Patterns between crown characteristics and radial increment in trees are similar during recovery and normal growth: a long-term example from old-growth forests

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Patterns between crown characteristics and radial increment in trees are similar during recovery and normal growth: a long-term example from old-growth forests

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Abstract: Crown traits and competition attributes have an important effect on tree radial increment. Relationships among these elements are modeled using the distributions of the crown characteristics in a given calendar year, but these patterns can differ through time. The suitability of the patterns during recovery and normal growth was investigated with the example of the fir *Abies alba* Mill. in old-growth forests. Generalized additive models (GAMs) for fir in the older (OG, trees aged 136 to 300 years) and younger (YG, trees aged 45 to 135 years) generations were developed. To test the validity of these GAMs, field data sets representing fir recovery and normal growth were used. In the case of fir in OG, crown transparency had the largest effect, explaining more than 25% of the variance. For fir in YG, relative crown length had the largest effect on tree growth, explaining more than 15% of the variance. The absolute relative prediction errors, $ARE_{\text{min}}$ and $ARE_{\text{max}}$, were less than 0.03 and 1.50 mm, respectively. The developed GAMs are suitable during recovery and normal growth, but the GAMs were fitted to a relatively small area which neglects climatic gradients and different disturbance types; this type of investigation should be continued.

Key words: pattern suitability, long-term field data, disturbances, forest management.
Introduction

Understanding tree resistance to disturbances and climate changes requires knowledge of relationships between crown traits, competition attributes and radial increment through time. Characteristics of tree crowns, such as their size, the shape of their tops, and the degree of deformation, are mainly the effect of competition. Dominant trees are characterized by higher growth rates, which are directly linked with, among other things, the close relationship between crown architecture and physiological processes (Aranda et al. 2012; Rathgeber et al. 2011; Fichtner et al. 2012, 2013). Suppressed trees with short crowns are characterized by lower photosynthesis productivity because of decreasing light capture efficiency and increasing path length for water transport (Niinemets 2010). However, the opposite pattern has also been described, suggesting that suppressed trees are more photosynthetically efficient than dominant trees (Reid et al. 2004). Small trees occupy their aerial growing space better and utilize their crowns to produce stem wood more efficiently than large trees, in the absence of competition (Larocque and Marshall 1994). Assimilative apparatus and stem increment might be mutually related (Seidling et al. 2012). Crown size can be used as a proxy variable for needle and leaf biomass, and it affects diameter at breast height (DBH) increment (Forrester 2013).

Studies on the relationships between crown characteristics and radial increment in old-growth forests are scarce (e.g. Norton et al. 2005; Fichtner et al. 2013, 2015; Juchheim et al. 2017). Crown traits respond sensitively to changes in tree condition; therefore, they are regarded as important indicators for individual tree growth assessments (Thorpe et al. 2010). Consequently, an understanding of the mechanisms of tree growth dependence on crown traits and competition attributes is crucial for better prediction of forest dynamics, thus supporting management decisions (Davi et al. 2008).

Complex interactions among abiotic, biotic and anthropogenic factors are the agents of disturbance in Central Europe (Cailleret et al. 2014; Kulakowski et al. 2017). In the second half of the twentieth century, disturbance and consequent decline in fir Abies alba Mill. resulted in changes in the species composition of...
stands (Becker 1989; Manion and Lachance 1992). Fir decline was closely linked to loss of vitality, crown and DBH increment reduction, and higher mortality. This process affects the stability of ecosystems and economic value of forests (Dale et al. 2001; Elling et al. 2009; Senf and Seidl 2017). At a larger spatiotemporal scale, fir decline led to a reduction in its distribution range (Feurdean and Willis 2008). In the Świętokrzyski National Park in Poland, the mortality of fir trees and DBH radial increment depression reached their maxima between 1970 and 1990 (Podlaski 2018). Generally, fir was in worse condition than beech (Fagus silvatica L.), pine (Pinus sylvestris L.), and larch (Larix decidua Mill. subsp. polonica [Racib.] Domin) (Podlaski 2004, 2005). Fir recovery began after 1990, and the proportion of moderately or severely damaged fir trees gradually decreased (Podlaski 2005). Similar trends have been observed in the Carpathians (e.g. Spiecker 1999).

