ECO-PHYSIOLOGICAL STUDIES ON YOUNG SCOTS PINE STANDS: III. PHOTOSYNTHATE ALLOCATION FOR NEEDLE GROWTH AND WOOD FORMATION IN CURRENT-YEAR SHOOTS

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SELOSTE:

NEULASTEN KASVUN JA PUUN MUODOSTUMISEN SUHDE YKSIVUOTISISSA MÄNNYN VERSOISSA

The proportions of needle and wood in current-year shoots in crown systems of young Scots pine *(Pinus* sylvestris L.) trees was studied. The proportion of needles out of the total shoot biomass increased according to the increasing number of the whorl counted from the apex. In the lower part of the crown system the needle biomass of newly-formed shoots was 50—60 fold compared to that of wood and bark biomass. In the upper part of the crown system the same ratio was 1—2. The variation in ratio between needle and wood biomass was whorl-specific and independent of tree class. The magnitude of the ratio was not related to the position of the tree in the stand nor to the prevailing light conditions within the stand.

INTRODUCTION

The availability of photosynthates for growth modifies the growth and structure of a tree stand. Especially, the allocation of photosynthates for different growth components, *i.e.* stem growth, crown growth, and root growth, determines the actual growth and structure of an individual member of tree stand as demostrated *e.g.* by PROMNITZ (1975). MONSI and MURATA (1970) have, among others, paid attention to the role of photosynthate allocation in tree growth and emphazised the influence of dry matter ditribution on the development of photosynthetic system.

Photosynthate allocation in plant growth is apparently associated with the light conditions inside the stand (cf. MONSI and MURATA 1970). Consequently, tree-to-tree variation in the photosynthate allocation system is apparently dependent on the position of the tree within the stand. On the other hand, tree-to-tree variation in the allocation of photosynthates for shoot and needle growth should exist owing to the importance of needle biomass in the survival of stand members.

The aim of the present paper is to investigate the allocation of photosynthates for needle growth and wood formation in current-year shoots in young Scots pine *(Pinus sylvestris* L.) trees. The main hypothesis is that there is within- and between-tree variation in the allocation system which is related to the position of the branches within a tree, and the position of the tree within a stand.

MATERIAL AND METHODS

The material consists of stands number 1—5 in the material by KELLOMÄKI and HARI (1980). The stands are situated near the Forest Field Station, University of Helsinki (60° 47′ N, 24° 18′ E, 150 m a.s.l.). The characteristics of these stands and the details of their measuring, environmental monitoring, the sampling of the study areas and whole tree analysis of the sample trees are described by KELLOMÄKI and HARI (1980).

The following sample tree characteristics were used in the present analysis: total length, diameter at height of 1,3 m above ground level, height of each whorl, needle biomass of each whorl divided into three age classes, amount of wood and bark in current year shoots, and the amount of respective needle biomass and the relative height of each tree. In addition, the photosynthetic light ratio for each whorl as well as the position coefficient for each sample tree were utilized in the analysis. These concepts are described by ILONEN *et al.* (1979) and KELLOMÄKI and HARI (1980).

RESULTS

The regression between the amount of wood and bark and respective neede weight of current-yearshoots for the first, second, third and fourth whorl from the apex are presented in Fig. 1. A shift to a steeper regression exists when the regression is related to whorl number. This trend is clear until the 13th—14th whorl as appears from Table 1. The subsequent values are also smaller than expected on the basis of the previous trend. The number of observations is, however, rather limited and the amount of variation explainable by the chosen regression model is also quite low.

The shift to steeper regressions is greatest in the first four whorls counting from the apex (Fig. 2 and Table 1). As a whole the dependence of the regression coefficients between needle and xylem growth in current-year-shoots on the number of the whorl is sigmoid, which levels off in the 13th and 14th whorl. In these whorls the needle biomass of the newly formed shoots is 50—60 fold compared to that of the xylem in the shoot. In the first whorl from the apex this ratio is 1—2 as appears from Table 2. In other words, the proportion of needle biomass increases at the expense of xylem in current-year shoots as the ratio between needle and xylem biomass in the same shoots is related to increasing whorl number from the apex (Fig. 3).

