Allocation of Above-ground Growth in *Pinus sylvestris* – Impacts of Tree Size and Competition

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The effect of tree age, size and competition on above ground growth allocation was studied with 69 *Pinus sylvestris* trees. Competition was described by tree-level indicators (needle density, crown ratio and height-diameter ratio). The stem, branch and needle growth were determined by stem and branch radial increments and tree level biomass analysis. Combined growth of compartments was strongly correlated with needle mass. Furthermore, tree age, size and competition indicators affected the allocation of growth among the compartments. The allocation of growth to stem and needle increased with tree age and size while the allocation of growth to branch decreased. The increasing crown ratio increased allocation of growth to branches. The combined growth of the components and separate growth of needles, branches and stem were related to needle mass. However, competition and tree size were significant additional explanatory variables when the stem, branch and needle growth were estimated according to needle mass. The growth efficiency increased with relative tree height and decreased with increasing needle density.

Keywords allocation, growth efficiency, Scots pine
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Symbols

γ_{b1} = Branch allocation ratio between stem and branch (= $i_{br}/(i_{br}+i_s)$)
γ_{b2} = Branch allocation ratio between stem, branch and needles (= $i_{br}/(i_{br}+i_s+i_n)$)
γ_{n2} = Needle allocation ratio between stem, branch and needles (= $i_s/(i_{br}+i_s+i_n)$)
γ_{s1} = Stem allocation ratio between stem and branch (= $i_s/(i_{br}+i_s)$)
γ_{s2} = Stem allocation ratio between stem, branch and needles (= $i_s/(i_{br}+i_s+i_n)$)
a = Branch cross sectional area at stem junction [mm^2]
b = Branch cross sectional area at first living sub-branch stem junction [mm^2]
S_a = Stem age
B_a = Branch age
B_{BM} = Regression model for branch woody biomass at branch level [g]
B_{GM} = Annual branch woody biomass growth at branch level [g/yr]
B_{NM} = Regression model for needle biomass at branch level [g]
c = a * (branch distance from the top/C_L)
C_A = Crown surface needle density (needle mass/surface area of crown cone) [kg/m^2]
C_{hr} = crown ratio (C_L/H)
C_L = Crown length [cm]
C_r = Crown radius [cm]
C_V = Crown volume needle density (Wf/volume of crown cone) [kg/m^3]
d = b * (branch distance from the top/C_L)
D_{bh} = Diameter at breast height [cm]
e = $b * B_a$
H = Tree height [cm]
H_D = Competition index (H/D_{bh})
H_{rel} = Relative height of sample tree (H/average height of the standing trees)
i_b = Branch biomass growth of tree during the last growing season [g/year]
i_{br} = Regression model for branch radius growth at branch level (Mäkinen 1999)
i_H = Tree height growth during the last growing season
i_n = Needle biomass growth of tree during the last growing season [g/year]
i_s = Stem biomass growth of tree during the last growing season [g/year]
i_{sr} = Stem radial growth at breast height (1.3 m) during the last growing season [mm/year]
i_{tot1} = Total growth of stem and branch ($i_s + i_{br}$) during the last growing season [g/year]
i_{tot2} = Total growth of stem, branch and needles ($i_s + i_{br} + i_n$) during the last growing season [g/year]
N_{eff1} = Needle efficiency in terms of stem and branch biomass growth (i_{tot1}/Wf)
N_{eff2} = Needle efficiency in terms of stem, branch and needle biomass growth (i_{tot2}/Wf)
N_{GM} = Regression model for needle biomass growth at branch level [g/year]
Wf = Tree level needle mass [g]

1 Introduction

Trees have ability to adapt their structure to environment (Davidson 1969, Whitehead et al. 1984, Schoettle 1990) by shifting the allocation and turnover rates of plant components. The effects of tree size and competition on tree structure can be seen even with the naked eye; but the phenotype of the tree does not indicate the current pattern of growth allocation. Instead, the current pattern of allocation among plant components must be determined from the representative growth characteristics.