The relationships between the crown characteristics and radial increment in trees are modeled using one-year data, representing the distributions of the crown traits and competition attributes in a given calendar year, but these patterns can differ through time, especially during decline versus recovery and among disturbances. The main objectives of this study are (1) to distinguish crown traits and competition attributes that have a significant influence on the radial increment of fir, (2) to model relationships between the crown characteristics and radial increment using data collected during fir recovery, and (3) to verify the suitability of the developed models using data representing fir recovery and normal growth.

Materials and methods

The study was carried out in the Świętokrzyski National Park (Central Europe, 50°50′–50°58′N, 20°48′–21°08′E) in the Święta Katarzyna, Święty Krzyż and Chelmowa Góra forest sections. In the investigated area, there are strictly protected forest reserves created in the 1920s. The main soil types are Dystric Cambisol and Haplic Luvisol (subtypes according to the IUSS Working Group WRB 2006). Four main plant associations occur: Dentario glandulosae-Fagetum Klika 1927. em. W. Mat. 1964, Abietetum polonicum (Dziub. 1928). Br.-Bl. & Vlieg. 1939, Querco roboris-Pinetum (W.Mat. 1981) J.Mat. 1988, and Tilio-Carpinetum

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*abietetosum* with *Larix decidua* Mill. subsp. *polonica* (Racib.) Domin (Matuszkiewicz 2008). The mean annual temperature was +5.9°C, and mean annual precipitation was 923 mm. The growing season lasted approximately 182 days.

**Field data**

A grid of the System of Information on Natural Environment (SINUS) covers whole Poland; the dimensions of the blocks and sub-blocks of SINUS are given in minutes (') and seconds (") of arc. SINUS consists of $P_0$ blocks ($10' \times 10'$); they are divided into 54 $P_1$ sub-blocks ($100.00'' \times 66.67''$; $6 \times 9 = 54$), next, each $P_1$ sub-block is divided into 4 $P_2$ sub-blocks ($50.00'' \times 33.33''$; $2 \times 2 = 4$), each $P_2$ sub-block is divided into 4 $P_3$ sub-blocks ($25.00'' \times 16.67''$; $2 \times 2 = 4$), etc. Points determining sub-blocks $P_2$ and $P_3$, comprising the investigated area of the Świętokrzyski National Park, were marked on small-scale maps (1:5000). In 1993 and 1994, sample points were randomly chosen in all $P_2$ sub-blocks covering the Święta Katarzyna and Święty Krzyż forest sections and in all $P_3$ sub-blocks covering the Chełmowa Góra forest section. In each $P_2$ or $P_3$ sub-block, 10 sample points were selected. In sub-blocks through which the forest section boundary passes, a proportionally smaller number of sample points was drawn. A total of 251 permanent sample points were chosen, traced out in the field and marked in the stands (for details, see Podlaski 2005).

One tree from the older generation (OG; fir trees aged 136–300 years) and one tree from the younger generation (YG; fir trees aged 45–135 years) were selected close to each sample point. These trees represented Kraft’s second class (Assmann 1961) in one-story stands or the upper canopy layer (> 2/3 top height; 100 according to IUFRO; Leibundgut 1956) in stands with a complex structure (see also Lebourgeois et al. 2014). According to this sampling design, 49, 39, and 29 fir trees from OG and 215, 205, and 200 fir trees from YG were sampled in 1994, 2004, and 2014, respectively (these were new trees each year, Fig. 1). The number of sampled fir trees was lower than the number of permanent sample points because there were no fir trees in the investigated generations near some of the points. In summary, (1) in 1994, the entire sample consisted of 49 and 215 fir trees selected from OG and
YG, respectively (trees coded A1994), (2) in 2004, it consisted of \(49 + 39 = 88\) and

\(215 + 205 = 420\) different fir trees (A2004 — the same trees sampled in 1994 and
trees coded B2004), and (3) in 2014, it consisted of \(49 + 39 + 29 = 117\) and

\(215 + 205 + 200 = 620\) different fir trees (A2014 — the same trees sampled in 1994,
B2014 — the same trees sampled in 2004 and trees coded C2014) (Fig. 1). From
1994 to 2004, and from 2004 to 2014, some trees reached the age of at least 136
years and passed from YG to OG.

