

Branching dynamics in young Scots pine

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TIIVISTELMÄ: OKSARAKENTEEN KEHITTÄMISEN DYNAMIIKKA NUORILLA MÄNNYILLÄ

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The development of shoot number and shoot properties was examined in successive shoot cohorts of young widely-spaced Scots pine trees (*Pinus sylvestris* L.) growing in a progeny trial. This was accomplished by reconstructing the branching process of the trees over a period of five years, from tree age 4 to 8. During this time the number of shoots in successive shoot cohorts increased rapidly, while at the same time the mean shoot length decreased. The decrease in shoot lengths from older to younger shoots was accompanied by a decline in the bifurcation frequency of the shoots. In general, rapid changes occurred in the branching characteristics during the early development of the trees. The variation in the branching characteristics was reflected in the development of the architecture and biomass production of the trees.

Työssä on tutkittu nuorten mäntyjen (*Pinus sylvestris* L.) oksarakenteen kehittämistä käyttäen aineistona kahdeksanvuotista jälkeläiskoetta. Puiden katsottiin rakentuneen modulaarisesti versoyksiköistä, joiden lukumäärän ja ominaisuuksien kehittyminen rekonstruoitiin viiden vuoden ajanjaksolle, ikävälille 4-8 vuotta. Tänä aikana versojen lukumäärä kasvoi nopeasti peräkkäisissä versokohorteissa, mutta samalla verson keskimääräinen pituus ja versojen haarautumisfrekvenssi pienenevät, mikä hidasti oksapituuden ja neulasmassan kasvunopeutta. Yleisesti ottaen oksimista kuvaavat tunnuksiset muuttuivat nopeasti puun alkukehityksen aikana. Oksimistunnuksissa oli suurta puiden välistä vaihtelua, mikä oli ilmeisessä yhteydessä puiden latvusarkkitehtuurin kehittämiseen ja tuotosominaisuuksiin.

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1. Introduction

The aerial architecture of most trees is developed by the serial repetition of organs by apical meristems. Usually the structure of a tree is derived from several meristems

through branching (Hallé 1986). Following this thought, a tree can be regarded as an integrated complex of modules, usually shoots, linked together to constitute a hier-

archy of these elementary structures (White 1979). The division of the individual, i.e. the genet, into its modular units of structure allows the use of the demographic approach in the study of tree morphology and growth dynamics of trees (Steingraeber et al. 1979, Maillette 1982a,b, Franco 1985, Jones 1985, Kellomäki and Väisänen 1988, Kuuluvainen et al. 1988).

In trees of modular structure even small differences in the branching characteristics can cause considerable changes in the overall tree architecture (Fisher 1984). This is because, in the branching process the effect of the differences in these genetically determined shoot characteristics is multiplied (Gottlieb 1986). It is also possible that the actual mechanisms controlling growth may be mainly located within the shoot-modules (Watson and Casper 1984, Waller and Steingraeber 1985). Therefore, in tree growth studies and in tree breeding, special attention should be paid to the effect of shoot properties and branching characteristics on the development of tree architecture,

2. Material and methods

21. Material

The sample included 12 Scots pine trees from a progeny trial in the Tuunaansaari test orchard at the Punkaharju tree breeding station of the Finnish Forest Research Institute (61°48'N, 29°17'E, alt 85 m above sea level). Four full-sib families with different crown structures were selected for this study. One family was a crossing between plus trees from Southern Finland, the other was from Central Finland and the third was from Northern Finland. The father tree of the fourth family was an exceptionally narrow-crowned and thin-branched tree E 1101 (Mikola 1985). The trees were growing on a fallow field with wide-enough spacing to prevent crown contacts between the adjacent trees. The measurements were carried out after growth cessation in August 1985. The growing conditions, as well as the measurement procedure of the sample trees

dry matter partitioning and the biomass production capacity of trees (Ford 1984).