The growth of merchantable timber is known to be dependent on tree age, size, and competition of a tree (Anderson 1975). Recently, the need to understand the behaviour of the unmerchantable compartments (branch, needles, roots and bark) has increased due to an increasing number of physiologically based models aiming to predict tree growth and while the significance of the unmerchantable compartments in the carbon budget of trees is dominating. Fine roots alone have been reported to account for more than 50 % of the total net primary production of a forest ecosystem (Ågren et al. 1980, Grier et al. 1981, Fogel 1983, Vogt et al. 1986). Furthermore, tree size and competition may influence the productivity of needles (Perry 1985, Ryan and Waring 1992, Hubbard et al. 1999).

The effects of competition on growth allocation have been studied earlier with younger trees. Nilsson (1993) concluded that increased competition increases allocation of growth to the stem and decreases growth allocation to needles in *Pinus sylvestris*. Further, he noticed that *Picea abies* was less plastic to competition than *Pinus sylvestris*. Vanninen and Mäkelä (2000) also found that increasing competition increased allocation to stem wood growth in older *Pinus sylvestris* trees. However, empirical studies on growth allocation in old and large trees are very few, although it is clear from physiological (Mäkelä 1997, Hubbard et al. 1999) and mechanical (Cannel and Dewar 1994) points of view that the observed pattern of growth allocation cannot necessarily be generalised from young to old trees.

The estimation of the annual above ground growth through destructive measurements becomes more difficult with old trees, particularly, due to the development of the branch system. The measurement of stem growth is relatively easy using methods of stem analysis. The needle growth can be estimated according to measurements of the youngest needle sets, but the branch growth is more complicated because it includes both radial and axial components. Branch growth has often been estimated at the stand level by comparing estimates of branch biomass in a cross-sectional age series (Madgwick et al. 1977, Linder and Axelsson 1982, Axelsson and Axelsson 1986, Kuuluvainen and Kanninen 1992, Nilsson and Gemmel 1993). Nilsson and Albrektson (1993) made an intensive study with 16-year-old trees in which branch growth was estimated as the difference between the biomass of shoot axes of consecutive whorls. However, there are only few studies on the development of branch growth in individual trees over the lifetime of trees.

In this paper, the effects of tree size and competition on allocation of above ground components were studied by means of destructive biomass analysis. Further, the ratio of different growth components and needle mass (needle efficiency) were studied as a function of tree age, size and competition. The present study is an extension of earlier work on growth allocation between needles and stem (Vanninen and Mäkelä 2000), now including the branch growth and a larger number of trees.

2 Material and Methods

2.1 Material

The material consisted of a total of 69 *Pinus sylvestris* trees collected during three different sampling years 1994, 1996 and 1997. The material represents trees of different age and competition. Competition was described by tree-level indicators. Sample stands were located in southern Finland and differed in age and stocking density (Table 1). All sites represented the *Vaccinium myrtillus* site type, determined by understory vegetation (Cajander 1925). The stands sampled in 1994 and 1996 have been described earlier by Mäkelä and Vanninen (1998) and the 1997 stand by Vanninen and Mäkelä (2000).

Table 1. Stand characteristics.

Stand	Location	Mean age [years]	Density [N/hectare]	Basal area [m^2/hectare]	Year
5d	61°48´N, 24°19´E	16	18727	21	1997
5s	61°48´N, 24°19´E	15	2584	10	1997
1d	61°48´N, 24°19´E	27	2675	28	1994
1s	61°48´N, 24°19´E	37	1105	20	1994
47d	61°20´N, 25°00´E	41	2914	35	1996
47s	61°20´N, 25°00´E	41	693	23	1996
45d	61°17´N, 27°00´E	71	1070	33	1996
45s	61°17´N, 27°00´E	71	455	19	1996

Table 2. Sample tree characteristics.

