

WOOD PRODUCTION AND STRUCTURE IN RELATION TO BUD ACTIVITY IN SOME SOFTWOOD AND HARDWOOD SPECIES

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Summary. The duration of cambial activity, and change in wood structure from early to latewood, are considered in relation to the initiation of scale and foliage leaves, and shoot extension, in *Picea abies*, *Pseudotsuga menziesii*, *Quercus robur*, *Fraxinus excelsior*, and *Fagus sylvatica*. The initiation of cambial activity appears to be associated with the production of the first scales at the shoot apex, but the cessation of cambial activity does not appear to coincide with the end of primordial initiation at the apex. In *P. abies* and *P. menziesii* leaf initiation continues at a rapid rate for several weeks after cambial activity has ceased. In *Q. robur*, *F. excelsior*, and *F. sylvatica* cambial activity continues longer than leaf initiation. The decline in vessel or tracheid diameter is not consistently related to the change from initiation of scales to initiation of foliage leaves. In the ring porous hardwoods the rapid decline in vessel diameter at the end of the earlywood coincides with the cessation of shoot elongation, but in the other species vessel or tracheid diameter declines steadily from the beginning of the earlywood.

INTRODUCTION

The aim of this paper is to explore the relationships between cambial activity, the production of primordia at the shoot apex, and shoot elongation. It has long been recognised that there is an association between budbreak and the reactivation of the cambium after a dormant period (Priestley, 1930), and it is generally accepted that this renewal of activity is triggered off by auxin produced by the dormant buds (Romberger, 1963). Far less is known about what controls the onset of cambial dormancy, and so limits the duration of wood production. Cambial activity continues for several weeks after the cessation of shoot elongation in many tree species (Denne, 1974), and it has been suggested that this may be associated with the continued production of leaf primordia at the shoot apex (Priestley & Scott, 1936; Denne, 1974).

In tree species having determinate shoot growth, it is generally assumed that earlywood production is associated with the leaf expansion phase of shoot growth, while latewood is produced after leaf expansion has ceased (Larson, 1969). However, it is also possible that the change from early to latewood may be associated with the change from the initiation of scales to foliage leaves at the apex, for in shoots with determinate growth the first primordia to be produced in the spring develop into bud scales, while

the primordia produced later in the season become the foliage leaves of the following year.

The work described in this paper was designed firstly to find out if the duration of wood production is related to the duration of primordial initiation at the shoot apex, and secondly to see if the seasonal change from early to latewood is coincident with the change from production of scales to foliage leaves. Cambial activity, shoot elongation, and initiation of primordia were compared in two conifer species (*Picea abies* (L.) Karst. and *Pseudotsuga menziesii* (Mirb.) Franco), in two porous hardwoods (*Quercus robur* L. and *Fraxinus excelsior* L.), and in one diffuse porous hardwood (*Fagus sylvatica* L.).

MATERIALS AND METHODS

Shoot samples were taken from trees of *Picea abies* (L.) Karst. at weekly intervals, and from *Pseudotsuga menziesii* (Mirb.) Franco, *Quercus robur* L., *Fraxinus excelsior* L., and *Fagus sylvatica* L. at fortnightly intervals, from early May 1975 until mid October 1975. Five trees from each species were selected for uniformity of date of budbreak, all the trees being at the early budburst stage at the beginning of May 1975. The trees selected were between 2m and 4m high, growing in an open canopy. Each sample consisted of a minimum of 10 shoots from each species. Terminal shoots were collected from major branches originating 1m to 2m from ground level, with the terminal bud growing in at least 60% of the outside light intensity. The light intensity was measured with a Megatron D7 lightmeter in diffuse light from overcast weather conditions, about mid-day. Shoots with a second flush of growth were excluded from the sample.

The terminal bud of each shoot was dissected for the count of scale and foliage leaf primordia within one hour of collection. A primordium was counted as present when visible as an external bump on the apex at $\times 50$ magnification. For the conifer species, the number of foliage leaf primordia was estimated by multiplying the mean number of primordia present per parastichy spiralling around the apex by the number of parastichies (Cannell & Willett, 1975). For the hardwoods, the time of change from scale to foliage leaf initiation was determined retrospectively from the mean number of scales eventually produced, since scales could not be distinguished from foliage leaves at the time of initiation.

