

# Modelling individual tree diameter growth for Norway spruce in the Czech Republic using a generalized algebraic difference approach

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## Abstract

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Individual tree-based growth models precisely describe the growth of individual trees irrespective of stand complexity. These models are more useful than the stand-based growth models for effective management of forests. We developed an individual tree diameter growth model for Norway spruce (*Picea abies* /Linnaeus/ H. Karsten) using permanent research plot data collected from Krkonoše National Park in the Czech Republic. The model was tested against a part of the Czech National Forest Inventory (NFI) data that originated from the western region of the country. Among various models derived by a generalized algebraic difference approach (GADA), the GADA model derived from the Chapman-Richards function best suited to our data. Tree-specific parameters unique to each growth series, which describe tree-specific growth conditions, were estimated simultaneously with global parameters common to all growth series using the iterative nested regressions. The model described most of the variations in diameter growth for model calibration data ( $R^2_{\text{adj}} = 0.9901$ , RMSE = 0.5962), leaving no significant trends in the residuals. A test against NFI data also confirms that the model is precise enough for predictions of diameter growth for ranges of site quality, tree size, age, and growth condition. The model also possesses biologically desirable properties because it produces the curves with growth rates and asymptotes that increase with increasing site quality. The GADA model is path-invariant and therefore applicable for both forward and backward predictions, meaning that the model can precisely predict diameter growth at any past ages of the trees.

**Keywords:** base-age invariant approach; Chapman-Richards function; global parameters; tree-specific parameters; iterative nested regression; National Forest Inventory

Effective management of the forest is possible only when reliable information on present and future forest conditions is available. This information can be derived from forest growth and yield models. Modelling growth and yield has been an intrinsic part of forestry research for many years and still remains ac-

tive (VANCLAY 1994; PORTE, BARTELINK 2002). Forest growth models are useful tools for inventory updating, evaluation of silvicultural treatments, harvest scheduling, and management planning in general (GARCÍA 1994; AMARO et al. 2003). Based on management objectives and input data, growth models

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may be operational either at stand or tree level. Stand growth is often modelled using the mean attributes of structurally less complex stands, where these attributes are closer to individual tree attributes (PIENAAR, RHENEY 1995; HUUSKONEN, MIINA 2007). Stand growth models do not precisely describe the growth dynamics of individual trees in the structurally more complex stands, where competitive situations largely differ among individual trees. The individual tree-based growth models are therefore aimed at a more precise description of individual tree growth in structurally more complex stands (WYKOFF 1990; PRETZSCH et al. 2002; UZOH, OLIVER 2008; BOLLANDSÅS, NÆSSET 2009). These models offer a good possibility of exploring detailed management alternatives as they allow ample flexibility in forecasting tree growth regardless of species, size, age, and site quality (HASENAUER 2006; ADAME et al. 2008; UZOH, OLIVER 2008; PRETZSCH 2009; CRECENTE-CAMPO et al. 2010; SUBEDI, SHARMA 2011).

Modelling the radial growth of individual trees (diameter or basal area growth) is often a starting point. As compared to individual tree radial growth models, the number of individual tree height growth models developed so far is lower. It is due to limited access of growth modellers to height growth data. Individual tree diameter growth is more affected by competition than height growth. Thus, it would be relatively easier to describe competitive response to the growth of diameter in diameter growth models. A potential growth reduction approach is often used to obtain the expected diameter growth while developing individual tree-based growth models. These models are either estimated simultaneously with a modifier for competition (HUANG, TITUS 1995; ANDREASSEN, TOMTER 2003; UZOH, OLIVER 2008; BOLLANDSÅS, NÆSSET 2009) or estimated separately (BIGING, DOBBERTIN 1992; PRETZSCH et al. 2002; SHARMA, BRUNNER 2016). This study applies a technique similar to the former one, where tree-specific parameters unique to each growth series are estimated simultaneously with global parameters common to all growth series using the iterative nested regressions. This technique is suitable for parameter estimation of the base-age invariant model (CIESZEWSKI, BAILEY 2000; KRUMLAND, ENG 2005).