Stand	Number of sample trees				Diameter [a] [cm]		Tree height [m]	
	H_D 1 [b]	H_D 2 [b]	H_D 3 [b]	Total N/ plot	Mean	Range of variation	Mean	Range of variation
5d	1	2	4	7	4.6	2–9	5.1	4–8
5s	1	2	-	3	7.7	6–10	6.8	6–7
1d	1	5	7	13	10.1	5–16	11.5	10–13
1s	2	10	3	15	14.0	9–19	13.6	11–15
47d	-	3	6	9	11.9	6–19	13.6	12–17
47s	1	2	-	3	19.3	16–24	17.1	15–18
45d	-	3	12	15	18.0	12–26	22.0	18–27
45s	-	3	1	4	20.7	17–24	22.1	19–25

[a] Stem diameter at 1.3 meter height without bark.
[b] H_D, tree slenderness, is defined as height divided by breast height diameter (Mäkinen 1999). The classification limits for H_D 1–H_D 3 are 70–100, 100–160, 160–250 respectively. H_D 1 represents the most dominant trees and H_D 3 the most suppressed trees.

The selection of sample trees differed slightly in different years, but in all years the objective was to sample trees in a representative range of the competition (Mäkelä and Vanninen 1998, Vanninen and Mäkelä 2000). In 1996 and 1997, the trees were first divided into dominant (100 thickest trees per hectare) and the rest as suppressed trees, and these groups were further divided into three subclasses of equal cumulative basal area. Trees were sampled from each of these subclasses so as to represent the whole diameter range of the stand. In 1994, all the standing trees were arranged by breast height diameter into subclasses of equal cumulative basal area and five trees were sampled from each subclass. The deviation of sampled trees by size is presented in Fig. 1 and the distribution of sample tree material by stand, stocking, and competition and tree slenderness (H_D = the ratio of height to breast height diameter) is presented in Table 2.

Stem and branch dimensions were measured for the regression analyses of needle and branch biomass and needle growth estimates. Measured variables were: branch diameter at the stem junction and at the lowest live sub-branch, whorl number, stem diameter below the whorl and the distance of the whorl from the top. All the measurements were considered at the end of the growing season. Ten sample branches were taken systematically throughout the crown length from each tree for needle and branch biomass estimation. The sample branches were separated into needles and branchwood. In the measurements in 1996, the needles in each sample branch were

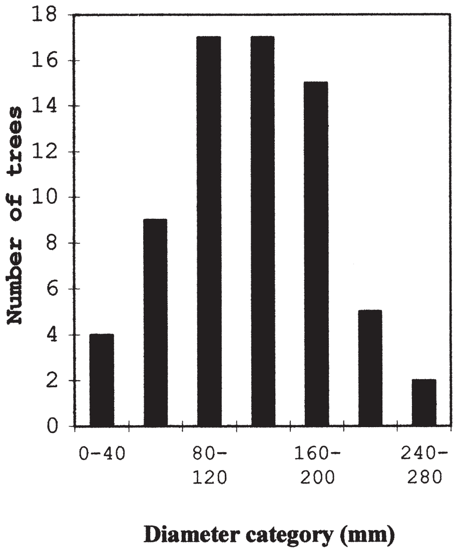

Fig. 1. The frequency distribution of sample trees by breast height diameter classes.

further divided into age classes to estimate needle biomass growth. Then the separated compartments were dried 48 h at 105 °C.

For stem analysis, a minimum of 9 stem disks were taken from different heights: 10 cm, 50 cm, 130 cm, at the middle of the bole below the crown base, at crown base, and at 25%, 50%, 75% and 90% of the length of the live crown from the base of the crown. The sampling heights of the stem disks were not exactly same with the dataset of 1994 (Mäkelä and Vanninen 1998). For the stem volume and stemwood density determinations the diameters of each sample disks were measured into two opposite directions for heartwood, sapwood and over the bark. The fresh volume of each disk was measured by immersion and dry weight after drying (48 h, 105 °C).