Cambial activity and wood structure were measured from sections taken at the mid-point of the 1974 internode below the terminal bud. For *Picea abies* and *Pseudotsuga menziesii* wood production was measured as the mean radial number of tracheids (including tracheids in the cambial zone which were fully expanded, in which secondary wall thickening was not yet complete), assessed from the mean of four radii from each section. The initiation of cambial activity was defined by the presence of expanding xylem elements around at least half the circumference of the stem. The cessation of wood production was determined by the appearance of dormancy in the cambial region;

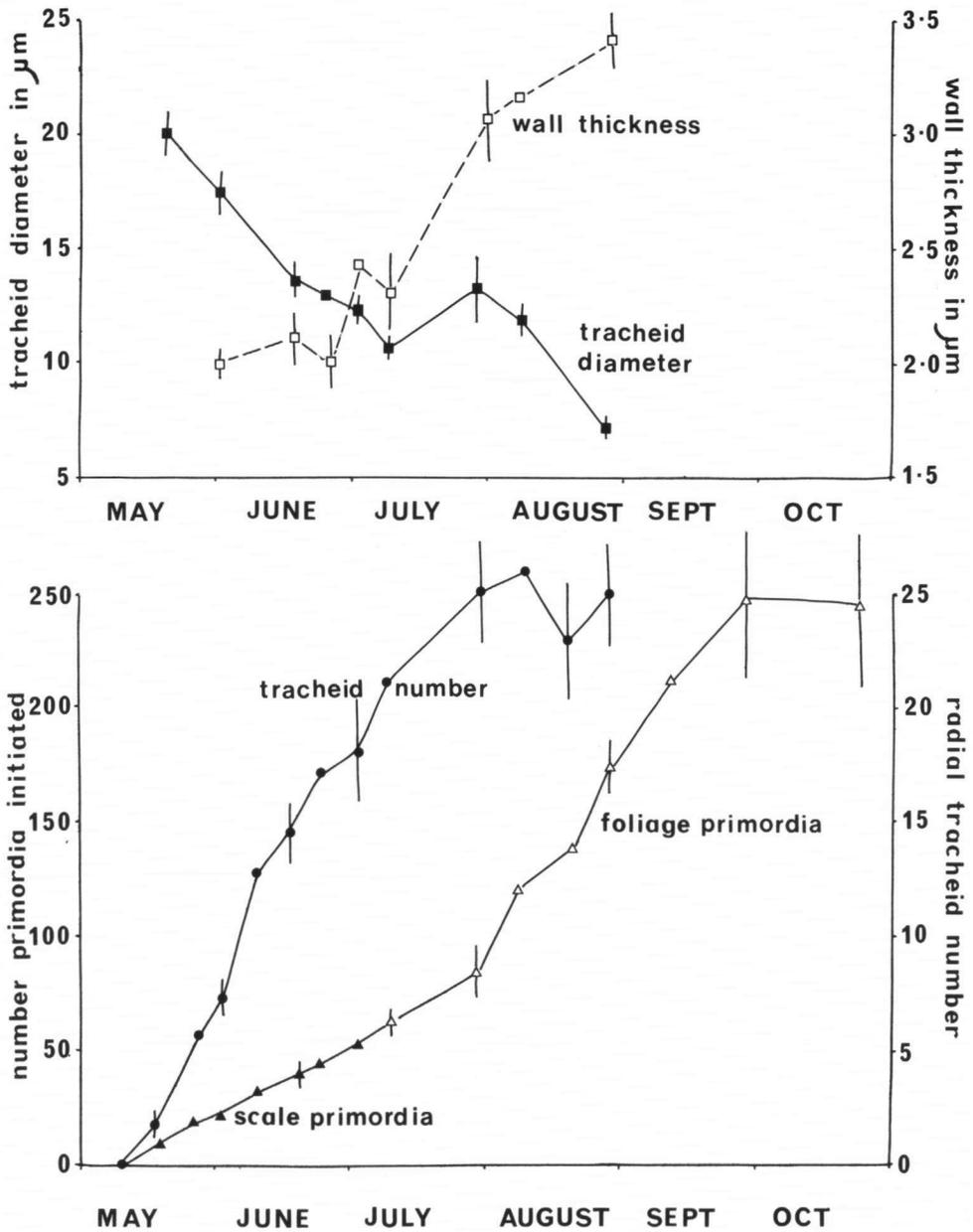


Fig. 1. Seasonal change in radial tracheid number, initiation of scale and foliage leaves, and tracheid dimensions in *Picea abies*. Vertical lines show $SE \times t_{0.05}$ on each side of the mean.

tracheid numbers were too variable between trees to allow the end of xylem increment to be estimated reliably from the tracheid number curve (as seen in Fig. 1).

