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Original article

Patterns in individual growth, branch population dynamics, and growth and mortality of first-order branches of *Betula platyphylla* in northern Japan

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Abstract – Growth of individual trees, population dynamics of first-order branches within individuals, and growth and mortality of first-order branches were followed for two years in an plantation of *Betula platyphylla* in central Hokkaido, northern Japan. The data were analyzed by stepwise regressions. The relative growth rate in terms of above-ground biomass of individuals was negatively correlated with a log-transformed competition index (ln(*CI*)), which was calculated for each individual from the size and distance of its neighbours. The change in branch number within an individual was also correlated with ln(*CI*). The growth and mortality of branches was correlated with the size of branches, size of individuals, growth of individuals, relative height of branches, and ln(*CI*). Generally, the patterns revealed by the regressions were consistent with what was expected and can be used as references against which the behavior of more detailed process-based models can be checked.

***Betula platyphylla* / branch population dynamics / competition / branch growth / branch mortality**

Résumé – Modèles de croissance individuelle, dynamique de développement des branches et croissance et mortalité des branches du *Betula Platyphylla.* La croissance des arbres individuels, la dynamique de développement des branches de premier ordre sur les arbres individuels ainsi que la croissance et la mortalité des branches de premier ordre ont été étudiées pendant deux ans dans une pépinière de *Betula Platyphylla* de la région centrale du Hokkaido dans le nord du Japon. Les modèles de croissance individuelle, la dynamique de développement des branches et la croissance et la mortalité des branches ont été analysées selon leur régression progressive. Le taux de croissance relatif en termes de biomasse aérienne des arbres individuels s'est avéré en rapport inverse à l'index de concurrence des grumes (ln(CI)), après calcul pour chaque individu d'après la taille et l'éloignement de ses voisins. Le changement du nombre de branches sur un même individu est également en rapport avec ln(CI). La croissance et la mortalité des branches s'est avérée en rapport avec la taille des branches, la taille des individus, la croissance des individus, la hauteur relative des branches et ln(CI). En général, les modèles mis en évidence par les régressions sont conformes aux hypothèses avancées et peuvent servir de référence pour le contrôle d'autres modèles plus détaillés.

***Betula platyphylla* / dynamique de développement des branches / compétition / croissance des branches / mortalité des branches**

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1. INTRODUCTION

An individual tree is constructed from structural units growing and iterating within an individual [12, 45], and can be thought of as a population of structural units [45]. Thus far, various components of an individual plant such as branches, shoots, and metamers [34] have been used as the structural unit, or module, of a tree. In this paper, the term "module" is defined, following Harper [13], as "a repeated unit of multicellular structure, normally arranged in a branch system."

The spatial and static aspects of a module population within a tree can be expressed by the spatial distribution of modules within a tree. The distribution of modules is important because it determines the crown form and the amount of light captured by the crown; future growth is determined by the amount of captured light. Previous studies have reported the size and location of modules and angles between modules [e.g. 1, 4-6, 19, 26, 33].

The dynamic aspect of a module population within a tree can be expressed by the change in the number of modules within a tree. The number of modules is changed through the birth and death of modules [13]. Some studies have described the population dynamics (birth and death) of modules within trees [e.g. 18, 25, 28]. If the size of modules under consideration can change, the change in size (growth) of modules must also be considered [15, 16].

In reality, the spatial and dynamic aspects of module population within a tree are closely related. The distribution of modules determines the distribution of resources (e.g. light) which determines the dynamics of local module population. The dynamics of local module populations, in turn, determines the future distribution of resources. Thus, development of a tree should be understood as the dynamics (birth, death, and growth) of modules which occupy certain three-dimensional spaces within a tree [8, 15, 39].

The distribution of resources is largely affected by the presence of neighbouring individuals (or modules of neighbouring individuals) [2, 10]. This implies that the spatial distribution and sizes of neighbouring individuals (i.e. competitive status of the target individual) must be considered to better understand the module population dynamics within individuals interacting with neighbours. However, the relationship between module population dynamics within individuals and the competitive status of the individual is not fully understood, while the relationship between local competition and the size or growth of individuals is well-documented [e.g. 3, 42, 44].

In quantifying module population dynamics, some morphological traces such as bud scars or annual rings can be used for reconstructing the history of the development of modules [e.g. 4, 18, 31, 32, 39]. However, it is sometimes difficult to estimate module mortality by such reconstruction methods because these methods reconstruct the past of only presently living organs. In consequence, direct information about the branches that have already been shed cannot be obtained. Continuous observations of modules provide more detailed information on module population dynamics [16, 24, 27, 28].

For species with an erect main stem and lateral branches that are clearly distinguishable from the main stem, first-order branches (branches attached directly to the main stem) are a convenient unit for describing tree structure. The distribution of first-order branches is important because it determines the shape of the whole tree crown. For example, Kellomäki and Väisänen [18] reported the dynamics of the first-order branch population within individual trees of *Pinus sylvestris*. Jones and Harper [15] quantified the growth of first-order branches of *Betula pendula* by the number of buds or higher-order branches within branches, and analysed the effect of neighbouring trees. Although many tree architecture models include birth, mortality, and growth of branches [e.g. 17, 30], these processes are not well understood for first-order branches of trees.

In this paper, we analyze data obtained from a plantation of *Betula platyphylla* var. *japonica* (Miq.) Hara whose architecture is suitable for the observation of first-order branches. We use a simple index to express the competitive status of individual trees, and report 1) the patterns in growth of individuals, 2) population dynamics of first-order branches within individuals, and 3) how growth and mortality of first-order branches are related to the size and height of branches, the competitive status of individuals, and the size and growth of individuals.