Table 3. Model characteristics for branch level branch biomass [g] (B_{BM}), needle biomass (B_{NM}) and needle biomass growth [g] (N_{GM}) models used for calculating the tree level estimates.

Stand/plot	Model	Variables [a)]	Range of r^2
5d	B_{BM}	a, B_a	0.71–0.99
5d	B_{NM}	b, d	0.62–0.95
5s	B_{BM}	a, B_a	0.81–0.98
5s	B_{NM}	b, d	0.67–0.87
1d	B_{BM}	a, b, e	0.86–0.97
1d	B_{NM}	b, d	0.68–0.83
1s	B_{BM}	a, b, e	0.92–0.95
1d	B_{NM}	b, d	0.86–0.90
47d	N_{GM}	b, d	0.50–0.97
47d	B_{BM}	a, c	0.91–0.99
47d	B_{NM}	b, d	0.50–0.98
47s	N_{GM}	b, d	0.86–0.98
47s	B_{BM}	a, c	0.89–0.98
47s	B_{NM}	b, d	0.77–0.91
45d	N_{GM}	b, d	0.66–0.98
45d	B_{BM}	a, c	0.77–0.99
45d	B_{NM}	b, d	0.66–0.99
45s	N_{GM}	b, d	0.59–0.97
45s	B_{BM}	a, c	0.88–0.96
45d	B_{NM}	b, d	0.86–0.98

[a)] For definitions, see the list of abbreviations.

2.2 Methods

Total needle dry mass (*Wf*) was estimated for each tree with the help of branch level linear regression models that were explained by branch diameter and position in the crown (Table 3). In order to find the most consistent variables for branch level needle biomass models (B_{NM}), all the sampled branches were first combined and the independent variables were selected using the best-subset-regression method. Models using those variables were further fitted separately for each tree, or, in the case of the 1994 dataset, for each sampling class (Mäkelä and Vanninen 1998) (Table 3). *Wf* was the sum of the branch-level masses of the tree, determined using the estimated treewise models. The annual tree level needle dry weight growth (i_n) was analysed for the sample trees of 1996. Branch level needle growth was approximated from the sample branches as the average needle mass of the two latest needle cohorts. The method for calculating tree level needle growth, i_n, from sample branches was the same as for calculation total needle mass. Branch level needle growth models (N_{GM}) were fitted for the sample branches of each sample tree separately (Table 3).

The annual branch growth, B_{GM}, was determined using branch woody biomass models (B_{BM}) (Table 3), developed in the same way as the B_{NM}- and N_{GM}-models. The growth of each living branch was calculated as the difference of branch biomass (Table 3) at the end of the growing season (measuring time) and the biomass before the growing season. The branch biomass before the growing season was estimated by backdating the variables used in the B_{BM} model to the time before the growing season. The backdating was done using the branch radial growth model (1) developed by Mäkinen (1999) and recorded whorl distance measurements from the sampling trees.

$$\log(i_{br}) = a_0 + a_1 i_{sr} + a_2 * H_D + a_3 B_a + a_4 \log(B_a) \tag{1}$$

where i_{sr} (mm) = stem radius growth at breast height (mm), H_D = stem height/stem diameter during the last growing season (cm), B_a = branch age, $a_o = 1.78213$, $a_1 = 0.24944$, $a_2 = –0.007256$, $a_3 = –0.06326$ and $a_4 = –0.40300$ (Mäkinen 1999).

The branch radial growth model of Mäkinen 1999 was developed using data sampled from 19 even aged thinning experiments on pure *Pinus sylvestris* stands in southern and central Finland (12 trees/stand, totally 229 trees). Stands aged between 22–76 years. The differences between the current and backdated branch biomasses of each living branch were calculated and combined to tree level branch growth for the last growing season (i_b).