The measurement and classification of the sampled fir trees was conducted in
1994 and 1995 (for A1994), in 2004 and 2005 (for A2004 and B2004), and from
2014 to 2015 (for A2014, B2014, and C2014) (Fig. 1). In 1994, 2004, and 2014, the
measurements taken included DBH (two crosswise measurements, with the first from
the side of the slope), height to tree crown and total tree height (Table 1; Figs. 2, 3).
Next, the crown traits and competition attributes were visually estimated (Jaworski et
al. 1988). The crown transparency, the degree of crown deformation and the degree
of forest canopy density around the fir crown were determined (separately for the
light and shaded parts) according to the percentage of needle loss, the loss of crown
volume, and the percentage of crown confinement (Table 1; Figs. 2, 3). In 1995,
2005, and 2015-2017, two increment cores were taken per tree. The first time a tree
was sampled it was cored to the pith: 1995 — A1994, 2005 — B2004, 2015–2017 —
C2014. For trees that had been previously bored, the core covered approximately 30–
(Fig. 1). The fir trees were bored as close to ground level as possible in order to
determine their age. Increment coring will always incur some risk of negative
impacts on the cored tree; coniferous trees sustain little serious damage (van
Mantgem and Stephenson 2004). During these investigations, holes were left to heal
naturally. Closing the hole often creates even more suitable conditions for the
development of pathogens. The increment borer was carefully cleaned and
disininfected with fungicide. Increment coring has not influenced the mortality of the
cored fir trees. For most fir trees, especially for mature trees, due to wood decay, it
was not possible to obtain complete, undamaged increment cores.
Identifying decline and recovery processes

Decline and recovery processes are closely linked to rapid changes in the tree radial increment. Using a binocular microscope, every tenth annual ring was marked on the increment cores, and the width of all annual rings was measured to the nearest 0.01 mm (two instruments were used — GP-3 and CODIMA). The individual series of tree-ring widths were cross-dated. The $t$ value (Baillie and Pilcher 1973) and the collinearity of the increments (Gleichläufigkeit; Eckstein and Bauch 1969; Buras and Wilmking 2015) were considered quality criteria. The matching of chronologies was considered reliable when it reached a minimum $t$ value of 3.5 and a minimum collinearity of 70% for a 50-year overlap. Radial increment trends of fir trees in OG and YG were approximated using a cubic smoothing spline with the desired equivalent number of degrees of freedom (ndf): 

$$\text{ndf} = 0.15 m$$

where $m = m_{OG}$ or $m = m_{YG}$ is the number of years in the analyzed periods for OG and YG; $m_{OG} = 171$ years (1844–2014) and $m_{YG} = 111$ years (1904–2014). A cubic smoothing spline was applied to all individual series of tree-ring widths of OG and YG, respectively. The degree of smoothness is controlled by the smoothing parameter, which was 0.4978 and 0.5620 for OG and YG, respectively.

Patterns between crown characteristics and radial increment of fir

The generalized additive model (GAM) is a useful tool for modeling the nonlinear relationships between a set of explanatory variables and a response variable. The GAM for OG and YG, were constructed to model radial increment during a recovery period (1985 to 1994) as a function of tree characteristics at the end of that period (data collected on the trees in 1994); data from the sample A1994 was used. The assumption is that if the tree characteristics stay the same in the future, the tree will continue to grow as it has in the past. The initial GAMs included all predictors (Table 1):

$$\log(\mathbb{E}[\text{INC}_{85\_94_i}]) = \beta_0 + s_1 (\text{DBH}_{94_i}) + s_2 (\text{LEN}_{94_i}) + s_3 (\text{DEF}_{94_i}) + s_4 (\text{NOA}_{94_i}) + s_5 (\text{SIZ}_{94_i})$$
and
\[ \text{INC}_{85-94} = E \left[ \text{INC}_{85-94} \right] + e_i \]
where \( E[\bullet] \) is the expected value, \( \text{INC}_{85-94} \) is the periodical DBH radial increment from 1985 to 1994 (mm), \( \text{INC}_{85-94} \sim \text{gamma} \), \( s_i(\bullet) \) is the smooth function, \( \beta_0 \) is an intercept, \( \text{DBH}_{94}, \text{LEN}_{94}, \text{DEF}_{94}, \text{DEFOR}_{94}, \text{CONF}_{L}_{94}, \text{CONF}_{S}_{94} \) are the variables that were considered as predictors (for details, see Table 1); \( e_i \) is the residual error on the scale of the response and \( i \) varies from 1 to \( N_{OG} \) and from 1 to \( N_{YG} \), where \( N_{OG} \) and \( N_{YG} \) are the number of investigated trees belonging to OG and YG, respectively. Thin plate regression splines and P-splines were used (Wood 2006).