2. MATERIALS AND METHODS

2.1. Study site and data collection

At the end of the growing season in 1993, a square plot (10 m × 10 m) was set up in an eight-year-old artificial plantation of *Betula platyphylla* in Shintotsukawa, central Hokkaido, northern Japan. *B. platyphylla* is a common deciduous tree in Hokkaido. It is a typical early-successional tree species characterised by its fast growth and shade-intolerance [21-23]. *B. platyphylla* produces two distinct types of shoots: long shoots and short shoots [9, 20]. Long shoots, which determines the overall crown shape, usually develop as lateral branches of parent long shoots [20]. In this study, we analyzed

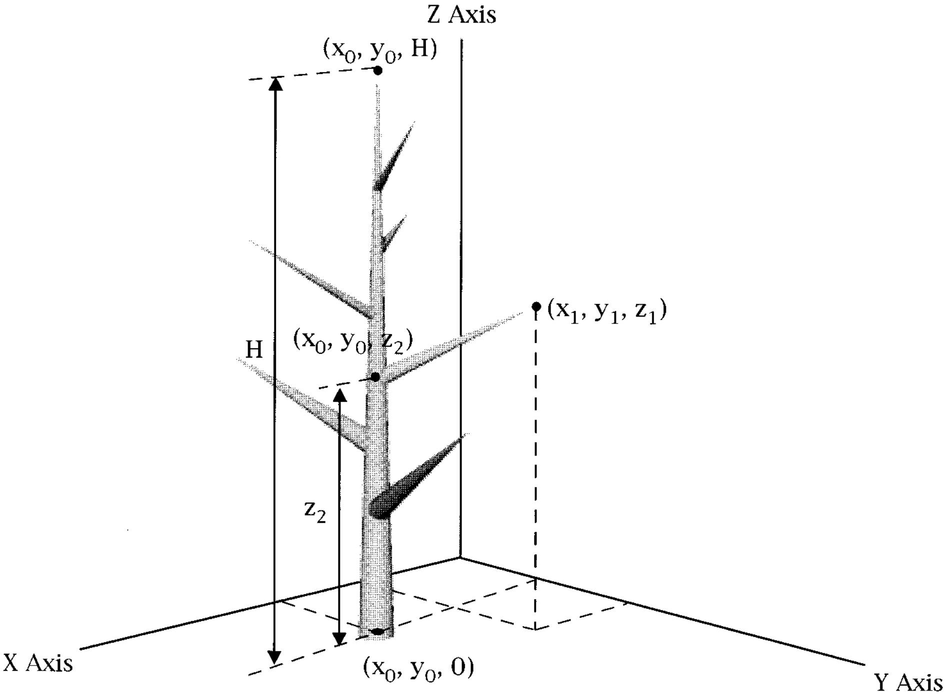

Figure 1. Diagram of the various measurements made on each tree during the study. (x_0, y_0, H): three-dimensional coordinates of the leader shoot tip, (x_1, y_1, z_1): three-dimensional coordinates of the tip of a branch, (x_0, y_0, z_2): three-dimensional coordinates of the base of a branch, (x_0, y_0, 0): three-dimensional coordinates of the base of the main stem of an individual. H: height of the leader shoot tip (tree height), z_2: height of the base of a branch.

the growth and mortality of first-order branches > 5 cm in length. First-order branches < 5 cm were not included.

All individuals within the plot were numbered. For each individual, diameter at breast height (*Dbh*), height of the leader shoot tip (tree height; denoted as H in *figure 1*), and the three-dimensional coordinates of the base of the main stem ((x_0, y_0, 0)) were recorded in 1993.

The three-dimensional coordinates of the tip ((x_1, y_1, z_1)) and base ((x_0, y_0, z_2)) of all first-order branches (> 5 cm in length) were determined with a measuring pole. If the main stem was not vertical, the x- and y-coordinates of the leader shoot tip and the bases of first-order branches were not (x_0, y_0) (i.e. the leader shoot tip was not at (x_0, y_0, H)). In this case, the horizontal deviation of the leader shoot tip from the base of the main stem was determined and necessary corrections were made in the coordinates of the leader shoot and the bases of first-order branches. In general, horizontal deviations of the leader shoot tips were small: the average deviation was 24.3 cm.

At the end of each growing season in 1994 and 1995, the same measurements were repeated so that dynamics data in two sequential one-year intervals (1993-1994 and 1994-1995) were available. In the measurements in 1994 and 1995, the deaths of first-order branches and three-dimensional coordinates of the first-order branches that developed in the current year were recorded. All the variables used in the equations are given in *table I.*

2.2. Biomass estimation

The branch length (*BL*) of the first-order branches was calculated from the three-dimensional coordinates of the base and tip of the branches, and then converted to foliar biomass (*FBbm*) and woody biomass (*WBbm*) using allometric equations. In 1995, thirty first-order branches, 15 of which were in the upper half of crowns and the rest of which were in the lower half, were sampled from trees in the same plantation adjacent to the 10 m × 10 m plot in order to develop equations that estimate *FBbm* and *WBbm* from *BL*. The sampled branches were taken to the laboratory and separated into foliar and woody components. The two components were dried and weighed. Log-transformed *FBbm* and *WBbm* were regressed on log-transformed *BL*.

The effect of the vertical position (upper half of crowns *vs.* lower half) of branches on the allometric equations was tested by analysis of covariance because the light intensity associated with the vertical position in crowns often affects the morphology and allocation of branches and leaves [25]. The branch vertical position had a significant effect on the intercept term in the

Table I. Description of variables used in equations.

Variable	Unit	Description
Individual level		
H	cm	Tree height (height of the leader shoot tip)
Dbh	cm	Diameter at breast height
Sbm	g	Biomass of main stem
$Agbm$	g	Above-ground biomass including main stem, branches, and leaves
$Agbm_i$	g	Above-ground biomass of the *i*-th neighbour
$AgbmI$	g year^{-1}	Above-ground biomass increment per year
$RgrAgbm$	g g^{-1} year^{-1}	Relative growth rate in terms of above-ground biomss per year
HI	cm year^{-1}	Height increment per year
$RgrH$	cm cm^{-1} year^{-1}	Relative growth rate in terms of tree height per year
B	year^{-1}	Birth rate of first-order branches per tree per year
D	year^{-1}	Death rate of first-order branches per tree per year
ΔN	year^{-1}	Change in first-order branch number per tree per year
CI		Competition Index
NN		Number of neighobouring trees within 2 m from a target tree
d_i	m	Distance from the *i*-th neighbor to a target tree
Branch level		
BL	cm	Length of a first-order branch
$FBbm$	g	Foliar biomass of a first-order branch
$WBbm$	g	Woody biomass of a first-order branch
$TBbm$	g	Total (foliage and woody) biomass of a first-order branch
BH	cm	Height of the base of a first-order branch
RBH		Ratio of the height of the base of a first-order branch to tree height
BE	cm year^{-1}	Elongation of a first-order branch per year
$FBbmI$	g year^{-1}	Increment in foliar biomass of a first-order branch per year
$WBbmI$	g year^{-1}	Increment in woody biomass of a first-order branch per year
$TBbmI$	g year^{-1}	Increment in total biomass of a first-order branch per year
BM	% year^{-1}	Branch mortality rate per year