The first base-age invariant model was derived using an algebraic difference approach – ADA (BAILEY, CLUTTER 1974). This makes direct use of the measured diameter-age series without the need of interpolation or extrapolation to determine diameter at base age if diameter is not measured at that age (CIESZEWSKI, BAILEY 2000; KRUMLAND, ENG 2005; NORD-LARSEN 2006). Therefore, a base-invariant

model is the most suitable to permanent sample plot data (NORD-LARSEN 2006; SHARMA et al. 2011). This only allows one parameter of the model to be subject-specific (tree-specific in our case), and the model derived by ADA may produce the anamorphic curves which would have a common asymptote (CIESZEWSKI 2003). CIESZEWSKI and BAILEY (2000) developed a more advanced base-age invariant model using generalized ADA (GADA), which allows more than one parameter to be subject-specific. The GADA model produces polymorphic curves with multiple asymptotes, which are biologically desirable properties (CIESZEWSKI 2003). The GADA model can be used to fit short time-series data, even if there is no common base age in the time series (GARCÍA 2005; SHARMA et al. 2011). Since GADA is a mathematically robust and biologically realistic modelling approach, all models derived by GADA exhibit much appealing results. This is the reason why GADA has become a standard of developing dominant height growth models (DIÉGUEZ-ARANDA et al. 2005; CIESZEWSKI et al. 2007; MARTÍN-BENITO et al. 2008; NORD-LARSEN et al. 2009; SHARMA et al. 2011), stand basal area growth models (BARRIO ANTA et al. 2006; CASTEDO DORADO et al. 2007), and tree biomass model (TANG et al. 2017).

To the authors' knowledge, GADA has been applied only for stand-based growth modelling and tree biomass modelling, but not for individual tree-based growth modelling to date. Thus, we developed an individual tree diameter growth model applying GADA by which global parameters common to all growth series were estimated simultaneously with tree-specific parameters unique to each growth series, using the iterative nested regressions (CIESZEWSKI et al. 2000; KRUMLAND, ENG 2005). We used two different data sets of Norway spruce: one for model calibration and the other for model validation. The first data set originated from the permanent research plots located across the Krkonoše National Park, while the second data set originated from the Czech national forest inventory. The proposed model can be applied for a precise prediction of future diameter growth that can be useful for estimating volume growth, biomass and carbon amounts of Norway spruce forests in the Czech Republic.

## MATERIAL AND METHODS

In this study, we used two data sets: model calibration and model validation data sets, in order to develop and validate the diameter growth model, respectively. Validation data originated from differ-

ent inventory designs and locations, and therefore these data had different characteristics and represented different growing conditions from those of the model calibration data. We briefly describe these data in the following subsections.

**Model calibration data.** We used model calibration data collected from Norway spruce stands in the Krkonoše National Park in the Czech Republic (Fig. 1a). The Park with an area of 363 km<sup>2</sup> was first declared in 1963 on the Czech-Polish border in the Krkonoše Mountains (synonymous to Giant Mountains). The park area was extended to 550 km<sup>2</sup> as a protection zone in 1968. In 1992, this park was included as a bilateral Biosphere Reserve in the list of the World Network of Biosphere Reserves. Forest stands are distributed at the altitudes between 400 and 1,370 m a.s.l. within the park (VACEK, HEJČMAN 2012), and precipitation, temperature and length of growing season vary with altitude and aspect. Mean annual precipitation varies from 860 to 1,260 mm, mean annual temperature from 2.6 to 6.1°C, and growing season length ranges from 35 to 150 days (VACEK et al. 2015). Norway spruce is a dominant species covering about 87% of the area in the park, while European beech (*Fagus sylvatica* Linnaeus), European larch (*Larix decidua* Miller), rowan (*Sorbus aucuparia* Linnaeus) or silver fir (*Abies alba* Miller) cover less than 12%, and the rest of the area is covered by mountain pine and other shrubby species. Based on the canopy layers, regeneration, dead wood stocks, damage, and developmental stages of stands, 830 circular permanent research plots (PRPs) of 500 m<sup>2</sup> in size were established by following the protocols developed by the Field-Map technology of the IFER – Monitoring and Mapping Solutions, Ltd. (IFER 2016). All measurements were done with a specific permission obtained from the park authority.

