

Chapter (non-refereed)

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21. ANALYSIS OF THE VARIATION WITHIN SITKA SPRUCE, LODGEPOLE PINE AND LOBLOLLY PINE

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Unlike most agricultural crops, forest tree species are genetically not far removed from their wild progenitors, and are only just beginning to be domesticated. Whereas genecologists study patterns of natural variation in native species, ecophysiologicalists are more concerned with physiological and morphogenic processes which underly that natural variation. What is the physiological basis of forest tree yield? What yield-determining processes offer the greatest opportunities for genetic improvement? And how can these processes be identified and exploited by tree breeders?

Attention has been devoted, in the main, to the 2 most important commercial tree species in Britain, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Dougl.) which grow native over a wide area in western North America, and are genetically very heterogeneous. Some work has also been done on loblolly pine (*Pinus taeda* L.) in the southern USA, where tree improvement work is more advanced. Work being done in ITE on Sitka spruce and lodgepole pine complements that of the Forestry Commission, which is gaining information empirically on the field performance of different provenances and elite-tree progenies of these species.

1. Research needs and approaches

There are 3 ways in which knowledge of yield physiology can aid tree improvement. Foremost, it should help define early selection criteria. Obviously, tree breeders cannot afford to wait for final harvest to evaluate genotypes, and the sooner inferior genotypes can be rejected, or superior types exploited, the more cost-effective the breeding programme. Second, physiologists can help breeders define 'ideotypes' (ideal plant types), determine whether these ideotypes are in practice being selected, and help plan crosses between complementary parents to produce the ideal combinations of attributes. Third, physiological understanding can help prevent errors of judgement and indicate what is possible. Are opportunities for genetic gain being missed, or being overrated?

Genetically different populations of trees have been grown by ITE and the Forestry Commission, and attempts have been made to analyse the nature of inherent growth differences. These analyses have contributed information of 3 kinds. First, they have provided a more complete description of

differences in height growth by analysing its less complex components and subcomponents. Second, the analyses have provided some understanding of how particular phenotypes result from the interaction between growth components, and between genotypes and environments. Third, by analysing differences among provenances, open-pollinated progenies, controlled-cross progenies and clones, we have automatically obtained some information on the patterns of variation and inheritance of various attributes.

2. Descriptive analyses of the components of growth

Yields of field crops have been characterised in terms of numbers of ears, grains per ear, weight per grain, etc. The annual height increments of conifers can be analysed in a similar way.

2.1 Leader length = length per flush x numbers of flushes

Unlike *Pinus taeda*, which can produce 4-5 flushes per year in Arkansas, northern pines, and most mature north temperate spruces, produce only one flush of growth per year from an overwintered preformed bud. But, young *Picea sitchensis*, for instance, can produce second flushes, called 'lammas' or 'free' growth (see Figure 44). Young progenies, prone to produce second flushes, were found to grow outstandingly well at good sites and poorly at poor sites, an adaptation worth exploiting on good sites but not elsewhere (Cannell & Johnstone, 1979).

2.2 Length per flush = length per stem unit x numbers of stem units

A stem unit is a node plus internode in the strict sense—a needle plus its associated section of stem. The total annual complement of stem units produced by a conifer shoot is equal to the total number of primordia produced at the shoot apical meristem. When there is only one spring flush of growth from an overwintered bud, shoot growth is said to be 'predetermined', because all primordia were produced during the previous year. Inherent variation in the length of the single spring flush produced by provenances and progenies of lodgepole pine is attributable, almost entirely, to differences in numbers of primordia already present in the overwintering buds. That is, it is associated with the activity of the apical meristems during the previous year rather than with the extent to which the preformed shoots elongate (Cannell *et al.*, 1976). However, in Sitka spruce there is additional inherent variation in the extent to which the preformed stem units elongate, and

