 5) which is presumed to occur after midwinter.

The two key planks of the interpretation of the height growth pattern are:

- (i) That the biological starting point for the annual cycle of shoot elongation be accepted as being in early summer to midsummer (cf. Bollmann & Sweet 1976) when the number of unelongated fascicle primordia below the apex is at a minimum, on the basis that elongation must follow differentiation, and elongation tends to be minimal or at least subordinate to differentiation shortly after this time.
- (ii) That the autumn elongation, which is extremely variable in extent, is essentially a “head start” on the spring flush.

The reckoning that the annual shoot extension stage starts after the spring (to early summer) flush can be applied to many other pines, especially cool-temperate species with strictly monocyclic growth. If, however, the “autumn” enlargement of the sealed bud

represents a negligible proportion of the annual height growth, any reference date between spring flushes can be satisfactory, but the practical appeal of using a common reference date (or period) for both height and diameter growth is strong.

The autumn elongation is interpreted as a facultative phenomenon which occurs under much more restricted conditions than does the main spring flush. Such conditions appear to override the primary seasonal cue, postulated to be decreasing photoperiod, which tends to suppress shoot elongation.

## **INTERRELATIONSHIPS BETWEEN PHENOMENA OF HEIGHT AND DIAMETER GROWTH STAGES**

The switch from producing latewood to earlywood reflects an abrupt change from tracheids with small diameters and thick walls to ones with larger diameters and thinner walls. This presumably reflects a change in basic phenological state of all the meristems involved in elongation of shoots and needles, although the low temperatures early in the season may prevent the state being expressed in rapid elongation. The much more gradual transition from earlywood to latewood in the growth ring is noteworthy in itself. It can be readily explained on the basis that the wood being produced reflects an integration of the state of elongation of meristems in the crown above that point. It would thus reflect the nature and amount of plant growth substances exported by the elongating meristems, and possibly an influence of the competing carbohydrate "sink" represented in those meristems. Such meristems are located on numerous shoots which vary widely in vigour. Elongation of stem and needles continues later on the more vigorous shoots, which would mean a gradual change in the average state of the elongation meristems in the crown.

## **FACTORS INFLUENCING FEATURES OF HEIGHT GROWTH STAGES**

The detailed timing and the definition of annual stages of height growth can be modified by several factors in addition to the postulated influence of daylength shift, and an understanding of these effects is helpful. While these factors have been mainly covered by Cremer (1973), Bollmann & Sweet (1976, 1979), and Bollmann *et al.* (1986) it is appropriate to summarise present understanding.

### **Drought**

Where *P. radiata* is grown, water deficits occur mainly in summer and early autumn. Lack of height growth during this period is therefore unremarkable. However, continued diameter growth and data on soil water and leaf water potentials may rule out water stress as a factor that prevents significant height growth during this period. Jackson *et al.* (1976) have shown that autumn elongation is more readily checked by drought conditions than is the main spring flush (*see also* Cremer 1973). A secondary effect of drought, namely, reduced nitrogen availability through drought affecting the upper soil layers, may be significant. In the absence of some of the more usual seasonal cues, drought can produce seasonal or quasi-seasonal discontinuities (Lanner 1966).

### **Nutrient Status**

High soil nitrogen appears strongly conducive to autumn growth. Personal observations on the amount of autumn growth occurring on sites of differing nitrogen status have been

corroborated by Will & Hodgkiss (1977) and Cremer (1973, Fig. 1A). This can have important consequences for tree form, partly because autumn elongation often occurs preferentially in the lateral buds in semi-juvenile trees, leading to the well-known condition “retarded leader”, and partly because of a general tendency for low nitrogen to restrict lateral growth more than leader growth.

High nitrogen tends to maintain a balance, rather than an alternation, between primordial initiation and differentiation, on the one hand, and elongation on the other hand. In addition to promoting autumn elongation, high nitrogen promotes continuous growth in very young seedlings of *P. radiata*, in contrast to strongly episodic growth that is evident under nitrogen deficiency in glasshouse pot trials. A tantalising parallel exists in forage production of pasture grasses, which is boosted by high nitrogen outside the peak season rather than during it.

### Temperatures

Autumn elongation tends to be greater on warmer sites (Bollmann & Sweet 1976, 1979; cf. Tennent 1986), in both absolute terms and the proportion of total annual elongation. Indeed, the timing of all processes of extension growth seems to be earlier on warmer sites. The facultative autumn elongation has the appearance of becoming progressively more active towards the winter solstice, but actual height growth may not accelerate because of the general slowing effect of falling temperatures.