The regression between the needle and xylem biomass in the same shoots represents trees in different position in the stands, *i.e.* dominant trees as well as suppressed trees. Especially in the upper parts of the crown system, the whorl-specific regressions hold well and no further explantion power was obtained when the tree position was included in the analysis. The variables describing the light climate within the stand, *i.e.* photosynthetic light ratio per whorl and position coefficient per tree, did not increase the proportion of the explained variation in the regressions. Even the relative height of the tree gave no further explanation.
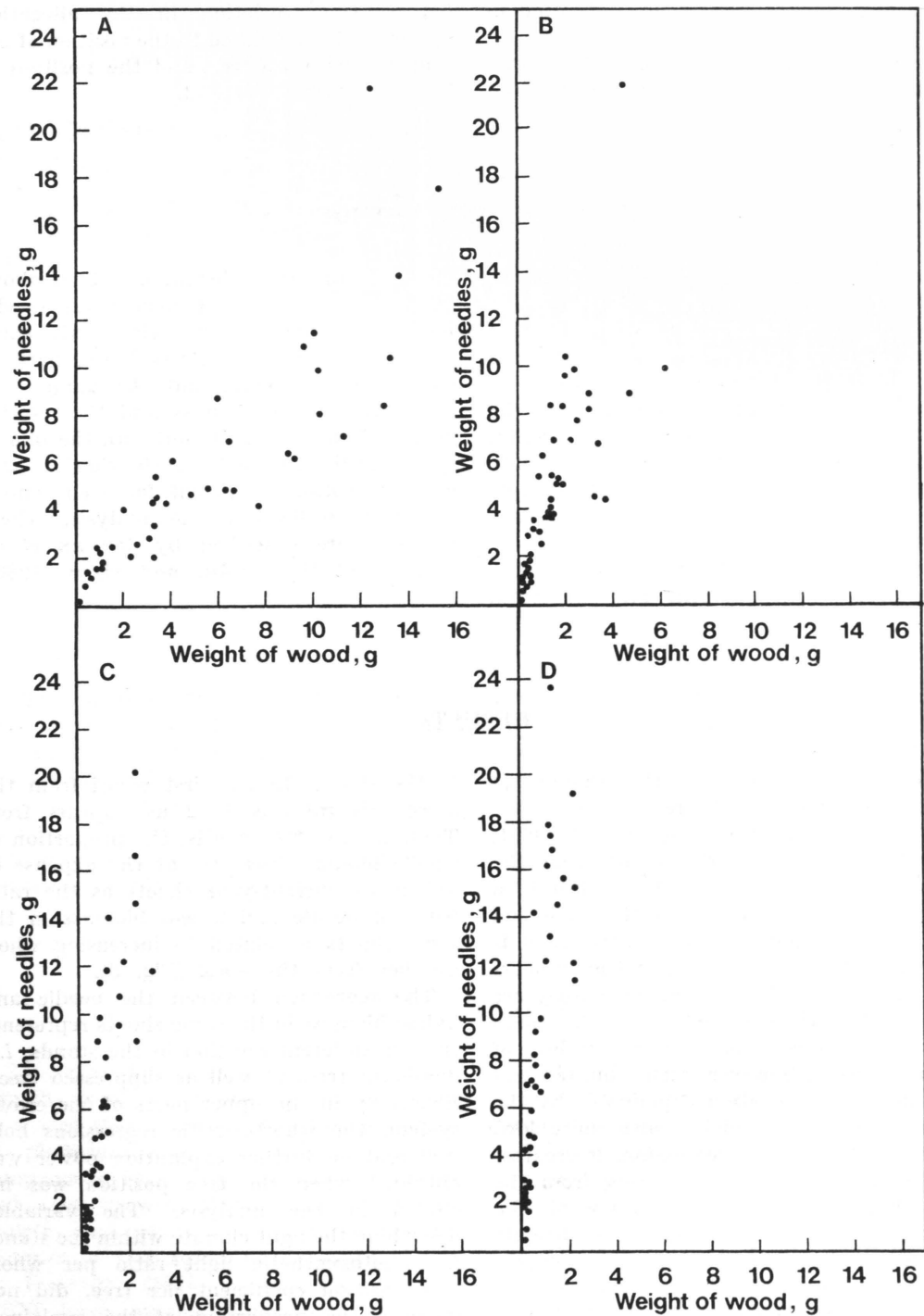
Fig. 1. Regression between dry weight of wood and weight of needles: A: in first whorl from apex, B: in second whorl from apex, C: in thrid whorl from apex, D: in fourth whorl from apex.
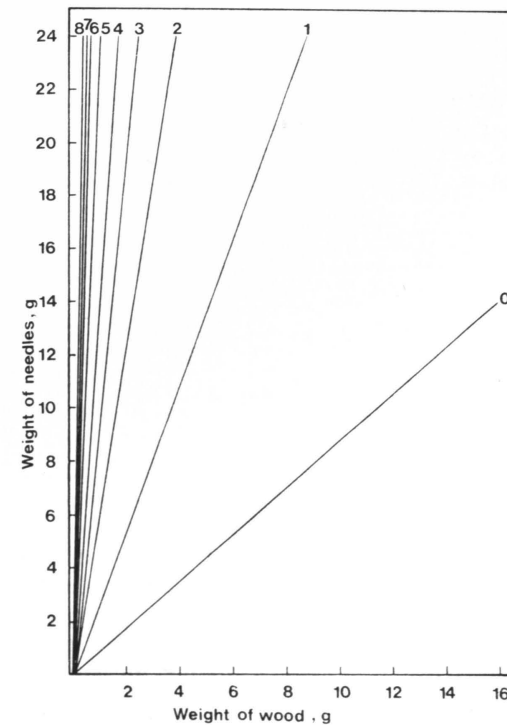
Fig. 2. Fitted curves for regression between dry weight of wood and weight of needles in the first through ninth whorls from the apex. For parameters of the models see Table 1.
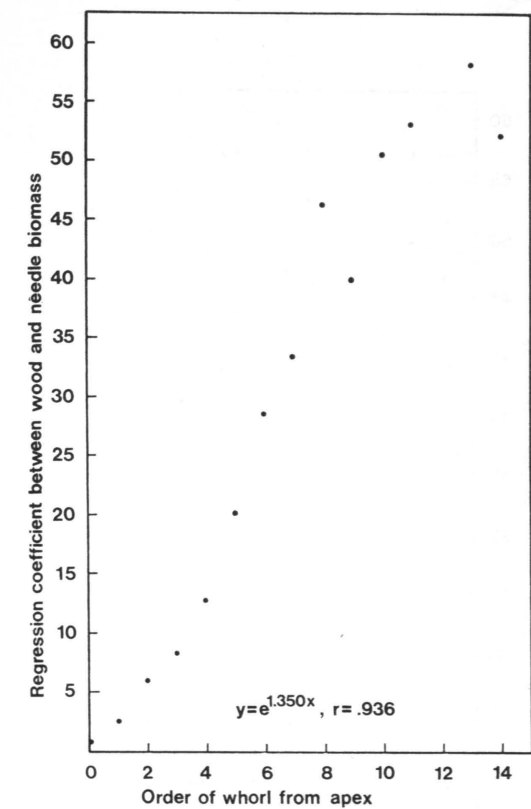