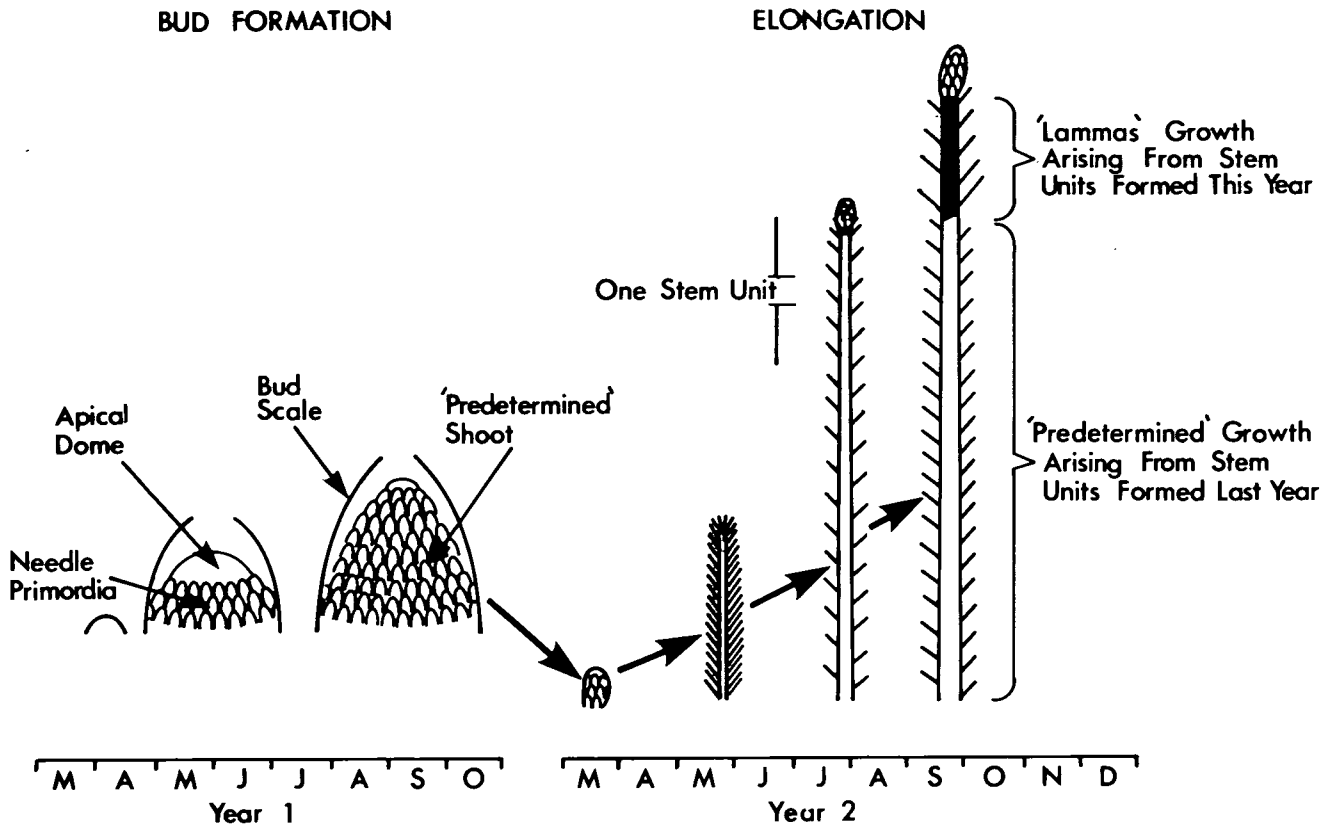


Fig.44 Stages in the development of the leading shoot of Sitka spruce.

in loblolly pine there is inherent variation in stem unit elongation on the long second flush.

2.3 Length per stem unit = numbers of cells x length per cell

Observations suggest that differences in lengths of stem units result primarily from differences in cell numbers, set up during the early stages of shoot elongation, rather than from differences in the extent to which cells elongate (Baxter & Cannell, 1978).

2.4 Numbers of stem units = duration of stem unit initiation x rate of initiation

Because the number of preformed stem units is an important, and somewhat neglected, variable in conifers, detailed studies were made of stem unit initiation by following the seasonal activity of shoot apical meristems of different genotypes: apical meristems become active before bud-burst, and remain active long after bud-set. The seasonal duration of initiation was found to be important in all species examined, especially the prolongation of activity into late summer and autumn (Cannell & Willett, 1975).

In lodgepole pine, inherently different rates of primordia production at shoot apices are also important. These rates depend on the sizes of primordia relative to the size of the apical domes, and also on mean cell generation times.