There seems to be general agreement (Jackson *et al.* 1976) that low-temperature inhibition of growth in *P. radiata* is usually almost immediately reversible, and thus does not represent true dormancy.

### Latitude

At low latitudes (where daylength varies little) in combination with the absence of a dry season, *P. radiata* typically shows no clear annual growth stages in either height or diameter growth (Lanner 1966). Height growth can be continuous, with no visible discontinuities, pollen shedding can occur throughout the year, and growth rings may not be discernible. While individual shoots might show some growth discontinuities, such discontinuities are often not synchronised from shoot to shoot within the tree (Jackson *et al.* 1976)

### Genotype

Casual observations, and quantitative studies (Bollmann & Sweet 1976, 1979; Jackson *et al.* 1976; Will & Hodgkiss 1977) all point to marked differences between genotypes in their propensity for autumn elongation and in its detailed features.

### Ontogenetic Stage

Associated with maturation are major changes in the seasonal pattern of shoot extension. In the first few months after germination, shoot elongation is continuous and appears to be closely matched to primordial initiation. Such “free growth”, which is associated with green apical tufts, represents virtually a steady state. As the tree gets older the growth tends to be more episodic, particularly under low nitrogen. There is a steady progression towards the

production of large, sealed, "preformed" buds in which the initials are formed long before the shoot elongation occurs (Bollmann & Sweet 1976, 1979). As the trees get older, shoot growth becomes more strictly seasonal in nature, this progression being virtually complete by the time trees are about 10 years old. During the transition, the spring growth flush, while it may be prominent, can be followed by one or more additional growth cycles which will overlap in elongation period to a lesser extent than the consecutive cycles within a compound bud elongating in spring. These additional cycles, which seem analogous to the so-called "summer shoots" reported in southern pines (Tepper 1963), may be viewed as supplementary to the strictly seasonal growth. They can, however, represent a large proportion of the annual extension, particularly in second- or third-year seedlings, and they can be highly asynchronous between individuals. A similar progressive increase in the seasonal entrainment of extension growth has been documented by Nørskov-Lauritsen (1963) for *P. taeda* L. in South Africa.

### Vigour of Shoot

Less vigorous shoots on the tree tend to be much less polycyclic (Cremer 1973). Indeed, the smaller branches are not only monocyclic, but they often lack the cluster of laterals at the end of the annual growth stage, which point is demarcated by the compressed parastichies which in turn are typically followed by a zone of pollen strobili and then the fascicles. Autumn elongation is usually less prominent, except that the zone of shoots bearing pollen strobili typically elongates before midwinter. This last feature creates a paradox whereby the least vigorous twigs, in which the pollen-bearing zone represents the greatest proportion of the annual growth stage, show the highest proportion of elongation in autumn. This feature is reflected in the seasonal growth measurements of small branches reported by Fielding (1955).

### Tree Size

It appears that maturation state is closely governed in *P. radiata* by tree size or, more specifically, by distance along stem axis from the original seedling root collar (cf. Libby *et al.* 1972). The effects of size in a tree grown as a seedling should therefore equate closely with maturation effects, although when a tree gets large and tall the declining vigour of extremities would bring its own effects (*see preceding paragraph*). In small adult-phase vegetative propagules, however, size differences can be associated with marked differences in seasonal timing of some processes of shoot extension (G.B.Sweet, pers. comm.).

## PRACTICAL IMPORTANCE

Apart from causing confusion, the discordance in seasonal discontinuities between height and diameter growth could cause systematic errors in estimating stem volumes at given ages. On many sites there could be an appreciable mismatch of externally recognisable height annual growth stages with the heights attained in midwinter. This mismatch can sometimes exceed 1 m. Where stem volumes are estimated by assuming certain taper functions, significant errors might arise, even though the volume of current leader between the visible discontinuity and midwinter height is minuscule. The midwinter heights, however, can be identified by detailed stem analysis, since they are reflected in the tops of the innermost sheaths of latewood. When this is done, volumetric errors arising from mismatches of heights

will be eliminated. Whether height growth stages are defined in terms of biological discontinuities or midwinter heights (the preferred mensurational criteria), demarcation of the stages can be difficult or laborious if not also destructive. For this, understanding of the situation can only help.

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