equation predicting *FBbm* (foliar biomass of a branch). For *WBbm* (woody biomass of a branch), the effect of the branch vertical position was not significant. The obtained equations are as follows:

$$\ln(FBbm) = 2.55\ \ln(BL) - 8.76,$$

for upper branches,

$$\ln(FBbm) = 2.55\ \ln(BL) - 8.47,$$

for lower branches ($r^2 = 0.96$: the model with a common slope and two specific intercepts for branches in the upper and lower parts of crowns), and

$$\ln(WBbm) = 1.01\ \ln(BL) - 0.85,$$

for all branches ($r^2 = 0.82$). Total branch biomass (*TBbm*) for each branch was estimated by summing *FBbm* and *WBbm*. To estimate the main stem biomass (*Sbm*), a published equation was used [41]:

$$Sbm = 1.83\ Dbh^2 H$$

where *Dbh* is the diameter at breast height (cm), and *H* is the tree height (cm). By summing the biomass of the main stem of a tree and all first-order branches attached to the tree (including the foliar and woody biomasses), the above-ground biomass (*Agbm*) was calculated for each tree.

2.3. Data analysis

At the individual level, the relative growth rate in terms of above-ground biomass (*RgrAgbm*: g g^{-1} year^{-1}), the annual birth rate (*B*: year^{-1}) and the death rate (*D*: year^{-1}) of first-order branches per individual, and the annual net change in branch number per individual ($\Delta N = B - D$, year^{-1}) were analyzed. To detect patterns in these variables, stepwise regressions were carried out in which tree sizes (*H*, *Dbh*, and *Agbm*) and a log-transformed competition index (*CI*: explained below) were used as candidates for independent variables.

To evaluate the competitive effect of neighbouring individuals, a competition index (CI) was calculated for each target individual:

$$CI = \sum_{i=1}^{NN} \frac{Agbm_i}{d_i^{\,2}} \quad (1),$$

where $Agbm_i$ is the above-ground biomass of the i-th neighbour, d_i is the distance from the i-th individual to the target individual, and NN is the total number of neighbours. Here, neighbours were defined as individuals within 2 m of the target individual. CI was calculated for individuals within the 6 m × 6 m center quadrat in the 10 m × 10 m plot, and individuals outside the center quadrat were used only as neighbours. CI was log-transformed because the distribution of CI was positively skewed and it performed well when transformed.

Branch elongation (*BE*), the increment in foliar biomass of a branch (*FBbmI*), the increment in woody biomass of a branch (*WBbmI*), and the increment in total (foliar and woody) biomass of a branch (*TBbmI*) were analyzed to detect patterns in branch growth. We used 12 variables as candidates for independent variables in the stepwise regressions. They were classified into five categories: (1) branch size = foliar biomass (*FBbm*), woody biomass (*WBbm*), and total biomass (*TBbm*) of a branch; (2) vertical branch position = height of the branch base (BH; z_2) and height of the branch base relative to tree height ($RBH = z_2 / H$; see *figure 1*); (3) competitive status = log-transformed competition index ($\ln(CI)$); (4) size of an individual = above-ground biomass (*Agbm*) and tree height (*H*); and (5) growth of an individual = above-ground biomass increment (*AgbmI*), relative growth rate in terms of above-ground biomass (*RgrAgbm*), height increment (*HI*), and relative growth rate in terms of height (*RgrH*). These independent variables were selected using a stepwise regression with $\alpha = 0.05$ used for the criteria for entering and being removed from the regression. Variables belonging to the same category had strong correlations with each other. Thus, they caused a problem of multicollinearity if more than one of them remained in the regression models. To reduce multicollinearity and to make it easier to interpret the results of the regressions, we did not allow more than one independent variable from a given category to remain in a regression model. To do this, we removed the variables that had poorer explanatory powers within each category.

Branch mortality is a discrete event. A datum can have either of two values: live or dead. A dichotomous dependent variable calls for special consideration both in parameter estimation and in the interpretation of goodness of fit [14]. We used the logistic regression to estimate the annual probability of mortality of a first-order branch (BM, % year^{-1}) [14]. This model takes the form:

$$BM = 100 / [1 + \exp(-X'\beta)]$$

where X' is the transpose of the vector of independent variables used to predict BM, and β is the vector of regression coefficients describing the relationship between the independent variables and BM. The logistic function has proven to be useful for developing models of the probability of mortality of individual trees [11, 29]. Estimation of regression coefficients was carried out by the maximum likelihood method. Usual measures of goodness of fit such as the coefficient of determination or the correlation coefficient are not appropriate for dichotomous variables. The appropriate test for significance of the overall independent variables in a model was provided by the likelihood ratio test in which the statistic G is tested using a Chi-square distribution [14]. The significance of each independent variable is tested by the Wald test [14]. As candidates for independent variables in the logistic regressions for BM, we used the same 12 variables as in the regressions of branch growth, and used the same rule in selecting independent variables.

All the regressions except for the logistic regression were done by PROC REG in the SAS statistical package [35] and the logistic regression was done by PROC LOGISTIC in SAS [36]. Because there was no significant year-to-year variance, dynamics data from the two intervals (1993-1994 and 1994-1995) were pooled for the analysis at the individual and branch levels.

3. RESULTS

3.1. Increment in diameter, height, and biomass of individuals

The number of individuals measured was 46, only one of which died during the measurement period. At the start of the measurement (1993), the tree density was 4 600 ha^{-1} (*table II*), and average *Dbh*, *H*, and *Agbm*

Table II. Density and tree size (mean ± S.D.) in a plantation of *Betula platyphylla* in Hokkaido, northern Japan.

Variable	1993	1995
Density (ha^{-1})	4 600	4 500
Dbh (cm)	2.01 ± 1.22	3.44 ± 1.77
Tree Height (cm)	324 ± 95	473 ± 125
Above-ground biomass (g)	5 161 ± 6 593	17 029 ± 17 057

(above-ground biomass of an individual) were 2.01 cm, 324 cm, and 5 161 g, respectively (*table II*). In the two-year measurement period, average *Dbh*, *H*, and *Agbm* increased to 3.44 cm, 473 cm, and 17 029 g, respectively (*table II*). The growth of the trees was very rapid; above-ground biomass tripled in the two-year interval.