For the diagnosis of collinearity among predictors, the variance inflation factor (VIF) was used; if VIF is greater than 10, multicollinearity is strongly suggested (McCullagh and Nelder 1989). The explanatory variables were selected according to the backward stepwise procedure (Wood and Augustin 2002). At each step, the significance of the predictors already included in the GAM was assessed; approximate \( p \)-values were obtained for testing the null hypotheses that the corresponding parameter coefficient (intercept) is zero (\( p \)-values were calculated with reference to the \( t \) distribution) and that the corresponding smooth term is zero (\( p \)-values were calculated with reference to the \( F \) distribution) (Wood 2006). The variable with the greatest \( p \) value (less significant) was excluded and the model was re-run. This step was repeated until only significant variables remained in the model.

The percentage of the variance explained by predictor \( pk \) was calculated using the formula:
\[ \text{VE}_{pk} = \left( \text{DE}_{fim} - \text{DE}_{rfm} \right) \times 100\% \]
where \( \text{DE}_{fim} \) and \( \text{DE}_{rfm} \) are the proportion deviance explained (DE) of the full final model (with \( pk \)) and the reduced final model (without \( pk \)), respectively. In the reduced final models the smoothing parameters were fixed for the comparison.
Validation of the developed GAM models

The fitted GAMs were validated with field data representing fir recovery (A2004, B2004; radial increment from 1995 to 2004) and normal growth (A2014, B2014, C2014; radial increment from 2005 to 2014). The crown traits and competition attributes were added to the GAMs as predictors. To evaluate the differences between the predicted and observed radial increments, the Spearman correlation coefficient ($\rho$) and the absolute relative prediction errors ($\text{ARE}_{\text{min}}$ and $\text{ARE}_{\text{max}}$) were used. After calculation of the respective $\rho$-values with 95% bootstrap confidence intervals (BCa CIs), the null hypothesis $H_0$: $\rho = 0$ (the alternative hypothesis $H_1$: $\rho > 0$) was tested using a permutation test with 999 iterations (Good 2000). The $\text{ARE}_{\text{min}}$ and $\text{ARE}_{\text{max}}$ are defined as:

$$\text{ARE}_{\text{min}} = \frac{\sum_{i=1}^{5} \min_i |\varepsilon_i|}{5 \text{ Inc}_{a,b}}$$

$$\text{ARE}_{\text{max}} = \frac{\sum_{i=N_p-4}^{N_p} \max_i |\varepsilon_i|}{5 \text{ Inc}_{a,b}}$$

where, after being sorted in ascending order, the five smallest ($\text{ARE}_{\text{min}}$) and largest ($\text{ARE}_{\text{max}}$) absolute values of the residual errors on the scale of the response $\varepsilon_i$ are summed; $\text{Inc}_{a,b}$ is the mean DBH radial increment from the year $a$ to the year $b$, and $N_p$ is the number of all analyzed trees.

The rejection of the null hypothesis in the case of the permutation test and the small values of the $\text{ARE}_{\text{min}}$ and $\text{ARE}_{\text{max}}$ suggest that the investigated GAMs can be used to predict radial increments.

All analyses were conducted within the R environment (R Development Core Team 2017); the mgcv package of R was also used (Wood 2004).

Results

Radial increment trends of fir

A cubic smoothing spline fitted the raw radial increment series; it reached
values from 1.07 to 3.13 mm and from 1.51 to 2.72 mm for fir in OG and YG, respectively (Fig. 4). The radial increment trends of fir in these generations were similar. A cubic smoothing spline highlights that the fir increment reached its minimum between 1980 and 1985. In this period, the mean radial increment of fir in OG and YG was less than 1.0 and 1.5 mm, respectively. Some fir trees reached the minimum annual increment below 0.05 mm. Most of the investigated fir trees did not reach the maximum annual increment above 4 mm. Aside from this period, such a long decrease and such low radial increment values were not observed throughout the entire investigated period, that is, from 1844 to 2014 (Fig. 4). After this period, fir trees have gradually been increasing their increment. This analysis confirms that in the Świętokrzyski National Park, fir recovery began after 1980 (1985).