Radial tracheid diameter, tracheid wall thickness, and vessel diameter, were means of the most recently matured cell in 20 radial files at each sample time.

With *Picea abies*, wood production and bud activity were also followed in shoots at reduced light intensity. Open sided hessian screens were placed over branches in a sector from each tree, reducing the light intensity down to one third of that received by branches outside the screen. The shading treatment was begun 24th June 1975, at the end of the shoot elongation phase of development.

RESULTS

The wood production and wood structure of *Picea abies* shoots are shown in relation to the initiation of scale and foliage leaves in Fig. 1. For all species sampled, the duration of wood production is compared with the duration of shoot elongation, and with the initiation of scale and foliage leaf primordia, in Fig. 2. The horizontal arrows in Fig. 2 indicate the variation between shoots at the beginning or end of each phase of activity; where the samples were too late, or too variable to give a dependable estimate, the points are queried.

In *Picea abies* the first tracheids began to differentiate during early budbreak, and this appeared to be coincident with the production of the first scale leaf primordia at the shoot apex (Fig. 1-2). Shoot elongation ceased at the end of June, about two weeks before the change from initiation of bud scales to initiation of foliage leaves. The pattern of production of primordia was closely similar to that described for *Picea glauca* (Moench) Voss (Pollard, 1973) and *Picea sitchensis* (Bong) Carr. (Cannell & Willett, 1975; Cannell *et al.*, 1976). In *Picea abies*, initiation of foliage leaf primordia continued at a rapid rate until mid to late September (Fig. 1-2). Cambial division ceased in early to mid August, about 6 to 8 weeks before the end of primordial initiation. Since tracheid dimensions changed from the beginning of the earlywood, the progress from early to latewood did not appear to be associated with either the cessation of shoot elongation or the shift from initiation of scale to foliage leaves at the apex (Fig. 1).

In all the species sampled, the beginning of wood production appeared to coincide with the initiation of the first bud scales (Fig. 2, except in *Fraxinus excelsior*, where this point was not determined). As has been pointed out by Longman & Coutts (1974), in oak the first formed vessels may originate from overwintering xylem mother cells, so the production of new wood does not necessarily indicate the reactivation of cambial division.

In *Pseudotsuga menziesii*, as in *Picea abies*, the apex continued to produce foliage leaf primordia at a rapid rate after the cessation of cambial activity (Fig. 2). But conversely, in the hardwood species cambial activity appeared to continue after the cessation of primordial initiation (Fig. 2).