The purpose of this study was to analyze the branching process and its stationarity in young, widely-spaced Scots pine (*Pinus sylvestris* L.) trees from different origins. This was accomplished by examining the development of shoot numbers, shoot properties and bifurcation frequencies of shoots in successive shoot age classes, i.e. shoot cohorts. The effect of the branching dynamics on tree architecture was discussed by utilizing the structural analysis of the sample trees presented in the paper by Kuuluvainen et al. (1988).

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are described in detail in Kuuluvainen et al. (1988).

22. Calculations

The analysis was a tree-by-tree analysis. The families were not used as calculation units, because of the small sample size and great within-family variation in tree characteristics (see Kuuluvainen et al. 1988).

The main method of study was frequency analysis and the calculation of means and variances of the shoot characteristics in the successive shoot cohorts.

The bifurcation rank order was determined for each shoot of the sample branches by using Strahler's (1957) centripetal ordering system (e.g. Borchert and Slade 1981). The ratio of the number of branches of one order to the number of branches of the next order constitutes the bifurcation ratio (R_b):

$$R_b = N_n \cdot (N_{n+1})^{-1} \quad (1)$$

where N is the total number of branches of an order and n is the order number. The bifurcation ratio for the entire tree was estimated by the formula (Motomura 1947):

$$R_b = (N - N_{\max}) \cdot (N - N_1)^{-1} \quad (2)$$

where N is the total number of branches of all orders, N_{\max} is the number of branches of the highest order and N_1 is the number of branches of the first order.

To estimate the needle mass loss in older shoots, the original amount of needles produced by older shoot cohorts was estimated as:

$$NM_{ij} = SL_{ij} \cdot SNMD_{1,j-1} \quad (3)$$

where NM_{ij} is the initial needle mass (g) in shoot cohort i ($i \geq 2$) in whorl j ($j \geq 2$, whorl number enumerated from the top of trees) and SL_{ij} is shoot length (cm) and $SNMD_{1,j-1}$ is shoot needle mass density per unit of shoot length (gcm^{-1}) in shoot cohort 1 in whorl $j-1$. According to this method, for example, the original needle mass of the 1-year-old shoot cohort of the second whorl was obtained by multiplying the shoot length by the needle density of the current year shoot cohort in the uppermost whorl, and so on.

3. Results

31. Number, length and bifurcation frequency of shoots

During the five years of tree growth, from tree age 4 to 8, the shoot number increased from older to younger shoot cohorts rapidly (Fig. 1), as did the total number of shoots. There existed, however, considerable between-tree differences in the rates of increase and in the number of shoots in each shoot cohort. As a result, at the end of the observation period, when all the trees were 8 years old, the between-tree differences in shoot numbers were notable. For example, the highest number of shoots in the current year shoot cohort was 746, while the minimum was 224.

The increase in shoot number was accompanied by a decrease in mean shoot length in all whorls from older to younger shoot cohorts. Within a shoot cohort the mean shoot length increased from older (lower) to younger (upper) whorls (Fig. 2).

The mean number of daughter shoots per parent shoot, referred to as the mean bifurcation frequency of shoots, decreased rapidly from older to younger shoot cohorts. However, the first branching in the 5th (lowest) whorl was an exception: the bifurcation frequency was higher in the 3-

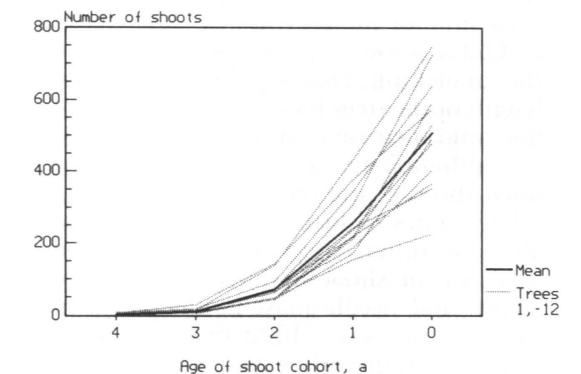


Fig. 1. The increase in shoot number in succeeding shoot cohorts in the sample trees. The 0 age class indicates "current year" shoots, i.e. shoots developed in 1985 when the trees were 8 years old. 1, age class indicate 1-year-old shoots, and so on.

year-old shoots than in the 4-year-old shoots. Within the shoot cohorts, the bifurcation frequency of shoots increased from lower to upper whorls (Fig. 3).