Patterns between crown characteristics and radial increment of fir

The VIF values were less than 3, indicating a lack of multicollinearity. Among the six variables, only the significant predictors were included in the final GAMs for fir trees of the analyzed generations. These models have the forms (Tables 2, 3):

$$\log(\text{INC}_{85-94}^{\text{OG}}) = \beta_{\text{OG}} + s_{\text{OG}}(\text{LEN}_{94}^{\text{OG}}) + s_{2\text{OG}}(\text{DEF}_{94}^{\text{OG}}) + \varepsilon_{\text{OG}}$$

$$\log(\text{INC}_{85-94}^{\text{YG}}) = \beta_{\text{YG}} + s_{\text{YG}}(\text{LEN}_{94}^{\text{YG}}) + s_{2\text{YG}}(\text{DEF}_{94}^{\text{YG}}) + s_{3\text{YG}}(\text{DEFOR}_{94}^{\text{YG}}) + s_{4\text{YG}}(\text{CONF}_{S}^{\text{YG}}) + \varepsilon_{\text{YG}}$$

where $\cdot^{\text{OG}}$ and $\cdot^{\text{YG}}$ indicate two investigated generations.

The $p$-values testing the significance of included terms were less than 0.001 for the relative crown length ($\text{LEN}_{94}^{\text{OG}}$ and $\text{LEN}_{94}^{\text{YG}}$), crown transparency ($\text{DEF}_{94}^{\text{OG}}$ and $\text{DEF}_{94}^{\text{YG}}$), degree of crown deformation ($\text{DEFOR}_{94}^{\text{YG}}$), and less than 0.05 for the degree of forest canopy density around the crown for the shaded part ($\text{CONF}_{S}^{\text{YG}}$) (Tables 2, 3).

In the case of fir in OG, crown transparency had the largest effect, explaining more than 25% of the variance. For fir in YG, relative crown length had the largest effect, explaining more than 15% of the variance. For all variables, the effective degrees of freedom are greater than one (estimated degrees of freedom greater than...
one denote nonlinear smoothers; Tables 2, 3, Figs. 5, 6).

The results show that the radial increments of the two investigated
generations are significantly affected by various sets of predictors, and among all the
analyzed variables, nonlinear relationships appear.

Suitability of the developed GAM models

The \( \rho \) coefficient between the predicted and observed radial increments
ranged from 0.7862 to 0.9413 for fir in OG and from 0.6999 to 0.8287 for fir in YG
(Table 4). For all \( \rho \)-values, the null hypothesis \( H_0: \ \rho = 0 \) was rejected. The absolute
relative prediction errors were less than 0.03 and 1.50 mm for the ARE\(_{\text{min}}\) and
\( \text{ARE}_{\text{max}} \), respectively (Table 4).

The conducted analyses indicate that the patterns among crown traits,
competition attributes and radial increments of the investigated fir trees are suitable

Discussion and conclusions

In the investigated area, the radial increment of fir in OG and YG followed
decreasing and increasing trends. These changes in radial increment were caused by
rapid environmental changes and at the same time reflected response of the trees to
environmental stress (e.g. Dobbertin 2005; Linares and Camarero 2012; Rydval and
Wilson 2012; Čavlović et al. 2015; Podlaski 2018; Podlaski et al. 2018). The tree-
ing widths of fir trees generally differed greatly during a recovery period and normal
growth. Crown length, crown transparency, crown deformation and forest canopy
density around the fir crowns changed together. The increase in crown length and the
decrease in crown deformation during fir recovery were consequences of the opening
of the canopy resulting from the death of a large number of trees during fir decline.

Under these conditions, fir has the ability to increase the growth of the main and side
shoots as well as to produce a secondary sunny crown (Dmyterko 2014).

Among all the investigated explanatory variables, the relative crown length
and the crown transparency had a significant effect on the radial increment of the two
investigated generations.

With the growth of the relative crown length, the radial increment of fir trees increased significantly. Trees with long crowns are characterized by efficient crown–stem physiological relationships. In selection and multilayered fir forests, trees with long crowns appear in all layers of the stand. Despite the lower level of light penetration, the long crowns allow even strongly shaded trees to achieve relatively high growth rates (Vieilledent et al. 2010). Consequently, higher structural complexity can be achieved by a wider variety of crown length classes, which in turn would benefit primary productivity in forest ecosystems (Morin et al. 2011). The crown length is considered to be an indirect measure of the photosynthetic capacity of the tree (Leites et al. 2009). In Austria, crown length accounted up to 14–47% of the variation in basal area increment, depending on tree species (Monserud and Sterba 1996).