Outside bark diameter at breast height (DBH) was measured for all trees with DBH ≥ 7 cm at two per-

pendicular directions with a metal calliper to the nearest 1 mm (hereafter termed as diameter). Total height and height to the crown base for at least five trees of dominating species and at least one for each of the other tree species were measured using a laser Vertex hypsometer (Haglöf Sweden, A.B., Sweden) to the nearest 10 cm. Ages for younger stands were derived from records of stand origin years and ages of mature stands were derived from the analysis of growth rings of the trees that were differentiated according to forest site types. The first measurement was done between May 2009 and December 2010, and the second measurement between June 2012 and July 2014, which resulted in about four years of growth period. Extremely large negative increments and positive increments were excluded assuming that they were due to measurement or recording errors.

**Model validation data.** Model validation data used in this study were a part of the Czech National Forest Inventory (NFI) data that represent only the western region of the country (Fig. 1b). Forests in this region consist of mixed species stands where Norway spruce is a dominant species. These stands are located at altitudes between 309 and 1,161 m a.s.l., and mean annual temperature and mean annual precipitation are 7.8°C and 675 mm, respectively. The circular sample plots with 500 m<sup>2</sup> area were established using the Field-Map technology of the IFER – Monitoring and Mapping Solutions, Ltd. (IFER 2016), and sample plots are located in a 2 × 2 km grid. The first measurement was done between 2001 and 2004 and the second measurement between 2010 and 2015, which resulted in about ten years of the growth period. We used only time-series data, i.e. only trees measured twice. This resulted in a selection of 514 sample plots that were used for our purpose. Other tree and stand characteristics on each NFI sample plot were measured following the inventory protocols developed by the Forest Man-

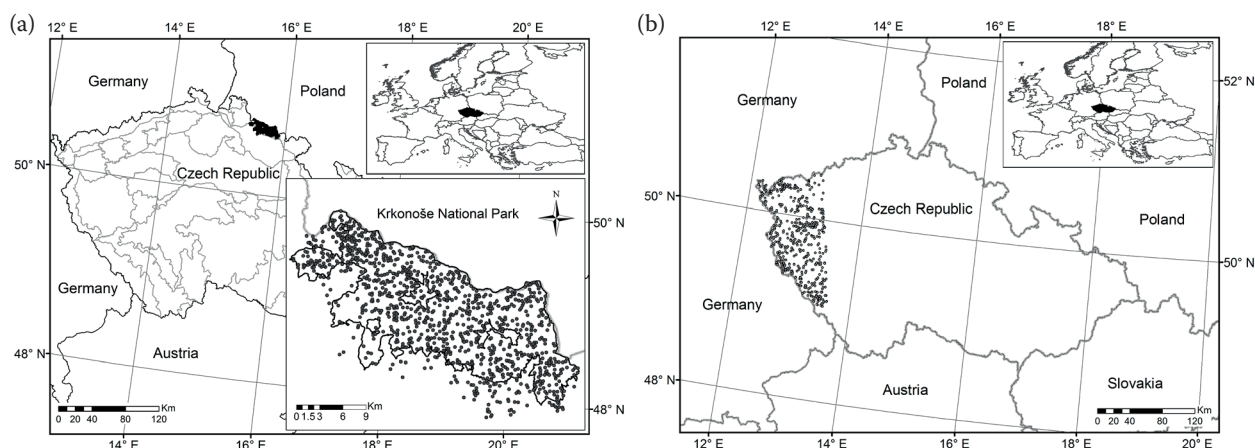


Fig. 1. Permanent research plots in the Krkonoše National Park (a), Czech National Forest Inventory sample plots (b)

agement Institute (FMI 2003). Details of sampling design and methods of measurement applied to NFI sample plots can be found in KUČERA (2015).

Summary statistics of both model calibration and validation data are presented in Table 1 and graphs of diameter-age series are presented in Fig. 2.