The between-tree variation in the bifurcation frequency of shoots in each shoot cohort was considerable, which in turn was reflected in the variable rates of shoot

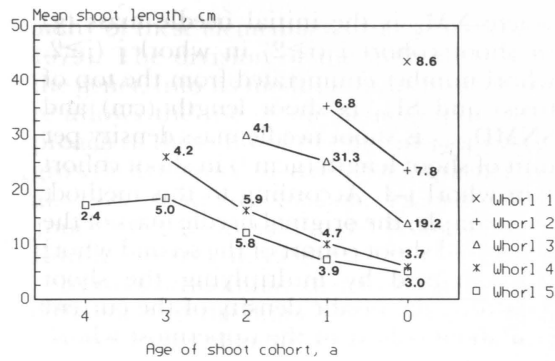


Fig. 2. Mean shoot length (cm) by shoot cohorts in whorls 1-5 (enumerated from the top of tree downward). Numbers indicate standard errors.

number increase as shown in Fig. 1. In general, the between-tree differences in bifurcation frequency decreased from older to younger shoot cohorts.

In spite of the decrease in shoot length and bifurcation frequency of shoots during the branching process, the total branch length of the trees increased steadily due to the rapid increase in shoot number. However, although the absolute increase continued through the observation period, the relative rates of increase rapidly decreased after the initial rise. The relative annual increases in shoot frequency, total shoot length and needle mass in the 3-year-old shoot cohorts were 510 %, 498 % and 442 %, respectively; thereafter these values rapidly declined being between 130 % and 260 % in the 1-year-old year shoot cohorts and already below 100 % in the current year shoot cohorts when the trees were 8 years old. (Fig. 4).

32. Bifurcation ratio and size distribution of shoots

The mean of the bifurcation ratio of the sample trees (R_b), calculated using eqn. 2, was 4.84, with a range from 4.4. to 5.8.

The size distribution of shoots was strongly skewed towards shorter shoots, which were also the youngest shoots: 60 % of the shoots were shorter than 10 cm and 32 %

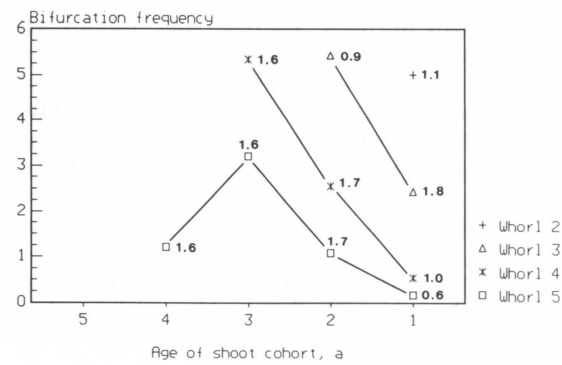


Fig. 3. The bifurcation frequency, i.e. the mean number of daughter shoots per parent shoot by shoot cohorts in whorls 2-5. Numbers indicate standard errors.

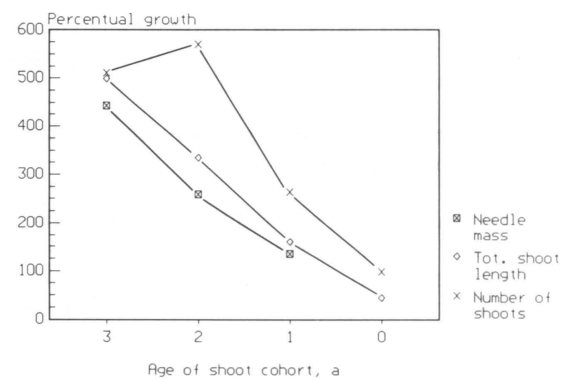


Fig. 4. The relative growth rate of needle mass (g), total shoot length (cm) and number of shoots by shoot cohorts in the sample tree material.

were shorter than 5 cm. This was obviously a consequence of the combined effect of the increase in shoot number and decrease in shoot size in succeeding shoot cohorts.