With the increase in crown transparency, the radial increment of fir trees decreased significantly. Fir trees usually have from 8 to 11 needle sets, which are necessary for optimal photosynthesis. Every lost needle results in a reduction in the tree radial increment. Previous studies have confirmed the relationship between crown transparency and tree ring widths (Drobyshev et al. 2007; Seidling et al. 2012; Eilmann et al. 2013). However, for many tree species, crown transparency and radial increment are only weakly related to each other (Bošelá et al. 2014). A reversed relationship may also occur between these two elements. In some tree species, precipitation in early summer is an important factor that controls their growth; for example, in the oak *Quercus robur* L., a lack of precipitation in early summer and the associated water deficit may consequently cause defoliation and a shift in the growth accumulation pattern, favoring investments in wood formation at the expense of the crown’s photosynthetic potential (Kelly et al. 2002).

The degree of forest canopy density around the fir crown estimated for the light part of the crown did not have a significant effect on the radial increment for fir trees in either generation. The reason might be that the sampled trees were from Kraft’s second class in one-story stands and from the upper canopy layer in stands with a complex structure.
The crown deformation and the degree of forest canopy density around the fir crown estimated for the shaded part of the crown showed a significant negative effect on the radial increment of trees in YG and no significant effect on that of trees in OG. Fir trees in YG usually grow in patches of various sizes characterized by high density. Under these conditions, competitive relations have a significant influence on the radial increment (Biging and Dobbertin 1992). Fir trees in OG are often characterized by random distribution and grow individually while surrounded by trees from lower biosocial classes (Szwagrzyk et al. 1997).

In Central Europe, fir is one of the most shade-tolerant tree species, and it can form uneven-aged forests with a complex vertical and horizontal structure (Podlaski 2019; Podlaski et al. 2019). When assessing forest management, one should pay more attention to increasing the tree diameter structural diversity of fir forests. For years, forest ecologists have recommended against planting even-aged pure stands. As a result of such recommendations, uneven-aged mixed-species stands have become a desirable management goal in Central Europe (Monserrud and Sterba 1996). The GAMs may be used for modeling the DBH structure of fir stands and predicting the radial increment of fir. Single-tree selection cuttings and group selection cuttings should shape biogroups consisting of several firs because the partial deformation and shading of fir crowns do not cause a significant reduction in their radial increment and vitality. The basic condition is appropriate height variation in the fir trees forming the biogroup, which prevents excessive shortening, deformation and shading of tree crowns.

The GAMs, which fit the nonlinear relationships, provide important information. An example of one possible use of the GAMs is the analysis of the relative crown length-radial increment relationship. In the case of fir trees in YG, extension of the relative crown length by up to at least 35% causes a significant increase in radial increment. Further extension of the crown increases growth to a lesser degree. However, if we want to obtain greater growth of fir trees after they have changed from YG to OG, then we must extend the crown early enough with appropriate crown thinning of up to at least 50% and at best up to 70%. For fir trees in OG, only a crown of 50–70% length ensures a significant increase in growth.
Understanding the relationships among crown traits, competition attributes and radial increment is crucial for forest ecology because growth is directly related to forest structure and biomass. The proposed GAMs may serve to assess the quality and efficiency of thinnings and cuttings. The GAMs need to be calibrated and adjusted to the local conditions. Basing on the relationships among crown traits, competition attributes and radial increments, local patterns can developed, thus decreasing the limitation of the models.

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References


Table 1. Explanatory variables considered in constructive of the generalized additive models (GAMs) of radial increment from 1985 to 1994.

<table>
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<th>Predictor</th>
<th>Abbreviation</th>
<th>Description</th>
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<tr>
<td>DBH (cm)</td>
<td>DBH_94</td>
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<td>Numerical (continuous)</td>
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<tr>
<td>Relative crown length (%)</td>
<td>LEN_94</td>
<td>Crown length divided by total tree height</td>
<td>Numerical (continuous)</td>
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<td>Crown transparency (%)</td>
<td>DEF_94</td>
<td>No defoliation – 0% loss</td>
<td>Categorical (ordinal)</td>
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<tr>
<td>Degree of crown deformation (%)</td>
<td>DEFOR_94</td>
<td>Regular crown – 0% loss</td>
<td>Categorical (ordinal)</td>
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<td>Degree of forest canopy density around the crown for the light part (%)</td>
<td>CONF_L_94</td>
<td>Free crown – 0%, crown entirely confined – 100%</td>
<td>Categorical (ordinal)</td>
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<tr>
<td>Degree of forest canopy density around the crown for the shaded part (%)</td>
<td>CONF_S_94</td>
<td>Free crown – 0%, crown entirely confined – 100%</td>
<td>Categorical (ordinal)</td>
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Table 2. Statistical characteristics of initial and final GAM for fir of the older generation (OG); estimated degrees of freedom greater than one denote nonlinear smoothers; abbreviations for the predictors see Table 1.