**Modelling approach.** The GADA model fits three-dimensional surfaces (stand age, diameter, subject-specific effects) in a way that directly estimates subject-specific effects (tree-specific effects in our case) as local parameters from the fitting procedures (CIESZEWSKI 2001; NORD-LARSEN 2006). For long-time-series data, the base function is fitted by individual diameter-age series in order to establish a relationship between theoretical variable  $X$  (unobserved variable, also known as growth intensity factor) and tree-specific parameters (CIESZEWSKI, BAILEY 2000). The  $X$  is a variable or a function of any number of variables that can include the effects of site quality, stand density or competitive interactions among the trees, and other physical and genetic factors. The  $X$  is continuous, monotonic and relevant to the modelled dynamics; and it can describe the relative rates of change in terms of direct functional relationships among the variables. Details about this theoretical variable  $X$  and its relationship with other variables are available in the literature (CIESZEWSKI, BAILEY 2000; CIESZEWSKI 2001, 2003; NORD-LARSEN 2006). The GADA-based diameter growth model is represented by a general functional form (Eq. 1):

$$d_1 = f(d_0, t_0, t_1, \mathbf{b}) \quad (1)$$

where:

$d_0, d_1$  – diameter measurements,  
 $t_0, t_1$  – age measurements,  
 $\mathbf{b}$  – parameter vector.

This formulation consists of global parameters that are transformed from the relationship of tree-specific parameters and theoretical variable  $X$  (Eqs 2–5). The resulting GADA model (Eq. 6) is mathematically robust and biologically realistic (CIESZEWSKI, BAILEY 2000). Our data have a short time series, i.e. it originated from two measurements, therefore it is not possible to formulate new GADA models as reported in the literature (CIESZEWSKI, BAILEY 2000; CIESZEWSKI 2003; NORD-LARSEN 2006; NIGH 2015). We therefore selected previously derived GADA models as our candidate models, which have frequently been used to fit dominant height-age or stand basal area-age trajectories of various tree species (DIÉGUEZ-ARANDA et al. 2005; BARRIO ANTA et al. 2006; CASTEDO DORADO et al. 2007; SHARMA et al. 2011).

Mostly GADA models are derived from the base functions of the fractional or exponential forms (CIESZEWSKI, STRUB 2008). The exponential form such as Chapman-Richards function (RICHARDS 1959; CHAPMAN 1961) is considered as an important paradigm to growth and yield modelling. In our case also, the GADA model derived from the Chapman-Richards function showed the smallest sum of squared errors, and therefore it was chosen for further analyses. Details of its derivation are presented below. The Chapman-Richards function we used as a base function is calculated as Eq. 2:

$$d = a_1 [1 - \exp(-a_2 t)]^{a_3} \quad (2)$$

where:

$d$  – diameter of the tree,  
 $t$  – age of the tree,  
 $a_1, a_2, a_3$  – asymptotic, rate and initial parameters of the function, respectively.

Table 1. Summary statistics of model calibration and validation data

Variable	Statistics [mean $\pm$ SD (range)]		
	model calibration data		model validation data
	monospecific stands	mixed species stands	mixed species stands
No. of sample plots	564	266	514
No. of trees per sample plot	15.2 $\pm$ 5.9 (2–33)	15.3 $\pm$ 5.1 (2–30)	22 $\pm$ 14.9 (4–77)
Basal area (m <sup>2</sup> ·ha <sup>-1</sup> )	27.6 $\pm$ 15.6 (0.4–66.2)	31.9 $\pm$ 14.9 (1.2–68.9)	41.5 $\pm$ 13.8 (1.4–73.8)
DBH (cm)	32.3 $\pm$ 10.9 (7–79.8)	34.9 $\pm$ 12.1 (7–75.5)	24.5 $\pm$ 9.8 (7–78.4)
QMD (cm)	31.9 $\pm$ 8.8 (7.3–64.3)	34.9 $\pm$ 8.6 (7.4–58.2)	25.7 $\pm$ 5.9 (8.4–55.8)
DBH range per sample plot (cm)	22.7 $\pm$ 9.4 (1.5–65.5)	30.6 $\pm$ 12 (2.4–67.1)	31.2 $\pm$ 10.2 (2–72.4)
Total height (m)	19.9 $\pm$ 7.9 (1.4–43)	24.5 $\pm$ 8.2 (3.5–45.4)	17.2 $\pm$ 9.8 (1.6–45.2)
Mean height per sample plot (m)	21 $\pm$ 6.9 (2.4–36.4)	24.5 $\pm$ 6.4 (4.3–37.4)	17.7 $\pm$ 5.1 (2.9–33.3)
Height range per sample plot (m)	6.6 $\pm$ 3.7 (1.6–25.2)	11.4 $\pm$ 6.2 (1.8–34.4)	25.8 $\pm$ 6.7 (2.1–43.4)
Stand age (yr)	85.4 $\pm$ 45.2 (9–236)	81.6 $\pm$ 37 (9–238)	68.2 $\pm$ 30.2 (10–196)