2.5 Sizes of apical domes, sizes of primordia, and mean cell generation time

A technique was developed to estimate the transverse growth rates of apical dome tissues and the sizes of primordia (Cannell, 1976). Making certain assumptions, it was possible to show that the average time taken for cell numbers to double at conifer apices was in the range 40-120 h, as in many herbaceous plants. But conifers can produce primordia exceptionally rapidly (up to one per hour) because they develop large apical domes (up to 1.6 mm diameter) and very small primordia (only 2-5% the size of the apical domes). There are, however, complex seasonal fluctuations in cell division rates, dome sizes, and primordia sizes. The most important factor affecting the amount of new tissue generated is the size of the apical domes—large domes are equipped to produce more cells per cycle of cell division than small domes. Curiously, very little evidence could be found for inherent differences in maximal rates of cell division. An important feature distinguishing genotypes of *P. contorta* and *P. sitchensis* was the rate at which they enlarged their apical domes in spring (Cannell & Bowler, 1978), possibly reflecting differences in the efficiency with which metabolites were supplied to, or utilized by, the apical meristems.

3. Analyses providing understanding of growth relationships and environmental responses

3.1 Branching and tree growth

The growth of young conifers is limited by the rate at which they can build up their foliage biomasses. Genotypes differ in this respect, not only because of differences in the growth of their individual shoots (analysed above) but also because of differences in branching. Each shoot produces branches in proportion to its own length and this proportion differs among genotypes. For instance, provenances of lodgepole pine have from 0.25 to 0.35 branches per cm of parent shoot whereas provenances of Sitka spruce have from 0.60 to 0.85 per cm. These differences are the cause of large differences in branchiness, needle biomass production and early dry matter production per tree when combined with differences in shoot growth. Trees with long shoots (leaders and branches) will produce many laterals, sub-laterals and so on, whereas trees with short shoots will build up their foliage biomasses much more slowly. Using a simple model, it was found that slow-growing individuals of an otherwise fast-growing provenance could mimic members of an inherently slow-growing provenance (Cannell, 1974).

3.2 Dry matter distribution

Are there inherent differences in the functional relationships between shoots and roots (allometric relationships)? How are these related to observable patterns of shoot growth? Are they reflected in differences in root:shoot weight ratios which may influence wind stability? Differences in root:shoot allometry were not found among provenances of Sitka spruce and lodgepole pine, but may be important in progenies of loblolly pine (Cannell *et al.*, 1979). However, inherent differences occur in seasonal patterns of dry matter distribution between shoots and roots. Briefly, genotypes which stop increasing in height early in the growing season (although they may continue bud development late into the autumn) develop relatively large, heavy root systems by the end of the year. This root:shoot 'imbalance' is 'corrected' the following spring, but is set up again in the autumn and may influence the wind stability of trees during winter (Cannell & Willett, 1976).

3.3 Photoperiod, temperature and stress responses

Many of the genotypic differences already described are linked with differences in response to photoperiod, temperature and water stress. Thus differences between genotypes in their propensity to produce late-summer growth are probably related to their responses to day length. In contrast, differences in the seasonal duration of apical meristematic activity probably have more to do with temperature responses. More information is needed on the onset and loss of frost hardiness in relation to (i) shoot apical activity and elongation, and (ii) the frost hazard in different British upland regions. Water stress responses may also be important—not surprisingly, they proved to be crucial to the success of genotypes of *P. taeda* in the southern USA (Cannell *et al.*, 1979).

4. Patterns of variation and inheritance

Studies of Sitka spruce provenances have confirmed their essentially clinal pattern of variation with latitude of origin in western North America. Lodgepole pine has a more discontinuous pattern of variation, with distinct differences in branching and physiology between coastal and inland populations, suggesting that coastal x inland hybridization might be profitable.

Variation among progenies of elite trees of Sitka spruce is being analysed. Also the inheritance of some traits is being assessed on (i) Forestry Commission controlled-cross experiments, where physiological complementation may explain some instances of hybrid vigour, and (ii) ITE clonal trials which are revealing a high degree of within-provenance genetic variation in traits which were formerly thought to be poorly inherited.

5. The future

Practical seedling screening procedures, which can be used by tree breeders to evaluate progeny differences, are required to (i) minimize the need for long-term field testing, and (ii) shorten the generation time. Additionally, more needs to be known about the inheritance of the different components of growth. Also, work is needed to test the assumption made by tree breeders that fast-growing individuals will produce fast-growing forests (Cannell, 1979).

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