33. Needle mass

The accumulation of needle mass closely corresponded to the increase in total branch length. The needle mass in successive shoot cohorts increased rapidly until the trees were 7 years old, after which the increase in needle mass of successive cohorts halted; the needle mass production in the 1-year-

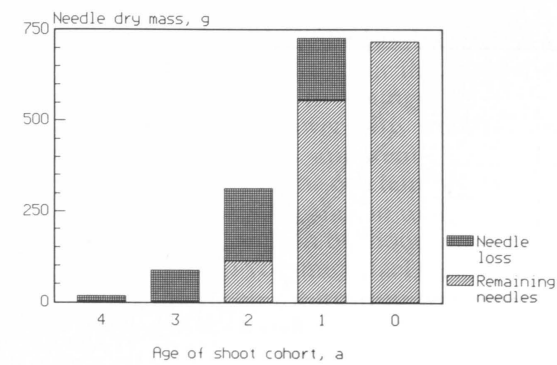


Fig. 5. The average development of needle mass production (g), needle mass loss (g) and amount of remaining needle mass (g) of a tree by shoot cohorts.

old and current year shoot cohorts were approximately equal (Fig. 5).

In general, only the three youngest shoot cohorts had living needles. In the 1-year-old and 2-year-old shoot cohorts the estimated losses of needle mass were 31 % and 64 %, respectively (Fig. 5), and the 3-year-old and 4-year-old shoot cohorts were already void of needles.

34. Branching characteristics as related to tree architecture

The present analysis on the branching dynamics of young Scots pine does not allow any firm conclusions to be drawn concerning the relationship between specific characteristics of the branching process and the development of tree architecture. However, some general remarks, based on the comparison of two opposite branching patterns, can be drawn.

In the architectural analysis of the pre-

sent sample tree material, Kuuluvainen et al. (1988) detected two highly different patterns of shoot distribution, which also indicated different biomass accumulation and allocation patterns. The first pattern was characterized by plagiotropic (horizontal) branches and had a layered branch structure with highly whorl-concentrated shoot distribution. This type was represented by a tree (tree 7) which was a descendant of the exceptionally narrow-crowned and thin-branched father tree E1101. The second branching pattern had more orthotropic (vertical) branches and exhibited a non-layered or 'bushlike' structure with rather even vertical shoot distribution. This type was represented by a tree (tree 10) from Northern Finland (Kuuluvainen et al. 1988).

The reconstruction of the branching process of these two sample trees with opposite architectures showed that, tree 7 produced longer shoots than tree 10 in all shoot cohorts, with the exception of the oldest shoot cohort, where the shoot lengths were almost equal (Fig. 6a). In all shoot cohorts tree 7 was also characterized by a higher bifurcation frequency of shoots when compared to tree 10 (Fig. 6b). Consequently, the rate of increase in shoot numbers in the successive shoot cohorts was higher in tree 7 when compared to tree 10 and the difference increased from older to younger shoot cohorts due to the multiplicative effect of bifurcation frequency of shoots in the branching process (Fig. 6c).

In addition to higher mean shoot length and bifurcation frequency of shoots, tree 7 was characterized by more plagiotropic shoot inclinations in all shoot cohorts when compared to tree 10 (Fig. 6d). This is probably an important characteristic underlying the development of the layered branch structure (Kuuluvainen et al. 1988).