QMD – quadratic mean DBH, SD – standard deviation



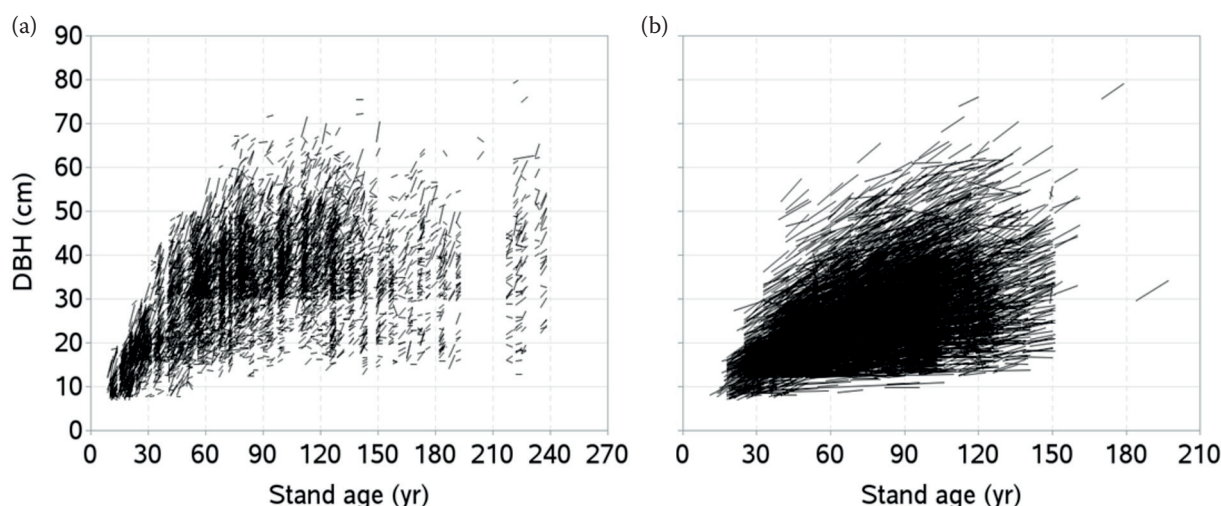


Fig. 2. Diameter-age series: model calibration (a), validation (b) data

The following parameters from Eq. 2 were considered as tree-specific parameters in our case (Eqs 3 and 4):

$$a_1 = \exp(X) \quad (3)$$

$$a_3 = b_2 + \frac{b_3}{X} \quad (4)$$

where:

$X$  – theoretical (unobserved) variable,

$b_2, b_3$  – global parameters.

Substituting these assumptions into Eq. (2) and solving for  $X$  with substitution of initial values ( $d_0$  and  $t_0$ ) for  $d$  and  $t$  would give out the algebraic solutions, as Eq. 5:

$$X_0 = \frac{1}{2} \left[ \Psi + \sqrt{\Psi^2 - 4b_3\phi} \right] \quad (5)$$

where:

$X_0$  – solution of  $X$  for initial diameter and age, and according to characteristics of biological growth theory, the root most likely to be real and positive,

$$\Psi = L_n d_0 - b_2 \phi,$$

$$\phi = L_n [1 - \exp(-b_1 t_0)],$$

$b_1, b_2, b_3$  – global parameters.

Then, the resulting GADA formulation would be as follows (Eq. 6):

$$d_1 = d_0 \left[ \frac{1 - \exp(-b_1 t_1)}{1 - \exp(-b_1 t_0)} \right]^{\left( \frac{b_2 + b_3}{X_0} \right)} \quad (6)$$

In preliminary analyses, we evaluated the hypothesis whether tree-specific parameters (derived from a functional relationship of a theoretical variable  $X$ , Eqs 2–5) were able to account for the variations caused by stand density or competition effects on diameter growth. For this, we included each of the sample plot-centred competition mea-

sures such as stand basal area – BA ( $\text{m}^2 \cdot \text{ha}^{-1}$ ) and stem number ( $N$ ) per hectare as a covariate into the GADA model using  $b_2$  as a function of  $Z$  in Eq. 6, as Eq. 7:

$$b_2 = \alpha_1 + \alpha_2 Z \quad (7)$$

where:

$\alpha_1, \alpha_2$  – parameters to be estimated,

$Z = \text{BA or } N$ .