3.2. Branch population dynamics within individuals

Ninety-seven percent (832 out of 862) of the new branches developed and grew longer than 5 cm in the same year that the main stem (parent shoot) developed. This implied that almost all of the new first-order branches (>5 cm in length) were sylleptic. The remaining (3%) of the new branches attained the threshold of 5 cm in the year following the development of the main stem. The birth rate of first-order branches per individual (B) was 10.7 year^{-1} in the 1993-1994 interval and 8.2 year^{-1} in the 1994-1995 interval (*table III*), which corresponded, on average, to 50.0 and 32.6% of the number of first-order branches in the previous year, respectively. The death rate of first-order branches per individual (D) was 7.8 year^{-1} in the 1993-1994 interval and 7.2 year^{-1} in the 1994-1995 interval (*table III*), which corresponded, on average, to 34.7 and 29.2% of the number of first-order branches in the previous year, respectively. In each of the two intervals, the mean birth rate of first-order branches was larger than the mean death rate although the difference was not significant in the 1994-1995 interval (p = 0.4% by paired t test with *d.f.* = 45 in the 1993-1994 interval, and p = 23.4% with *d.f.* = 44 in the 1994-1995 interval). The number of first-order branches per individual increased on average (*table IV*).

Table III. Branch number and change in branch number per tree in a plantation of *Betula platyphylla* in Hokkaido, northern Japan (mean ± S.D.; n = 46 for 1993 and 1994, n = 45 for 1995).

Year or Measurement Interval	Variable	
1993	Branch Number	24.6 ± 10.3
1994	Branch Number	27.5 ± 11.3
1995	Branch Number	29.0 ± 13.0
1993~1994	Birth Rate (B; year^{-1})	10.7 ± 4.3
1993~1994	Death Rate (D; year^{-1})	7.8 ± 3.3
1993~1994	Net Change (ΔN; year^{-1})	2.9 ± 5.2
1994~1995	Birth Rate (B; year^{-1})	8.2 ± 3.9
1994~1995	Death Rate (D; year^{-1})	7.2 ± 3.6
1994~1995	Net Change (ΔN; year^{-1})	0.8 ± 6.1

Table IV. Final models for variables at the individual level selected by the stepwise regressions. *Agbm*: above-ground biomass (g), *B*: birth rate of first-order branches (year^{-1}), *CI*: competition index, *D*: death rate of first-order branches (year^{-1}), *ΔN*: change in branch number (year^{-1}), *RgrAgbm*: relative growth rate in terms of above-ground biomass ($\text{g g}^{-1}\ \text{year}^{-1}$). ***, **, and *: significant at the 0.1%, 1%, and 5% levels, respectively.

Dependent Variable	n	$r2$	Final Model
RGR (Above-ground Biomass)	38	0.340***	$RgrAgbm = -1.30\ln(CI)^{**}$ $-\ 0.000\ 0130Agbm^{**}$ $+\ 0.87$
Birth Rate	38	0.126*	$B = -1.778\ln(CI)^{*}$ $+\ 10.927$
Death Rate	38	0.338***	$D = 0.000233Agbm^{***}$ $+\ 6.31$
Change in Branch Number	38	0.383***	$\Delta N = -3.76\ln(CI)^{***}$ $+\ 6.33$

3.3. Patterns in individual growth and branch population dynamics within individuals

Relative growth rate in terms of above-ground biomass of individuals (*RgrAgbm*) was most strongly related with log(*CI*) (log-translated competition index) (*figure 2a*), but log(*CI*) explained only 18% of the variance of *RgrAgbm*. Some of the unexplained variation was due to the above-ground biomass of an individual (*Agbm*). Inclusion of *Agbm* into the regression model as a further independent variable increased the coefficient of determination to 34% (*table IV*). The selected model indicated that *RgrAgbm* increased with decreasing competition and with increasing individual size. The birth rate of first-order branches per individual (B) had a negative relationship with ln(*CI*) whereas the death rate (D) had a positive relationship with *Agbm* (above-ground biomass of individuals) (*figures 2b, c; table IV*). The net annual change in first-order branch number per individual (ΔN) was negatively related to ln(*CI*) indicating that the first-order branch population within an individual grew rapidly for individuals with weak competition (*figure 2d; table IV*). The number of first-order branches decreased (i.e. $\Delta N < 0$) for individuals with strong competition though above-ground biomass increased even for these individuals (*figures 2a, d*). The regressions could account for 12.6 to 38.3% of the variance of the above four variables (*RgrAgbm*, B, D, and ΔN); more than half the variance remained unexplained. The final models for these variables, which were selected by the stepwise regressions, are tabulated in *table IV*.

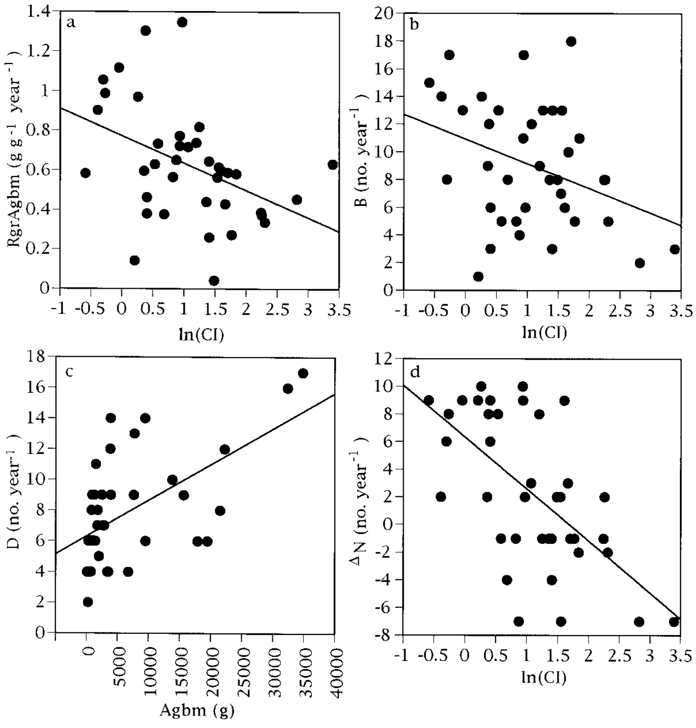

Figure 2. Effects of competition index and individual above-ground biomass on individual growth and branch population dynamics within individuals. a) relationship between relative growth rate in terms of above-ground biomass (*RgrAgbm*) and the logarithm of the competition index (ln(*CI*)). $RgrAgbm = -0.138\ \ln(CI) + 0.773$, $r^2 = 0.180$, $p < 1\%$. b) relationship between the birth rate of first-order branches per individual (*B*) and the logarithm of the competition index (ln(*CI*)). $B = -1.778\ \ln(CI) + 10.927$, $r^2 = 0.126$, $p < 5\%$. c) relationship between the death rate of first-order branches per individual (*D*) and the above-ground biomass of the individual (*Agbm*). $D = 0.000\,233 Agbm + 6.31$, $r^2 = 0.338$, $p < 0.1\%$. d) relationship between the annual net change in first-order branch number per individual (ΔN) and the logarithm of the competition index (ln(*CI*)). $\Delta N = -3.76\ \ln(CI) + 6.33$, $r^2 = 0.383$, $p < 0.1\%$.