Corresponding stemwood growth (i_s) was determined by stem analysis and wood density analysis. Stem analysis was carried out using the WinDendro and XlStem programs of Regent Instruments. Width of the annual ring was measured at all cardinal points (the inter-cardinal points also from the 1996 dataset) from each of the stem disks. The annual stem volume growth was calculated by the XlStem-program according to sample disks heights and measured annual radial growth from the disks. The wood density of stem was determined according to measured stem volumes and dry-fresh density. Stem volumes were calculated as the sum of the truncated cones defined by the consecutive sample disks. Stem volume was converted to mass piece by piece, using measurements of dry-fresh density in the sample disks and assuming that the density of a log between two disks was the average of the two density measurements. Stem volume growth was converted to stem biomass growth, i_s, using the mean dry-fresh density of each stem (= stem mass/stem volume). The calculated annual biomass increments were further combined to $i_{\mathrm{tot1}} = (i_s + i_b)$ and $i_{\mathrm{tot2}} = (i_s + i_b + i_n)$.

The competition was described by relative height (H_{rel}) and the height to diameter ratio (H_D). Some further characteristics were derived in order to describe the structure of the sample trees: crown ratio (C_{hr}) is the ratio of crown length to tree height, needle density of the crown cone area (C_A) and needle density of crown volume (C_V). The crown cone area and crown volume were calculated based on crown length (C_L) and crown basal area, which was determined on the basis of measured crown width at the crown base.

The relative growth allocation was studied by comparing the growth of different components. Because needle growth was measured only in the 1996 dataset, the growth allocation was calculated between stem (γ_{s1}) and branch (γ_{b1}) in the whole data set and between stem (γ_{s2}), branch (γ_{b2}), and needles (γ_{n2}) in the 1996 data set. The growth allocation coefficients were determined as follows:

$$\gamma_{i1} = i_i / (i_s + i_b) \qquad i = s, b \tag{2}$$

$$\gamma_{i2} = i_i / (i_s + i_b + i_n) \qquad i = s, b, n \tag{3}$$

Two different indeces were calculated for needle efficiency

$$N_{\mathrm{eff1}} = i_{\mathrm{tot1}} / Wf \tag{4}$$

$$N_{\mathrm{eff2}} = i_{\mathrm{tot2}} / Wf \tag{5}$$

The influence of competition on growth of different components was studied with regression analysis by first regressing growth component and needle mass (Eq. 6) and then testing several competition variables in the model

$$Y = a_1 * Wf + a_2 * X + a_0 \tag{6}$$

where Y is the growth component (i_{tot1}, i_{tot2}, i_b, i_n, i_s), Wf is needle mass, X is the additional explanatory variable, and a_0, a_1 and a_2, are regression parameters. Log-transformation was used with i_b because of the heteroscedastic variances between i_b and Wf.

The effect of competition on determined allocation coefficients (Eqs. 2–3) and needle efficiency

Table 4. Variables providing the best improvement to compartment specific growth model. The additional variables, X, providing the best improvement of fit to the simple regression (with $P<0.05$), are reported below. For abbreviations see the list of symbols.

Compartment (Y) [a]	Additional variable (X)	Effect	P-value	R^2	n
i_{tot1}	S_a	–	<0.001	0.81	69
i_{tot1}	C_{hr}	+	0.003	0.77	69
i_{tot1}	H	–	0.005	0.77	69
i_{tot1}	H_D	–	<0.001	0.80	69
i_{tot1}	H_{rel}	+	0.020	0.76	69
i_{tot1}	i_H	+	<0.001	0.83	69
i_{tot2}	S_a	–	0.048	0.91	31
i_{tot2}	C_{hr}	+	0.028	0.92	31
i_{tot2}	C_A	–	0.007	0.91	31
i_{tot2}	H_{rel}	+	0.022	0.92	31
i_{tot2}	i_H	+	<0.001	0.93	31
$\ln(i_b)$	S_a	–	0.003	0.55	69
$\ln(i_b)$	C_{hr}	+	0.002	0.56	69
$\ln(i_b)$	H_D	–	<0.001	0.79	69
$\ln(i_b)$	i_H	+	<0.001	0.61	69
i_n	C_A	–	0.036	0.91	26
i_n	C_L	+	0.046	0.93	31
i_s	S_a	–	0.007	0.79	69
i_s	C_A	–	0.020	0.90	69
i_s	H_D	–	0.004	0.79	69
i_s	H_{rel}	+	0.025	0.78	69
i_s	i_H	+	<0.001	0.81	69