However, no significant effect of each of them was found ( $P > 0.05$ ). Another alternative such as  $b_1$  or  $b_3$  as a function of  $Z$  was also evaluated, but the model did not converge either. This analysis showed that tree-specific parameters, which are unique to each growth series, were able to account for stand density effects or competition effects on diameter growth effectively. However, we were not able to evaluate the site quality effect using the site index. Alternatively, the sample plot dominant height calculated using the methods by SHARMA et al. (2011, 2016) was evaluated in a similar way as above, however its effect was not significant either.

In order to fit the GADA model (Eq. 6), we prepared data structure of the form (Eq. 8):

$$\begin{pmatrix} t_{1i} \\ d_{1i} \end{pmatrix}, \begin{pmatrix} t_{0i} \\ d_{0i} \end{pmatrix} \quad (8)$$

where:

$d_{1i}$  – diameter measurement at age  $t_{1i}$  for a tree  $i$ ,

$t_{0i}$  – mean of age measurements for a tree  $i$  ( $i = 1, 2, 3, \dots, n$ , with  $n$  – number of trees),

$d_{0i}$  – mean of diameter measurements for a tree  $i$  (also considered as a tree-specific parameter).

Instead of using  $t_{0i}$  as a starting value, any other value within the observed range could be used as

a starting value for estimating GADA models using the iterative nested regressions (CIESZEWSKI et al. 2000; KRUMLAND, ENG 2005). We assumed that temporal or serial autocorrelation was insignificant because of too short time series, but spatial autocorrelations caused by several numbers of trees within the same sample plot could be strong. In order to compute the spatial weight matrix, which is used to deal with spatial autocorrelations through the application of autoregressive error-structured modelling, the location of each tree was necessary (BANERJEE et al. 2014). However, no variable was available in our data to describe the location of each tree. We therefore applied the mixed effect modelling approach with a random effect parameter added to  $b_2$  in Eq. 6 while estimating model parameters. This approach is also assumed to describe all kinds of within-sample plot variations and autocorrelations effectively (VONESH, CHINCHILLI 1996; PINHEIRO, BATES 2000).

**Model estimation and evaluation.** We estimated the GADA model (Eq. 6) with restricted maximum likelihood in SAS macro NLINMIX (Version 9.4, 2013) (SAS Institute, Inc. 2013) using an expansion-around-zero method (LITTELL et al. 2006). Tree-specific parameter ( $d_{0i}$ ) unique to each growth series, which describes the tree-specific growth condition, was estimated simultaneously with global parameters common to all growth series using the iterative nested regressions (CIESZEWSKI et al. 2000; KRUMLAND, ENG 2005; SHARMA et al. 2011). An iterative procedure involved: (i) estimation of global parameters of the GADA model (Eq. 6), (ii) estimation of tree-specific parameters ( $d_{0i}$ ) using estimated global parameters in step (i), (iii) re-estimation of global parameters using new values of tree-specific parameters obtained in step (ii), (iv) procedures of step (ii) and (iii) were repeated until the sum of squared errors changed by a negligible magnitude.

The fitted models were evaluated using the sum of squared errors, adjusted coefficient of determination –  $R^2_{adj}$  and root mean squared errors – RMSE (MONTGOMERY et al. 2001). We examined the graphs of residuals plotted against each of the potential independent variables (stand basal area, quadratic mean diameter, stem number per hectare, dominant height) and simulated diameter-age curves overlaid on the measured data. We carried out the model validation, which is one of the most important tasks in growth modelling, as this provides credibility and confidence about the prediction models, using independent data. Model validation with independent data provides impor-

tant information in addition to the respective fit statistics obtained from the model calibration data (KOZAK, KOZAK 2003; YANG et al. 2004; SHARMA et al. 2011).