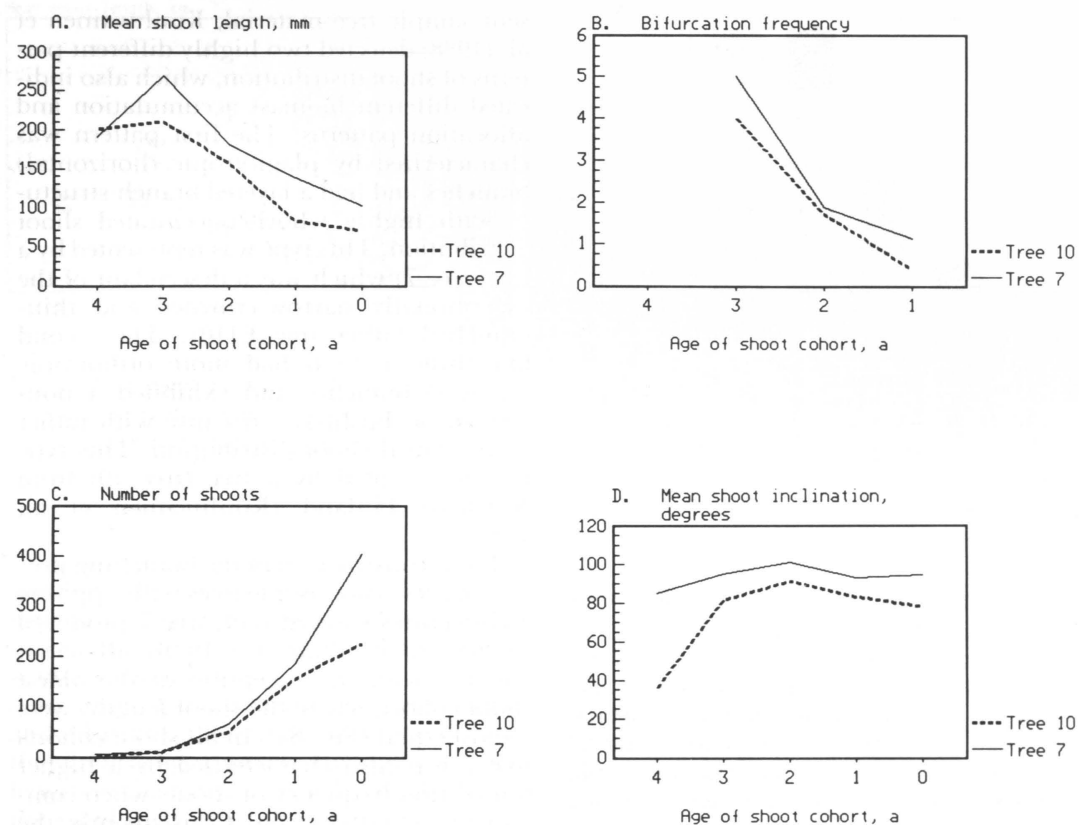


Fig. 6. a. Mean shoot length (cm), b. bifurcation frequency of shoots, c. number of shoots and d. mean shoot inclination (measured from vertical) by shoot cohorts in trees 7 and 10.

4. Discussion

Branching patterns and angles in woody plants play important roles in establishing both crown form and leaf position (Fisher 1984). The idea that a plant can be considered as an assemblage of rather similar basic units has proved fruitful when describing and interpreting the development of plant architecture (Harper and White 1974, Harper and Bell 1979, White 1979, Harper 1980, Waller and Steingraeber 1986). The advantage of this phytotic approach (Cusset 1982) in tree growth studies is that it allows one to analyze the processes and mechanisms of tree construction, which regulate the rate of dry matter ac-

cumulation and distribution in trees (Ford 1985).

In this study the demography of shoots units was examined during the development of young Scots pine trees. During the five years of growth, from tree age 4 to 8, the number of shoots in successive cohorts increased in an exponential manner, thus following the general growth form of modular organisms in their early stages (Harper and Bell 1979, Waller and Steingraeber 1985). The increase in total shoot length was, however, considerably reduced by the decrease in the mean shoot length and by the reduction in the bifurcation frequency

of shoots, i.e. the number of daughter shoots per parent shoot, in the branching process from older to younger shoot cohorts (see also Flower-Ellis et al. 1976, Kurttio 1986). This apparently facilitates the maintenance of the mechanical stability of tree structure (McMahon and Kronauer 1976) and the location of shoots more evenly in the crown volume (MacDonald 1983).