3.4. Patterns of branch growth

The results of the stepwise regressions for four variables representing branch growth (*BE*: branch elongation, *FBbmI*: increment in foliar biomass of a branch, *WBbmI*: increment in woody biomass of a branch, and *TBbmI*: increment in total biomass of a branch) were similar (*table V*). The selected independent variables had the strongest explanatory power within each category of the independent variables. For example, *RBH* (relative branch height) had stronger effects on *BE*, *FBbmI*, *WBbmI*, and *TBbmI* than did *BH* (branch height). Although most of the independent variables that remained in the final models were highly significant, the amounts of variance explained by the models were low, ranging from 9.7 to 22.0%.

We consistently found significant effects of the woody biomass of a branch (*WBbm*), the height of the branch base relative to tree height (*RBH*), and the logarithm of the competition index (ln(*CI*)) on the four

Table V. Final models for variables at the branch level selected by the stepwise regressions. *Agbm*: above-ground biomass of an individual (g), *AgbmI*: above-ground biomass increment of an individual (g year^{-1}), *BE*: branch elongation (cm year^{-1}), *BM*: branch mortality (% year^{-1}), *CI*: competition index, *FBbm*: foliar biomass of a branch (g), *FBbmI*: foliar biomass increment of a branch (g year^{-1}), *H*: tree height (cm), *HI*: height increment of an individual (cm year^{-1}), *RBH*: relative branch height, *TBbmI*: total (foliar and woody) biomass increment of a branch (g year^{-1}), *WBbmI*: woody biomass increment of a branch (g year^{-1}). ***, **, and *: significant at the 0.1%, 1%, and 5% level, respectively. †: *G* statistic is only for branch mortality.

Criterion Variable		*n*	r^2 or $G^\dagger$	Final Model
Branch Growth	Elongation	650	0.097***	$BE = 0.23 WBbm^{**} + 46.19 RBH^{***} - 4.30\ln(CI)^{***} + 0.08 HI^{**} - 17.46$
	Foliar Biomass	650	0.220***	$FBbmI = 0.61 WBbm^{***} + 25.28 RBH^{***} - 3.64\ln(CI)^{***} - 0.000\,33\, AgbmI^{*} - 16.66$
	Woody Biomass	650	0.097***	$WBbmI = 0.10 WBbm^{**} + 20.59 RBH^{***} - 1.92\ln(CI)^{***} + 0.04 HI^{**} - 7.83$
	Total Biomass	650	0.160***	$TBbmI = 0.76 WBbm^{***} + 48.21 RBH^{***} - 5.26\ln(CI)^{***} + 0.067 HI^{*} - 0.03 H^{*} - 22.27$
Branch Mortality		952	377.1***	$\ln[BM/(100-BM)] = -0.09\, WBbm^{***} - 10.62 RBH^{***} + 0.54\ln(CI)^{***}$ $- 0.000\,11 AgbmI^{***} + 0.000\,08 Agbm^{***} + 6.55$

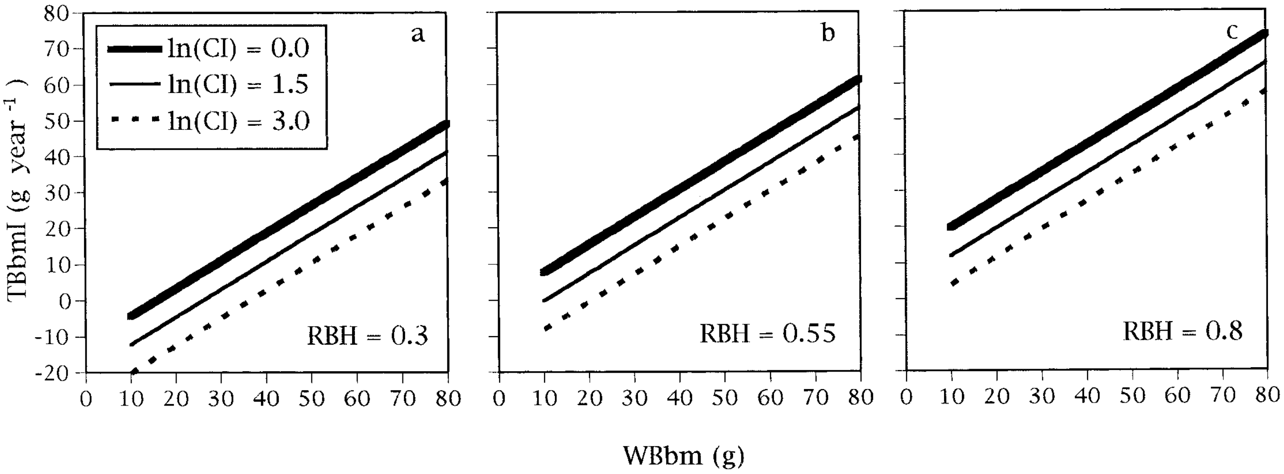

Figure 3. Predicted relationship between total (foliar and woody) biomass increment of a branch (*TBbmI*) and woody biomass of a branch (*WBbm*) with three levels of ln(*CI*) (0.0, 1.5, and 3.0) and three levels of *RBH* (a, 0.3; b, 0.55; c, 0.8). $TBbmI = 0.76\ WBbm + 48.21\ RBH - 5.26 \ln(CI) + 0.067\ HI - 0.03\ H - 22.27$. To calculate the predicted values, the mean values for *HI* (68 cm year^{-1}) and *H* (346 cm) were used.

variables for branch growth (*BE, FBbmI, WBbmI,* and *TBbmI*). *WBbm* and *RBH* had positive effects, and ln(*CI*) had negative effects. This indicated a major pattern in branch growth: branch growth tended to increase when branches were large and located in relatively high positions in crowns, and was affected less by competition from neighbours. As an example of this pattern, the predicted response of *TBbmI* related to *WBbm, RBH,* and ln(*CI*) is illustrated in *figure 3.* The predicted *TBbmI* was calculated using the obtained regression model (*table V*) with three levels of ln(*CI*) (0.0, 1.5, and 3.0), three levels of *RBH* (0.3, 0.55, and 0.8), and mean values of *HI* (68 cm year^{-1}) and *H* (346 cm). The figure shows the pattern clearly. The growth of smaller branches at lower positions within individuals was predicted to be negative.