## RESULTS

The model derived by GADA described most of the variations in diameter growth ( $R^2_{adj} = 0.9901$ , RMSE = 0.5962) and all parameter estimates are highly significant (Table 2). All tree-specific parameter estimates ( $d_{0i}$ ) observed in the final step of the iterative procedures in the nest regressions were logical, reflecting true local conditions of tree growth. The model fits also showed no heteroscedasticity problem in the residuals (Fig. 3), indicating that GADA formulation using the Chapman-Richards base function (considering tree-specific parameters as a function of theoretical or unobserved variable  $X$ , Eqs 2–5) best suited to our data. Even though there were substantial variations among diameter growth across stand ages (Fig. 2), where such variations also increased with stand age, more than 99% residuals confined to be within a narrow range ( $\pm 2$  cm) around zero (Fig. 3).

The test against validation data showed that the GADA model was able to precisely predict diameter growth for a wide range of ages and diameters without any pronounced trends in the prediction errors (Fig. 4). The prediction statistics calculated by the GADA model (Eq. 6) using parameter estimates in Table 2 are promising (i.e.  $R^2 = 0.9772$ , RMSE = 0.7583). Most of the observations were described adequately well by the model whereby more than 95% of prediction errors confined to be within a narrow range ( $\pm 2$  cm) around zero. However, the model was not able to precisely describe some extreme outlier observations.

The diameter curves simulated using parameter estimates in Table 2 passed through each of the diameter-age trajectories in both model calibra-

Table 2. Parameter estimates and fit statistics of Eq. 6 ( $R^2_{adj} = 0.9901$ , RMSE = 0.5962,  $P < 0.0001$ )

Parameter	Estimate	SE	<i>t</i> -Statistic
$b_1$	0.016143	0.000388	41.52
$b_2$	0.137024	0.00189	72.36
$b_3$	3.29387	0.04984	66.14

$R^2_{adj}$  – adjusted coefficient of determination, RMSE – root mean squared error,  $b_1$ ,  $b_2$ ,  $b_3$  – global parameters, SE – standard error, *t*-statistic – ratio of the estimated value of a parameter and its standard error