[a] See the list of symbols.

Table 5. Correlation table of variables best ($p<0.1$) describing the needle efficiency and growth allocation of sample trees. For abbreviations see the list of symbols.

Dependent variable	Independent variable	P-value	R	n
N_{eff1}	S_a	<0.001	–0.69	69
N_{eff1}	C_{hr}	0.005	–0.33	69
N_{eff1}	D_{bh}	<0.001	–0.45	69
N_{eff1}	F_A	<0.001	0.65	36
N_{eff1}	C_L	0.002	–0.36	69
N_{eff1}	H	<0.001	–0.55	69
N_{eff1}	i_H	<0.001	0.66	69
N_{eff2}	S_a	0.030	–0.39	31
N_{eff2}	D_{bh}	0.072	–0.32	31
N_{eff2}	C_A	0.001	–0.60	26
N_{eff2}	i_H	0.025	0.40	31
γ_{b1}	S_a	<0.001	–0.71	69
γ_{b1}	C_{hr}	0.005	0.33	69
γ_{b1}	D_{bh}	<0.001	–0.54	69
γ_{b1}	H	<0.001	–0.72	69
γ_{b2}	i_H	<0.001	0.54	69
γ_{b2}	S_a	<0.001	–0.77	31
γ_{b2}	D_{bh}	0.018	–0.42	31
γ_{b2}	H	<0.001	–0.64	31
γ_{b2}	i_H	<0.001	0.62	31
γ_{n2}	S_a	0.019	0.42	31
γ_{n2}	D_{bh}	0.065	0.33	31
γ_{n2}	H_D	0.074	–0.33	31
γ_{n2}	H	0.065	0.34	31
γ_{n2}	i_H	0.044	0.42	31
γ_{s2}	S_a	<0.001	0.62	31
γ_{s2}	H	0.002	0.53	31
γ_{s2}	i_H	0.006	–0.48	31

(Eqs. 4–5) were tested against measured tree size, age and competition characteristics using correlation analysis.

3 Results

Growth components were strongly correlated with needle mass ($r=0.86$ and 0.95 for i_{tot1} and i_{tot2}, respectively). In general, additional variables contributing to the estimation of growth can be interpreted as describing the light condition of the needles, such as the competition index, H_D, relative height, H_{rel}, crown ratio, C_{hr} or needle density, C_A (Table 4). Tree age decreased the growth with i_{tot1}, i_{tot2}, i_b and i_s (Table 4). Height growth, H_i, was positively correlated with needle growth, i_n. Wf alone was also a good predictor for i_n ($r=0.98$) and i_s ($r=0.88$), while there was more variation with i_b ($r=0.77$) (Fig. 2).

Variables describing tree size or age seemed to be related to growth allocation also. The γ_{b1} and γ_{b2} were negatively correlated with age and height and the opposite was the case for of γ_{s2} and γ_{n2} (Table 5). Height growth was positively correlated with γ_{b1} and $\gamma_{b2,}$ while γ_{n2} and γ_{s2} correlated negatively to height growth.