An independent variable representing individual growth (*HI*: height increment) had positive effects in three regressions (for *BE*: branch elongation, *WBbmI*: increment in woody biomass of a branch, and *TBbmI*: increment in total biomass of a branch) indicating that branch growth increased with increasing individual height growth. In one regression (for *FBbmI*: increment in foliar biomass of a branch), on the other hand, another independent variable representing individual growth (*AgbmI*: increment of above-ground biomass of an individual) had a negative effect. Tree height (*H*) had a weak negative effect on the total biomass increment of a branch (*TBbmI*).

3.5. Patterns of branch mortality

The effect of the overall selected independent variables in the logistic regression for *BM* (branch mortality rate) was highly significant ($G = 377.1$; $d.f. = 5$; $p < 0.1\%$), and the effect of each selected independent variable was also highly significant (*table V*). *BM* increased with decreasing woody biomass of a branch (*WBbm*), with decreasing height of the branch base relative to tree height (*RBH*), and with increasing competition (ln(*CI*)) (*table V*).

We found a major pattern in branch mortality similar to the pattern observed in branch growth: *BM* tended to decrease when branches were large and located in relatively high positions in crowns, and was affected less by competition from neighbours. The dependence of *BM* on *WBbm, RBH,* and ln(*CI*) is illustrated in *figure 4.* The predicted value of *BM* was calculated using the obtained regression model (*table V*) with three levels of ln(*CI*) (0.0, 1.5, and 3.0), three levels of *RBH* (relative branch height: 0.3, 0.55, and 0.8), and mean values of *AgbmI* (increment in above-ground biomass of an individual: 4613 g year^{-1}) and *Agbm* (above-ground biomass of an individual: 6 910 g). The figure shows a strong effect of *RBH. BM* was less than 30% irrespective of *WBbm* and ln(*CI*) if the branches were in the upper region of a crown (*RBH* = 0.8), whereas it was more than 50% if the branches were shorter than 38 cm and located in the lower region of a crown (*RBH* = 0.3).

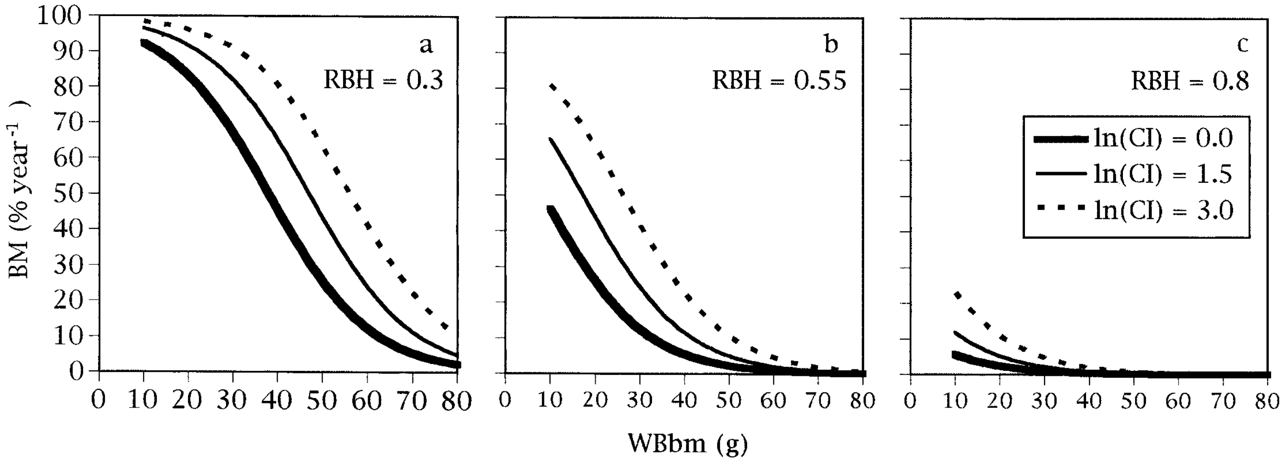

Figure 4. Predicted relationship between branch mortality (*BM*) and woody biomass of a branch (*WBbm*) with three levels of ln(*CI*) (0.0, 1.5, and 3.0) and three levels of *RBH* (a, 0.3; b, 0.55; c, 0.8). $\ln[BM/(100 - BM)] = -0.09\ WBbm - 10.62\ RBH + 0.54 \ln(CI) - 0.00011\ AgbmI + 0.00008\ Agbm + 6.55$. To calculate of the predicted values, the mean values for *AGM* (6910 g) and *AGMI* (4613 g year^{-1}) were used.

Two variables representing individual size (*Agbm*) and growth (*AgbmI*) were selected as significant factors in the logistic regression. Branch mortality was larger if the individual to which the branch was attached was large and growth of the individual was small.

4. DISCUSSION

The birth and death rates of first-order branches per individual of young *Betula platyphylla* ranged from 7.2 to 10.7 year^{-1} which were about a third of the number of branches in the previous year. Almost all of the new first-order branches (> 5 cm in length) developed as sylleptic shoots from the leader shoot; they were located in the upper part of the crowns. Branch mortality, on the contrary, was concentrated in the lower part of crowns (*figure 4*). Therefore, an individual *Betula platyphylla* shifts its crown upward by shedding about a third of its first-order branches in the lower part of the crown, and by developing almost as many new branches in the upper part of the crown. The rapid turnover rate of first-order branches, coupled with the rapid height growth, is an important characteristic of pioneer species such as *Betula platyphylla*.

This dynamic view of crown development of *Betula platyphylla* is consistent with the results of a previous study. Sumida and Komiyama [40] showed that the height of the base of the lowest first-order branch of *Betula platyphylla* was high compared with those of shade-tolerant species, and the maximum age of the branches was low. They inferred that the period of branch retention of *Betula platyphylla* was short (i.e. branch mortality was high), and concluded that it was a characteristic of crown development of shade-intolerant species [40].