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<td>$p$-value</td>
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<td>Intercept</td>
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<th>Estimated degree of freedom</th>
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<th>$p$-value</th>
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<td>$s$(DBH$_{94OG}$)</td>
<td>1.60</td>
<td>2.60</td>
<td>0.108</td>
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<tr>
<td>$s$(LEN$_{94OG}$)</td>
<td>2.76</td>
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<td>$s$(DEF$_{94OG}$)</td>
<td>1.31</td>
<td>25.00</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>$s$(DEFOR$_{94OG}$)</td>
<td>1.00</td>
<td>0.18</td>
<td>0.675</td>
</tr>
<tr>
<td>$s$(CONF L$_{94OG}$)</td>
<td>1.00</td>
<td>0.11</td>
<td>0.744</td>
</tr>
<tr>
<td>$s$(CONF S$_{94OG}$)</td>
<td>1.00</td>
<td>1.31</td>
<td>0.259</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Final GAM model</th>
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<tbody>
<tr>
<td>Parameter</td>
<td>Estimate</td>
<td>$t$-value</td>
<td>$p$-value</td>
</tr>
<tr>
<td>Intercept</td>
<td>2.3719</td>
<td>44.52</td>
<td>&lt; 0.001</td>
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<table>
<thead>
<tr>
<th>Smooth term</th>
<th>Estimated degree of freedom</th>
<th>$F$-value</th>
<th>$p$-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s$(LEN$_{94OG}$)</td>
<td>3.15</td>
<td>7.43</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>$s$(DEF$_{94OG}$)</td>
<td>1.27</td>
<td>32.69</td>
<td>&lt; 0.001</td>
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</table>
Table 3. Statistical characteristics of initial and final GAM for fir of the younger generation (YG); estimated degrees of freedom greater than one denote nonlinear smoothers; abbreviations for the predictors see Table 1.

<table>
<thead>
<tr>
<th>Smooth term</th>
<th>Estimated degrees of freedom</th>
<th>F-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s$(DBH_94_YG)</td>
<td>1.53</td>
<td>0.47</td>
<td>0.558</td>
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<tr>
<td>$s$(LEN_94_YG)</td>
<td>3.02</td>
<td>29.10</td>
<td>&lt; 0.001</td>
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<td>$s$(DEF_94_YG)</td>
<td>1.16</td>
<td>20.34</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>$s$(DEFOR_94_YG)</td>
<td>6.92</td>
<td>7.89</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>$s$(CONF_L_94_YG)</td>
<td>1.00</td>
<td>0.04</td>
<td>0.848</td>
</tr>
<tr>
<td>$s$(CONF_S_94_YG)</td>
<td>1.00</td>
<td>6.68</td>
<td>0.011</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Smooth term</th>
<th>Estimated degrees of freedom</th>
<th>F-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>$s$(LEN_94_YG)</td>
<td>2.81</td>
<td>29.68</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>$s$(DEF_94_YG)</td>
<td>1.47</td>
<td>14.97</td>
<td>&lt; 0.001</td>
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<td>$s$(DEFOR_94_YG)</td>
<td>3.86</td>
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<tr>
<td>$s$(CONF_S_94_YG)</td>
<td>3.19</td>
<td>2.93</td>
<td>0.020</td>
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</table>