A significant correlation with a decreasing slope was found between needle efficiency and variables related to tree size (height, diameter and age). On the other hand, needle efficiency was

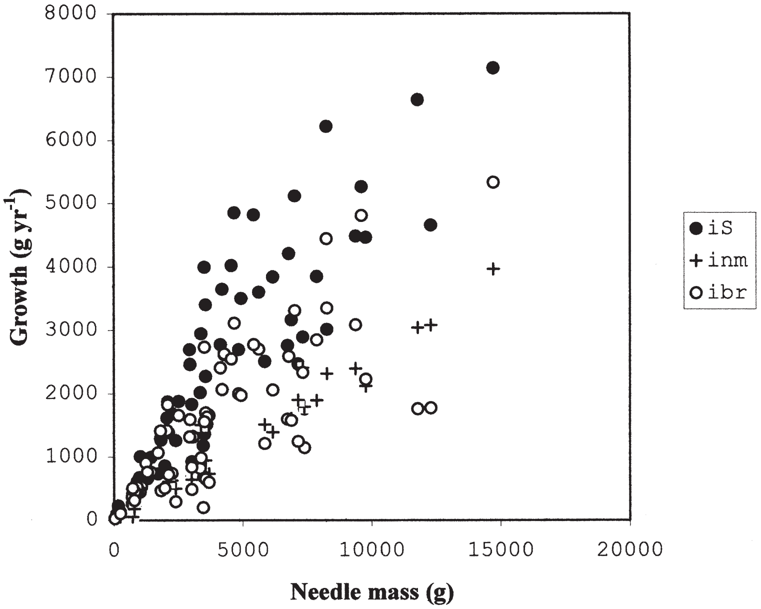

Fig. 2. The annual growth of stem (i_s), branches (i_{br}) and needles (i_{nm}) as a function of needle biomass.

greater in trees with larger crown ratio and faster height growth (Table 5).

4 Discussion

Branch growth was calculated by means of two statistical models. As the used branch radial growth model (Mäkinen 1999) was constructed for predicting timber quality it was based on the thickest branches of trees. It is possible that the radial growth of the thickest branches is greater than radial growth of average branch. If the branch radial growth model overestimates the radial growth of smaller branches, branch biomass growth would be overestimated also. However, the present results concerning allocation between the aboveground compartments were similar to those obtained by Nilsson (1993) for young *Pinus sylvestris* stands. The results of Nilsson (1993) indicate that growth allocation to stem wood increases with increasing tree size and further that intensified competition decreases allocation to branch wood.

In an earlier study (Vanninen and Mäkelä 2000), needle mass was found to be a good predictor of growth at the tree level, but variables describing competition and tree size improved the regression between growth and needle mass. The same was found in this study. Firstly, needle efficiency was affected by variables related to the light environment of the needles (H_r, C_V, C_A) indicating that trees receiving more light had more efficient needles. Secondly, the growth components (i_{tot1}, i_{tot2}, i_{br}, i_n, i_s) were affected by tree age and size. As the tree ages, one needle unit produced less growth in terms of determined growth components. While the effect of age on needle growth was also negative, but not statistically significant ($p = 0.53$), which may be due to the smaller dataset for determined needle growth component.

A commonly used explanation for the decrease in productivity with age of the tree is the increasing respiratory costs (Gower et al. 1996, Ryan et al. 1997a) as a result of increasing amount of respiring biomass, especially the woody compartments. This decreases the amount of net production available for growth. However, Lavigne and Ryan (1997) and Ryan et al. (1997b) have reported that the respiratory cost of wood does not increase sufficiently with age to account for the observed decrease in growth rates. Instead, changes in wood conductivity with tree age have been suggested to be responsible for the decrease in needle productivity (Ryan and Waring 1992, Hubbard et al. 1999). In addition, some empirical findings (Grier et al. 1981, Ingestad et al. 1981, Sprugel 1984) suggest that nutrient availability in soil may decrease as stands age. Ryan et al (in print) have recently published an interesting study where any of these (respiration, water conductivity and nutrients) explanations was not remarkable reason for the decreasing productivity of stand according to stand age.