The regression analyses in the present study revealed that individual tree growth expressed by the relative growth rate in terms of above-ground biomass (*RgrAgbm*) was affected by the competitive effect of neighbours (ln(*CI*)) (*figure 2a, table IV*). The change in the number of first-order branches within individuals (ΔN) was also affected by ln(*CI*) (*figure 2, table IV*). These results indicated that competition with neighbours, probably for light, is important in determining individual tree growth and branch population dynamics within individuals. However, the amounts of the variances that could be explained by the competition index (ln(*CI*)) were small. Similar patterns (i.e. competition affects the growth of individuals, but cannot explain a large amount of the variance in growth) have been found in some other studies [7, 37, 39].

The number of first-order branches of individuals that experience strong competition from neighbours can decrease though the above-ground biomass increases even for such individuals (*figures 2a, d*). The reduction in the number of first-order branches causes reductions in crown size and the amount of photosynthesis, eventually leading to the death of individuals. In the study plot, individual mortality was low (*table II*) indicating that the stand had not reached the self-thinning stage. However, the process leading to the deaths of individuals was found in a considerable number of individuals.

The regression analyses in the present study detected an important pattern in branch growth: larger branches in the upper part within crowns that experience less competition can grow more rapidly (*figure 3, table V*). A similar pattern has been found in *Betula pendula* by Jones and Harper [15] who reported that young branches located in the upper part of crowns and branches with less competition grow better. Maillette [27] also reported that growth of branches of *Betula pendula* expressed by the number of buds was larger in the upper part of the crowns than in the lower part. This pattern can be explained by the amount of light captured by the branches; larger branches in higher positions within individuals with less competition can intercept more light, resulting in better growth.

Tree development is often reconstructed by some morphological traces such as bud scars or annual rings [e.g. 4, 18, 31, 32, 39]. These methods, however, reconstruct the past of only presently living organs so that direct information about the branches that have already been shed cannot be obtained. This is probably the reason why few studies have dealt with branch mortality of hardwood trees. For some conifers, on the other hand, reconstruction methods are useful because dead branches are retained on stems for a long time [18, 25]. Data on branch mortality can be obtained by continuous observation of branches by non-destructive methods. The pattern detected in the present study regarding branch mortality was similar to the pattern in branch growth (i.e. *BE*: branch elongation, *FBbmI*: increment in foliar biomass of a branch, *WBbmI*: increment in woody biomass of a branch, and *TBbmI*: increment in total biomass of a branch): larger branches in the upper part within individuals that experience less competition have a higher probability of surviving (*figure 4, table V*). This pattern in branch mortality can be explained by the amount of light captured by branches. McGraw [28] reported a similar pattern in shoot mortality of a shrub, *Rhododendron maximum* in which the mortality of large shoots, which intercept more light, was lower than that of small shoots. The major patterns revealed by the regressions at the branch level (*figures 3, 4*) suggested that the growth and mortality of branches were largely determined by the amount of light captured by each branch, indicating an autonomy of branches [38].

Despite the autonomous behavior of branches, parts of an individual still depend on the other parts of the individual to various degrees [38, 43]. It is important to understand the extent to which modules are physiologically integrated to an individual plant in order to understand the architectural development of plants [38, 43]. In the regression analyses for branch growth and mortality, some suggestions of integration of modules were found. Throughout the regressions, the height of the branch base relative to tree height (*RBH*) had greater explanatory powers over the absolute height of the branch base (*BH*) which would be more closely related to the light condition in a stand. Moreover, variables representing individual size and growth (*HI*: height increment, *AgbmI*: increment in above-ground biomass, *H*: tree height, and *Agbm*: above-ground biomass) were found to be significant factors in the regressions. These results indicated that branch growth and mortality are influenced by the status of whole individuals and may suggest integration of modules in an individual. However, the effects of the variables representing individual growth and size cannot be easily interpreted. For example, *HI* had positive effects on *BE*, *WBbmI*, and *TBbmI*, while *AgbmI* had a negative effect on *FBbmI*. The underlying causal processes for these patterns are not clear and future research efforts should clarify the biomass allocation pattern between the branches and the main stem, and among the branches.

In all the regression analyses in the present study, the selected independent variables can explain significant amounts of the variances in the dependent variables, but the unexplained variances were large. This implies that, in modelling of tree development, the obtained regression models should be used with error variances. The obtained regression models can be used as references against which the behavior of more detailed process-based models can be checked.

In conclusion, the regression analyses revealed the patterns in individual growth (*RgrAgbm*: relative growth rate in terms of above-ground biomass), branch population dynamics within individuals (*B*: birth rate of branches, *D*: death rate of branches, and ΔN: change in branch number per year), branch growth (*BE*: branch elongation, *FBbmI*: increment in foliar biomass of a branch, *WBbmI*: increment in woody biomass of a branch, and *TBbmI*: increment in total biomass of a branch), and branch mortality (*BM*). Competition with neighbours affects both biomass growth of individuals and branch population dynamics within individuals. Large branches located in relatively higher positions within individuals that experience less competitive effects from neighbouring individuals grow rapidly and have large probabilities of surviving. These patterns in branch growth and mortality can be explained by the amount of light captured by each branch, suggesting branch autonomy. The obtained regression models can be used as references for further modelling.

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REFERENCES

[1] Bozzuto L.M., Wilson B.F., Branch angle in red maple trees, Can. J. For. Res. 18 (1988) 643-646.

[2] Canham C.D., Finzi A.C., Pacala S.W., Burbank D.H., Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees, Can. J. For. Res. 24 (1994) 337-349.

[3] Cannell M.G.R., Rothery P., Ford E.D., Competition within stands of *Picea sitchensis* and *Pinus contorta*. Ann. Bot. 53 (1984) 349-362.

[4] Ceulemans R., Stettler R.F., Hinckley T.M., Isebrands J.G., Heilman P.E., Crown architecture of *Populus* clones as determined by branch orientation and branch characteristics, Tree Physiol. 7 (1990) 157-167.

[5] Cluzeau C., Le Goff N., Ottorini J.-M., Development of primary branches and crown profile of *Fraxinus excelsior*, Can. J. For. Res. 24 (1994) 2315-2323.

[6] Doruska P.F., Burkhart H.E., Modeling the diameter and locational distribution of branches within the crowns of loblolly pine trees in unthinned plantations, Can. J. For. Res. 24 (1994) 2362-2376.

[7] Firbank L.G., Watkinson A.R., On the analysis of competition at the level of the individual plant, Oecologia 71 (1987) 308-317.