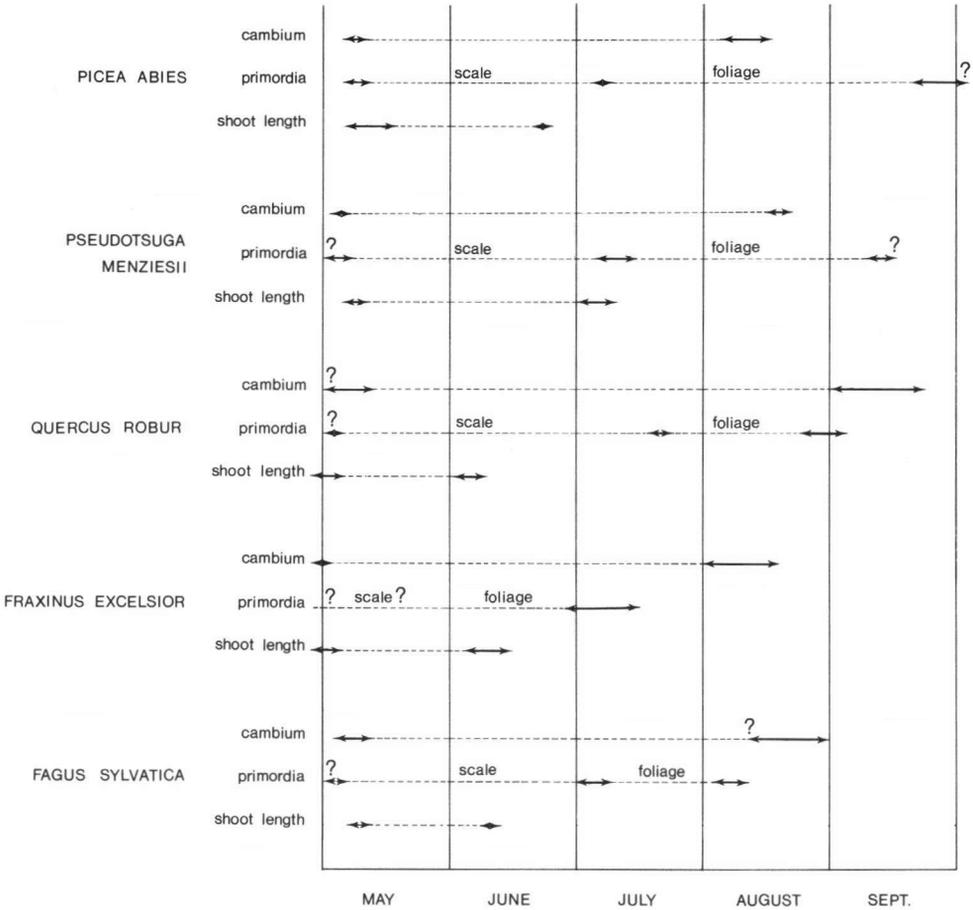


Fig. 2. Duration of cambial activity in relation to initiation of scale and foliage leaves and shoot elongation. Horizontal arrows indicate the variation between shoots at the beginning or end of each phase of activity.

The vessel diameter of *Quercus robur* and *Fraxinus excelsior* (Fig. 3) declined sharply from the earlywood ring to the latewood at about the time shoot elongation ceased. But in *Fagus sylvatica* vessel diameter decreased gradually across the ring, showing no obvious association between wood structure and shoot elongation, or with the change from scale to foliage leaf production (Fig. 3).

The duration of wood production was decreased by shading shoots of *Picea abies*, cambial division ceasing about the beginning of July, two weeks after the treatment began (Fig. 4). Primordial production ceased about the end of August in shaded shoots, and there was a significant reduction in the number of both scale and foliage leaves initiated at the apex (Fig. 4). Radial tracheid diameter was reduced by shading, but there was no significant effect on tracheid wall thickness (Fig. 5).

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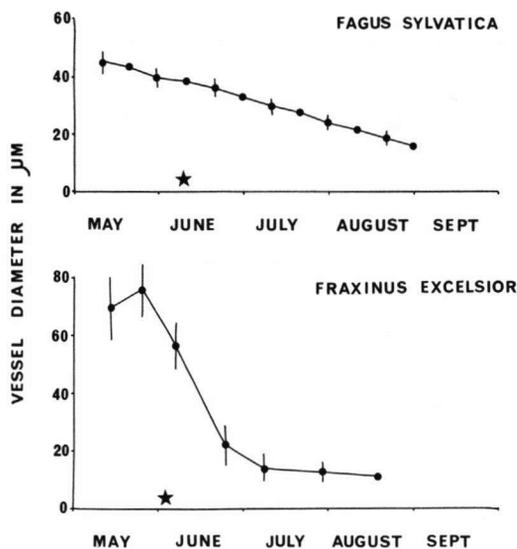


Fig. 3. Seasonal change in vessel diameter in *Fagus sylvatica* and *Fraxinus excelsior*. Vertical lines show $SE \times t_{0.05}$ on each side of the mean. ★ cessation of shoot elongation.

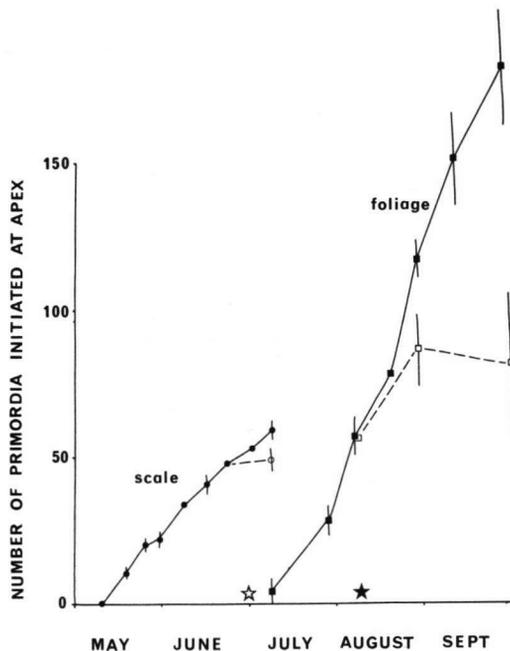


Fig. 4. Effect of light intensity on initiation of scale and foliage leaf primordia in *Picea abies*. Vertical lines show $SE \times t_{0.05}$ on each side of the mean.