Fig. 3. Dependence of parameters for regression between dry weight of wood and weight of needles in order of whorl from apex.

Table 1. Parameters for regression between wood and needle dry weight per whorl.[1])

Whorl number from apex	Regression coefficient	Standard deviation for regresion coefficient	R^2
0	.883	.045	.860
1	2.696	.169	.806
2	5.775	.342	.823
3	8.313	.554	.787
4	12.753	.792	.810
5	20.029	.183	.661
6	28.653	2.512	.688
7	33.394	2.985	.695
8	46.267	5.463	.589
9	40.350	5.222	.565
10	50.432	6.622	.586
11	53.016	6.298	.633
12	18.151	5.375	.226
13	58.023	8.061	.597
14	52.222	7.875	.603
15	72.490	10.841	.670
16	55.156	12.032	.553
17	43.581	11.529	.488
18	30.792	10.249	.530

[1]) A model $y = ax$ where y is needle weight and x shoot weight was employed in calculations.

Table 2. Mean values for ratio between needle growth and wood formation per whorl.

Whorl number from apex	Ratio between needle and shoot growth		
	n	$\overline{x}$	s
0	49	1.240	.629
1	47	3.690	1.308
2	47	6.918	3.390
3	45	11.760	6.005
4	45	18.236	10.124
5	44	26.558	18.099
6	43	32.984	28.844
7	34	39.845	31.564
8	29	57.299	75.693
9	30	49.922	65.792
10	23	54.319	44.595
11	24	51.367	53.034
12	17	59.118	46.405
13	14	71.738	61.477
14	14	61.571	43.863
15	10	88.500	46.371
16	8	62.125	42.616
17	8	43.625	35.741
18	4	25.500	13.503
Total	536	30.367	41.333
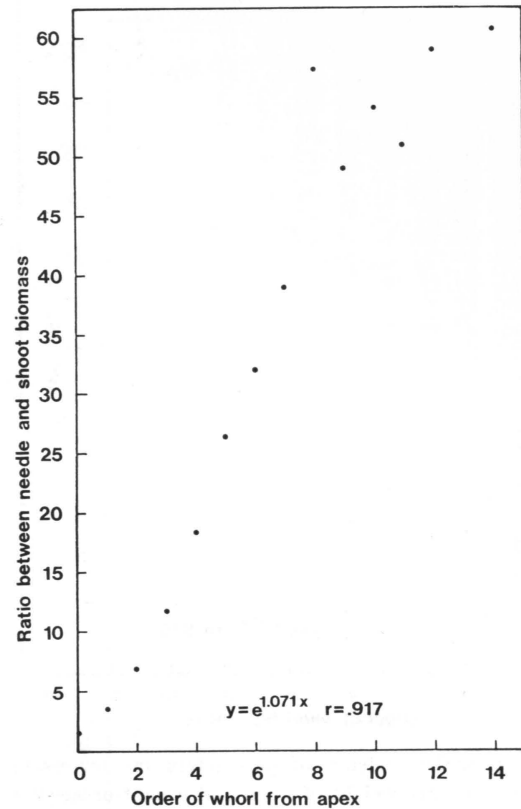
Fig. 4. Dependence of ratio between needle biomass and wood biomass on order of whorl from apex.

$$y = e^{1.071x} \quad r = .917$$

DISCUSSION

The regression between the amounts of needle and xylem biomass in the same shoot was whorl-specific and no significant correlation was found between this regression and tree position or availability of photosynthates. Therefore it is suggested that the allocation of photosynthates for needle growth and wood formation in current-year shoots of branches is profoundly affected by the genotype of the trees. Presumably this control system is tree-specific and one of the determinants affecting the growth and structure of the crown system.

The increasing proportion of needle biomass in the lower parts of the crown system is interpreted as adaption to the decreasing light conditions and increasing competition that exists in any even-aged stand within the closed canopy. For example, GRIME (1977) has suggested that the most prominent characteristic of competetive plants is the mechanism of phenotypic response which maximizes the capture of resources. The increased allocation of photosynthates for needle growth improves, under shaded conditions, the survival of the trees and branches through the increased amount of photosynthates made available for growth.

These mechanisms are advantageous, in particular, in environments where high rates of capture of energy, water and mineral nutrients can be maintained. The negligible influence of environmental factors on the allocation of photosynthates to needle and xylem growth may, however, indicates that the high rate of resource capture is not the only factor affecting the adaptation of cots pine to the changing environment. During the early phases of forest succession, when Scots pine characteristically dominates, the stable allocation system is more preferable. Under unpredicatable conditions as in the early phase of succession, such an allocation system of photosynthates is capable of improving the survival capacity (cf. BORMANN and LIKENS 1979, pp. 118—128). Therefore the negligible influence of environmental factors on the photosynthetic allocation system improves its reliability and enables the effects of unexpected conditions in community development to be avoided.

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SELOSTE:

NEULASTEN KASVUN JA PUUN MUODOSTUMISEN SUHDE YKSIVUOTISISSA MÄNNYN VERSOISSA

Tutkimuksessa on tarkasteltu neulasten ja puuaineen määrän suhdetta männyn *(Pinus sylvestris* L.) vasta muodostuneissa versoissa. Suhde kasvoi nopeasti siirryttäessä latvuksen yläosasta alaosaan. Alimmissa oksakiehkuroissa neulasia syntyi 50—60 kertaa enemmän kuin puuainetta muodostui. Latvuksen yläosassa neulasten määrä oli sen sijaan vain 1—2 kertainen puuaineen määrään verrattuna. Em. suhde oli oksakiehkurakohtainen. Suhteen suuruuden ja puun aseman tai metsikön sisäisen valaistuksen välillä ei voitu osoittaa tilastollisesti merkitsevää riippuvuutta.