Both the mean bifurcation frequency of shoots and mean shoot length, decreased from the top of crown downwards within shoot cohorts. As a result, the increase in branch length was considerably higher in the top part of the crown when compared to the lower crown portion; this appears to be the general pattern in pines (Jankiewicz and Stecki 1976). One reason for this may be differences in illumination (Ilonen et al. 1979, Viherä and Kellomäki 1983), although the regulating mechanism may be hormonal (Jankiewicz and Stecki 1976). In the two lowest and oldest whorls (4th and 5th) the mean bifurcation frequency of shoots had already fallen below one in the 1-year-old shoots. This is a clear sign of declining growth vigor, which precedes the onset of self-pruning.

The dynamics of early branching of Scots pine was characterized by rapid quantitative and qualitative changes. The relative growth rates in shoot number, total shoot length and needle mass decreased rapidly during the observation period. It is likely that this reduction in relative growth is mainly a consequence of the increased allocation of dry matter to supporting, non-productive woody structures in order to maintain the mechanical stability of tree architecture (e.g. Tilman 1988). Also, the differences and changes between shoot and root allocation may be important in this respect.

The results of this study show that the bifurcation frequency of shoots and bifurcation ratio of trees in young even-aged Scots pine from different origins can vary substantially. This supports the findings of Borchert and Slade (1981) and Steingraeber et al. (1979) that the bifurcation ratio can vary between individuals of the same species and contradicts the view often expressed in literature that the branching pattern within any species is approximate-

ly stationary (e.g. McMahon and Kronauer 1976). The range of the obtained R_b -values in comparable to the values given by Kurttio (1988) for young Scots pine and to the reported R_b -values for other *Pinus*-species (Oohata and Shidei 1971, McMahon and Kronauer 1976, Whitney 1976). In the present sample tree material the differences in the treewise bifurcation ratio were not found to be clearly related to any specific characteristics of tree architecture. This was apparently due to the fact that the bifurcation ratio does not bear any information on the physical properties of the shoot modules.

The development of crown architecture is of primary interest to tree growth studies, since the structure and aerial distribution of shoots determine the amount of intercepted radiation and the photosynthetic capacity of the tree (e.g. Oker-Blom et al. 1983, Kellomäki et al. 1984, Pukkala and Kuuluvainen 1987). The comparative analysis of growth dynamics of the tree with a layered branch structure and the tree with a non-layered and "bushlike" branch structure (Kuuluvainen et al. 1988) would suggest that the critical variables in the development of tree architecture are (i) shoot lengths, (ii) bifurcation frequency of shoots and (iii) shoot inclinations (see also Jankiewicz and Stecki 1976).

Long shoots and high bifurcation frequency together with plagiotropic shoot inclinations produced a layered branch structure, where shoots were situated in narrow horizontal whorl-layers. This branching pattern was related to both rapid biomass increase and high harvest index (Kuuluvainen et al. 1988), in spite of the fact that theoretically the branch mass needed to support a unit of needle mass should increase toward more horizontal branch inclinations (Morgan and Cannell 1988). On the other hand the non-layered or 'bushlike' branch structure, which indicated low biomass production, was characterized by considerably shorter mean shoot lengths, lower bifurcation frequencies of shoots and more orthotropic branches (Kuuluvainen et al. 1988). Although several factors may affect production, it is possible that these relationships between architecture and productivity are related to the

photosynthetic efficiency of the crown structure as determined by within-shoot, within-whorl and within-tree shading of foliage (Fisher and Honda 1979, Oker-Blom et al. 1983, Kuuluvainen et al. 1988).

In conclusion, there seems to exist pronounced and obviously genetically determined differences in the branching characteristics of young Scots pine trees from different origins. These differences are re-

flected in the development of both tree architecture and biomass and stemwood production capacities of the trees. However, we still need more knowledge on the mechanisms of tree construction as related to biomass production and partitioning, as well as, on the ecological role of varying tree architectures for maintaining forest stability in different environments.

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