- scale leaf primordia in full light,
- scale leaf primordia in one third full light,
- foliage leaf primordia in full light,
- foliage leaf primordia in one third full light,
- ★ cessation of cambial activity in full light,
- ☆ cessation of cambial activity in one third full light.

DISCUSSION

There does not appear to be a clear association between the duration of wood production and the duration of primordial initiation at the shoot apex. In the conifers *Picea abies* and *Pseudotsuga menziesii* cambial activity ceased while the apex was still producing foliage leaf primordia at a rapid rate, while conversely in the hardwoods *Quercus robur*, *Fraxinus excelsior*, and *Fagus sylvatica* cambial activity continued after leaf initiation had ceased. The causes of cambial dormancy are still obscure; cambial dormancy can be induced photoperiodically (Wareing, 1956), but it is not likely to be regulated solely by daylength since the onset of dormancy varies with light intensity within the tree (Denne, 1974). The present data confirm the effect of light intensity on the duration of cambial activity, wood production ceasing soon after shading shoots of *Picea abies*. Shading also reduced the duration of apical activity, decreasing the numbers of both scale and foliage leaves initiated. But since cambial activity ceased

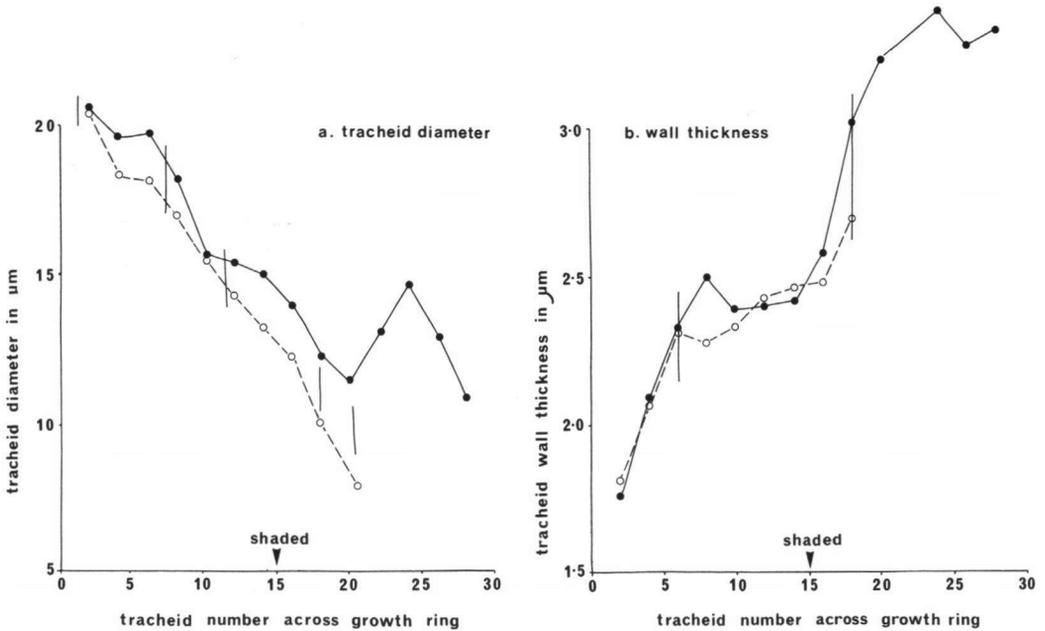


Fig. 5. Effect of light intensity on tracheid dimensions in *Picea abies*. Vertical lines show least significant difference at $P = \pm 0.05$.

●—● full light,
 ○—○ one third full light,
 ▼ beginning of shading treatment.

before the initiation of foliage began in these shaded shoots, it does not seem likely that cambial dormancy is associated with any particular stage in the ageing of foliage leaf primordia.