[8] Franco M., The influence of neighbours on the growth of modular organisms with an example from trees, Philos. Trans. R. Soc. Lond. B. 313 (1986) 209-225.

[9] Fujimoto S., On the growth characteristics branching into long shoots and short ones, Trans. Meet. Hokkaido Branch Jan. For. Soc. 34 (1987) 163-165.

[10] Goldberg D.E., Components of resource competition in plant communities, in: Grace J.B., Tilman D. (Eds.), Perspectives on Plant Competition, Academic Press, San Diego, 1990, pp. 27-49.

[11] Hamilton D.A. Jr., A logistic model of mortality in thinned and unthinned mixed conifer stands of northern Idaho, For. Sci. 32 (1986) 989-1000.

[12] Harper J.L., The population biology of plants, Academic Press, London, 1977.

[13] Harper J.L., The concept of population in modular organisms, in: May R.M. (Ed.), Theoretical Ecology: Principles and applications, Blackwell Scientific Publications, Oxford, 1981.

[14] Hosmer D.W., Lemeshow S., Applied logistic regression, John Wiley & Sons, New York, 1989.

[15] Jones M., Harper J.L., The influence of neighbours on the growth of trees. I. The demography of buds in *Betula pendula*, Proc. R. Soc. Lond. Ser. B. 232 (1987) 1-18.

[16] Jones M., Harper J.L., The influence of neighbours on the growth of trees. II. The fate of buds on long and short shoots in *Betula pendula*, Proc. R. Soc. Lond. Ser. B. 232 (1987) 19-33.

[17] Kellomäki S., Kurttio O., A model for the structural development of a Scots pine crown based on modular growth, For. Ecol. Manage. 43 (1991) 103-123.

[18] Kellomäki S., Väisänen H., Dynamics of branch population in the canopy of young Scots pine stands, For. Ecol. Manage. 24 (1988) 67-83.

[19] Kershaw J.A. Jr., Maguire D.A., Crown structure in western hemlock, Douglas-fir, and grand fir in western Washington: trends in branch-level mass and leaf area, Can. J. For. Res. 25 (1995) 1897-1912.

[20] Kikuzawa K., Leaf survival and evolution in Betulaceae, Ann. Bot. 50 (1982) 345-353.

[21] Kikuzawa K., Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees, Can. J. Bot. 61 (1983) 2133-2139.

[22] Koike T., Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees, Pl. Sp. Biol. 3 (1988) 77-87.

[23] Koike T., Autumn coloring, photosynthetic performance and leaf development of deciduous broad-leaved trees in relation to forest succession, Tree physiol. 7 (1990) 21-32.

[24] Lehtilä K., Tuomi J., Sulkinoja M., Bud demography of the mountain birch *Betula pubescens* spp. *tortuosa* near tree line, Ecology 75 (1994) 945-955.

[25] Maguire D.A., Branch mortality and potential litterfall from Douglas-fir trees in stands of varying density, For. Ecol. Manage. 70 (1994) 41-53.

[26] Maguire D.A., Moeur M., Bennett W.S., Models for describing basal diameter and vertical distribution of primary branches in young Douglas-fir, For. Ecol. Manage. 63 (1994) 23-55.

[27] Maillette L., Structural dynamics of silver birch. I. The fates of buds, J. Appl. Ecol. 19 (1982) 203-218.

[28] McGraw J.B., Effects of age and size on life histories and population growth of *Rhododendron maximum* shoots, Amer. J. Bot. 76 (1989) 113-123.

[29] Monserud R.A., Sterba H., Modeling individual tree mortality for Austrian forest species, For. Ecol. Manage. 113 (1999) 109-123.

[30] Perttunen J., Sievänen R., Nikinmaa E., Salminen H., Saarenmaa H., Väkevä J., LIGNUM: A tree model based on simple structural units, Ann. Bot. 77 (1996) 87-98.

[31] Remphrey W.R., Davidson C.G., Branch architecture and its relation to shoot-tip abortion in mature *Fraxinus pennsylvanica*, Can. J. Bot. 70 (1992) 1147-1153.

[32] Remphrey W.R., Davidson C.G., Spatiotemporal distribution of epicormic shoots and their architecture in branches of *Fraxinus pennsylvanica*, Can. J. For. Res. 22 (1992) 336-340.

[33] Remphrey W.R., Powell G.R., Crown architecture of *Larix laricina* saplings: quantitative analysis and modelling of (nonsylleptic) order 1 branching in relation to development of the main stem, Can. J. Bot. 62 (1984) 1904-1915.

[34] Room P.M., Maillette L., Hanan J.S., Module and metamer dynamics and virtual plants, Adv. Ecol. Res. 25 (1994) 105-157.

[35] SAS institute, SAS/STAT user's guide, Cary, USA, 1990.

[36] SAS institute, SAS/STAT software: changes and enhancements, Cary, USA, 1996.

[37] Schellner R.A., Newell S.J., Solbrig O.T., Studies on the population biology of the genus *Viola* IV. Spatial pattern of ramets and seedlings in three stoloniferous species, J. Ecol. 70 (1982) 273-290.

[38] Sprugel D.G., Hinckley T.M., Schaap W., The theory and practice of branch autonomy, Annu. Rev. Ecol. Syst. 22 (1991) 309-334.

[39] Stoll P., Weiner J., Schmid B., Growth variation in a naturally established population of *Pinus sylvestris*, Ecology 75 (1994) 660-670.

[40] Sumida A., Komiyama A., Crown spread patterns for five deciduous broad-leaved woody species: ecological significance of the retention patterns of larger branches, Ann. Bot. 80 (1997) 759-766.

[41] Takahashi Y., Asai T., Kikuzawa K., On biomass estimation of *Betula platyphylla* var. *japonica* forest stand in Nayoro, Bull. Hokkaido For. Exp. St. 12 (1974) 29-37.

[42] Wagner R.G., Radosevich S.R., Neighborhood predictors of interspecific competition in young Douglas-fir plantations, Can. J. For. Res. 21 (1991) 821-828.

[43] Watson M.A., Casper B.B., Morphogenetic constraints on patterns of carbon distribution in plants, Annu. Rev. Ecol. Syst. 15 (1984) 233-258.

[44] Weiner J., Neighborhood interference amongst *Pinus rigida* individuals, J. Ecol. 72 (1984) 183-195.

[45] White J., The plant as a metapopulation, Annu. Rev. Ecol. Syst. 10 (1979) 109-145.