<table>
<thead>
<tr>
<th>Sample</th>
<th>$\rho$ (95% CI – BCa CIs)</th>
<th>Permutation test $p$</th>
<th>$\text{ARE}_{\text{min}}$ (mm)</th>
<th>$\text{ARE}_{\text{max}}$ (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>GAM for fir of the older generation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A2004</td>
<td>0.9084 (0.8042–0.9534)</td>
<td>0.001</td>
<td>0.0243</td>
<td>0.3802</td>
</tr>
<tr>
<td>B2004</td>
<td>0.9413 (0.8647–0.9790)</td>
<td>0.001</td>
<td>0.0100</td>
<td>0.3046</td>
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<tr>
<td>A2014</td>
<td>0.7896 (0.6169–0.8935)</td>
<td>0.001</td>
<td>0.0046</td>
<td>1.3764</td>
</tr>
<tr>
<td>B2014</td>
<td>0.8040 (0.6453–0.8999)</td>
<td>0.001</td>
<td>0.0097</td>
<td>0.9015</td>
</tr>
<tr>
<td>C2014</td>
<td>0.7862 (0.5386–0.9133)</td>
<td>0.001</td>
<td>0.0214</td>
<td>0.3430</td>
</tr>
<tr>
<td><strong>GAM for fir of the younger generation</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>A2004</td>
<td>0.8099 (0.7442–0.8628)</td>
<td>0.001</td>
<td>0.0070</td>
<td>0.6598</td>
</tr>
<tr>
<td>B2004</td>
<td>0.8133 (0.7481–0.8659)</td>
<td>0.001</td>
<td>0.0027</td>
<td>0.6403</td>
</tr>
<tr>
<td>A2014</td>
<td>0.6999 (0.6176–0.7618)</td>
<td>0.001</td>
<td>0.0025</td>
<td>1.0309</td>
</tr>
<tr>
<td>B2014</td>
<td>0.8287 (0.7580–0.8777)</td>
<td>0.001</td>
<td>0.0050</td>
<td>0.7023</td>
</tr>
<tr>
<td>C2014</td>
<td>0.7859 (0.6938–0.8500)</td>
<td>0.001</td>
<td>0.0017</td>
<td>0.8028</td>
</tr>
</tbody>
</table>

$\rho$: Spearman correlation coefficient between the predicted and measured radial increments for ten-year periods with 95% bootstrap confidence intervals (BCa CIs); permutation test: the null hypothesis $H_0$: $\rho = 0$ ($H_1$: $\rho > 0$); $\text{ARE}_{\text{min}}$ and $\text{ARE}_{\text{max}}$: absolute relative prediction errors.
Figure captions:

**Fig. 1.** Codes of sample fir trees; A – trees were chosen in 1994, crown measured and characterized in 1994, 2004, and 2014, trees cored in 1995, 2005, and 2015-2017; B – trees were chosen in 2004, crown measured and characterized in 2004 and 2014, trees cored in 2005 and 2015-2017; C – trees were chosen in 2014, crown measured and characterized in 2014, trees cored in 2015-2017.

**Fig. 2.** Dendrometric parameters, crown traits and competition attributes of sample fir trees from the older generation (OG) (see also Fig. 1); min, mean, max, mean ± sd (boxes) (a, b, c, d, f) and mean, max values (e); during investigated periods some trees passed from YG to OG.

**Fig. 3.** Dendrometric parameters, crown traits and competition attributes of sample fir trees from the younger generation (YG) (see also Fig. 1); min, mean, max, mean ± sd (boxes) (a, b, c, d, f) and mean, max values (e); during investigated periods some trees passed from YG to OG.

**Fig. 4.** The raw radial increment series at breast height and the growth trend (a cubic smoothing spline) of fir trees in the older generation (OG) (a) and in the younger generation (YG) (b).

**Fig. 5.** The final GAM for fir in the older generation (OG). The response is expressed in mean deviation form (the value of zero on the y-axis is the mean of the response). Each component is also centred, and thus, each panel represents how the response changes relative to its mean with changes in the component. Panels show the estimated effects (solid curves) with 95% confidence limits (dotted lines) for the relative crown length (a) and crown transparency (b). The number in each y-axis caption is the effective degrees of freedom of the component being plotted.

**Fig. 6.** The final GAM for fir in the younger generation (YG). The response is
expressed in mean deviation form (the value of zero on the y-axis is the mean of the response). Each component is also centred, and thus, each panel represents how the response changes relative to its mean with changes in the component. Panels show the estimated effects (solid curves) with 95% confidence limits (dotted lines) for the relative crown length (a), crown transparency (b), degree of crown deformation (c), and degree of forest canopy density around the crown for the shaded part (d). The number in each y-axis caption is the effective degrees of freedom of the component being plotted.
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