Possibly cambial dormancy may be determined at a certain stage in apical development not associated with leaf initiation; as pointed out by Cannell & Willett (1975) primordia may continue to be differentiated from the apical dome after meristematic activity has slowed down in the apex. However, in *Robinia pseudacacia* L. wood production continues after bud abortion (Wareing & Roberts, 1956), continued cambial activity being dependant on auxin produced by the mature leaves (Digby & Wareing, 1966). But on the other hand some recent work in our laboratory (unpublished) suggests that in *Picea abies* the buds are essential to maintain wood production, cambial dormancy being induced by removing the terminal buds at any stage of the growing season, without removing the current leaves.

The change in wood structure from early to latewood does not appear to be related to the production of scale or foliage leaf primordia. Nor does the change in type of primordium initiated coincide with the end of shoot elongation. In the ring porous hardwoods the sharp decline in vessel diameter at the end of the earlywood began about the time that shoot elongation ceased, but there was no clear association between

change in wood structure and duration of shoot growth in *Fagus sylvatica* or in the conifers. However, that does not necessarily mean that wood structure is independent from leaf expansion, for a second flush of shoot growth is usually associated with reversion to the earlywood type of wood structure in both conifers and hardwoods. In *Populus* Larson (1976) showed that specific phases of leaf development have a strong influence on vessel production in the wood; from that, Larson suggested that the proportion of vessel to fibre might be determined by the relative durations of leaf production and retention of mature leaves after leaf production. Also, in *Picea sitchensis* work on effects of light intensity indicated that the amount of latewood increases with the duration of cambial activity (Denne, 1974); some preliminary work in our laboratory suggests a similar relationship in *Quercus robur* and *Fagus sylvatica*.

Further work is needed to elucidate the factors which limit the duration of cambial activity in both hardwoods and softwoods. If the duration of cambial activity is not linked physiologically to the duration of leaf initiation at the apex, this would enhance the possibilities of selection for extended wood production without necessarily increasing the period of shoot elongation in the following season. In other words, it should be possible to select for increase in sturdiness; amongst other advantages this would improve stability to wind. If the production of earlywood is causally associated with shoot elongation, selection for an extended period of cambial activity would also increase the proportion of late to earlywood in the growth ring.

REFERENCES

- CANNELL, M. G. R., S. THOMPSON, & R. LINES. 1976. An analysis of inherent variation in shoot growth within some north temperate conifers. In: 'Tree physiology and yield improvement' (eds. M. G. R. Cannell & F. T. Last).
- CANNELL, M. G. R. & S. C. WILLETT. 1975. Rates and times at which needles are initiated in buds on differing provenances of *Pinus contorta* and *Picea sitchensis* in Scotland. Can. J. For. Res. 5: 367-380.
- DENNE, M. P. 1974. Effects of light intensity on tracheid dimensions in *Picea sitchensis*. Ann. Bot. 38: 337-345.
- DIGBY, J. & P. F. WAREING. 1966. The relationship between endogenous hormone levels in the plant and seasonal aspects of cambium activity. Ann. Bot. 30: 607-622.
- LARSON, P. R. 1969. Wood formation and the concept of wood quality. Yale Univ. Sch. For. Bull. 74.
- LARSON, P. R. 1976. The leaf-cambium relation and some prospects for genetic improvement. In 'Tree physiology and yield improvement' (eds. M. G. R. Cannell & F. T. Last).
- LONGMAN, K. A. & M. P. COUTTS. 1974. Physiology of the oak tree. In: 'The British Oak' (eds. M. G. Morris & F. H. Perring).
- POLLARD, D. F. W. 1973. Provenance variation in phenology of needle initiation in white spruce. Can. J. For. Res. 3: 589-593.
- PRIESTLEY, J. H. 1930. Studies in the physiology of cambial activity III. The seasonal activity of the cambium. New Phytol. 29: 316-354.
- PRIESTLEY, J. H. & L. I. SCOTT. 1936. A note upon summer wood production in the tree. Proc. Leeds phil. lit. Soc. 3: 235-248.
- ROMBERGER, J. A. 1963. Meristems, growth and development in woody plants. Techn. Bull. U.S. Dept. Agric. For. Service. 1293.
- WAREING, P. F. 1956. Photoperiodism in woody plants. A. Rev. Pl. Phys. 7: 191-214.
- WAREING, P. F. & D. L. ROBERTS. 1956. Photoperiodic control of cambial activity in *Robinia pseudacacia* L. New Phytol. 55: 356-368.