The nutrient content of the needles may also cause differences in the productivity of the needles (Ågren 1996). According to nitrogen productivity theory (Ågren 1985) the productivity of needles increases according to their nitrogen concentration. However, nutrient concentrations of plant parts, *Pinus sylvestris,* (e.g. needles, wood) have not been observed to show a decreasing trend with stand age (Helmisaari 1990, Helmisaari 1992, Augusto et al. 2000). The ratio of stand level needle mass to fine root mass, often interpreted as an indicator of nutrient availability (Santantonio 1989), has also been observed to be relatively independent of stand age in *Pinus sylvestris* (Vanninen and Mäkelä 1999). Although no foliar nutrient analysis was carried out in this study, it would therefore appear that a shortage of foliar nutrients may not be a major factor limiting growth in the older *Pinus sylvestris* trees of the present data set.

The observed change in stem wood allocation with tree age or height is supported by the empirical findings of Albrektson and Valinger (1985) and Vanninen and Mäkelä (2000). Tree height and age are highly correlated ($r=0.92$ in this material) and according to the pipe model theory an increase in tree height increases the allocation to stem wood, assuming that the relative growth rate remains the same (Mäkelä 1986). Hence, tree height is probably a more reliable explanatory variable for the changes in allocation of stem wood than tree age.

The pattern of allocation of growth to needles was similar to stem, but the changes with tree height were just below statistical significance ($p=0.065$). In order to maintain tree vitality, the growth allocated to needles should exceed or at least equal the senescence rate of needles, which is greater than the senescence rate of the stem sapwood or branches. Needle mass, Wf, was strongly correlated with tree age and height, implying that needle growth should increase considerably with tree age and height. A similar increase in stem growth, however, may weaken the correlation between allocation of growth to needles and tree height or age. This could be a reason for not observing a statistically significant relation between allocation of growth to needles and tree height or age.

The allocation pattern of branch growth seemed to be related to the pattern of height growth. At the time of rapid height growth, just before canopy closure, the allocation of growth to branches increased. In contrast, in older and taller trees where height growth was slow, the allocation of growth to branches decreased. At the same time, there is usually less competition between trees and the light conditions are more stable, also reducing branch shedding and crown rise. The significance of growing space for growth allocation (Monsi and Murata 1970, Farmer 1976, Siemon et al. 1976, Mäkelä 1986, Mäkelä 1997) is reflected in the positive effect of C_{hr}, and C_r, on allocation of growth to branch. As the lower branches are exposed to more light, the senescence of those branches decreases and crown ratio increases. Crown radius, C_r, was significant for allocation of growth to branch (γ_{b1} and γ_{b2}); the wider the crown the greater the share of growth allocated to branches. Therefore, the growth allocation to branch may be decreased in favour of stem wood under severe competition (Cannell 1989, Brix and Mitchell 1983, Lavigne 1988, Nilsson and Albrektson 1993).

Although it was concluded that needle efficiency decreased with age and size, stem growth was nevertheless very strongly correlated with current needle mass (Fig. 2). This seemed to be because the decreasing trend in total growth was compensated by an increasing trend in growth allocation to the stems. We can therefore expect models predicting stem growth from needle mass or crown size to function fairly well over the rotation time of a stand (Mitchell 1975).

Allocation patterns differ among tree species, hence it may not be justified to generalise the present results to other tree species. For example, changes with tree age and size are faster in pioneer species than climax species and, further, shade tolerant species respond differently to competition than shade intolerant species (Waring 1987, Givnish 1986).

In a summary, the decreasing trend found in the total above-ground needle efficiency seemed to be mainly due to a decrease in the branch growth (i_{br}), while growth of stem, (i_s), needles, (i_n), remains surprisingly stable with age in the present data set. This may be partly due to the fact that increasing maintenance costs (or decreasing production) due to a larger size are partly compensated by an increase in the availability of light, which normally takes place at least in managed older stands.

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