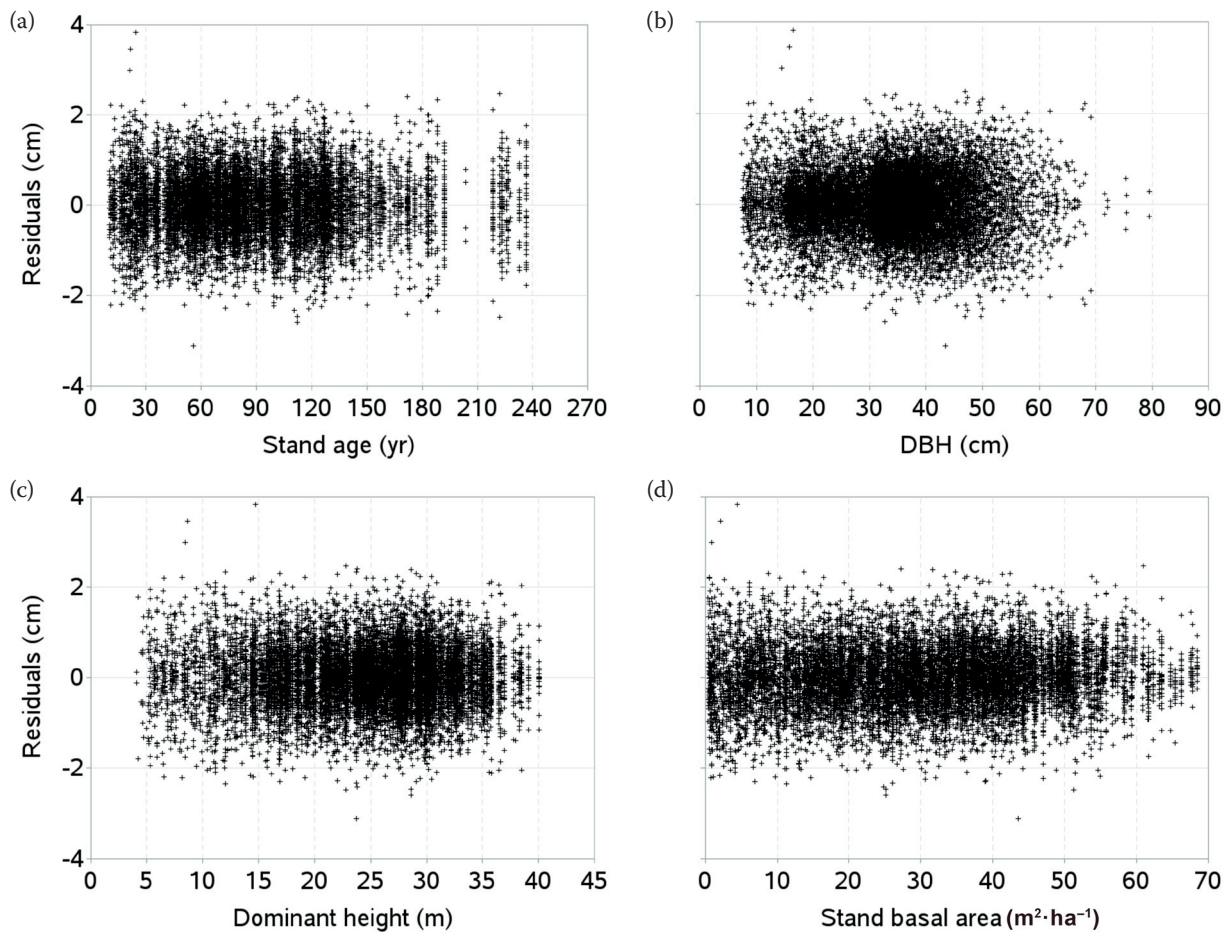


Fig. 3. Residuals of GADA model (Eq. 6) using parameter estimates in Table 2 for calibration data: stand age (a), diameter at breast height – DBH (b), dominant height (c), stand basal area (d)

tion and validation data even though there were significantly large variations in diameter growth across stand ages and site qualities (Fig. 5). Both measured diameter-age trajectories in these data and simulated curves appeared relatively steeper in younger stands with better sites. However, the simulated curves appeared flatter for older stands (age > 150 years for model calibration data) than the

measured diameter-age trajectories for most of the stands with all site classes. This resulted in slightly larger residuals and prediction errors for a number of older trees in both data sets. This could be much more clearly visible when residuals and prediction errors were examined by PRP. The model also produced the curves with growth rates and asymptotes that increased with increasing site quality.

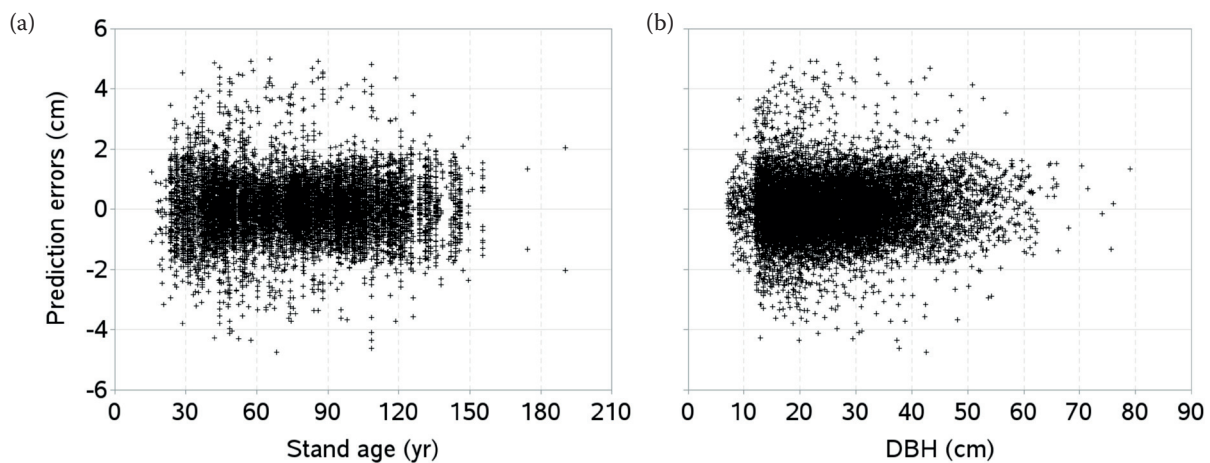


Fig. 4. Prediction errors of GADA model (Eq. 6) using parameter estimates in Table 2 for model validation data: stand age (a), diameter at breast height – DBH (b)



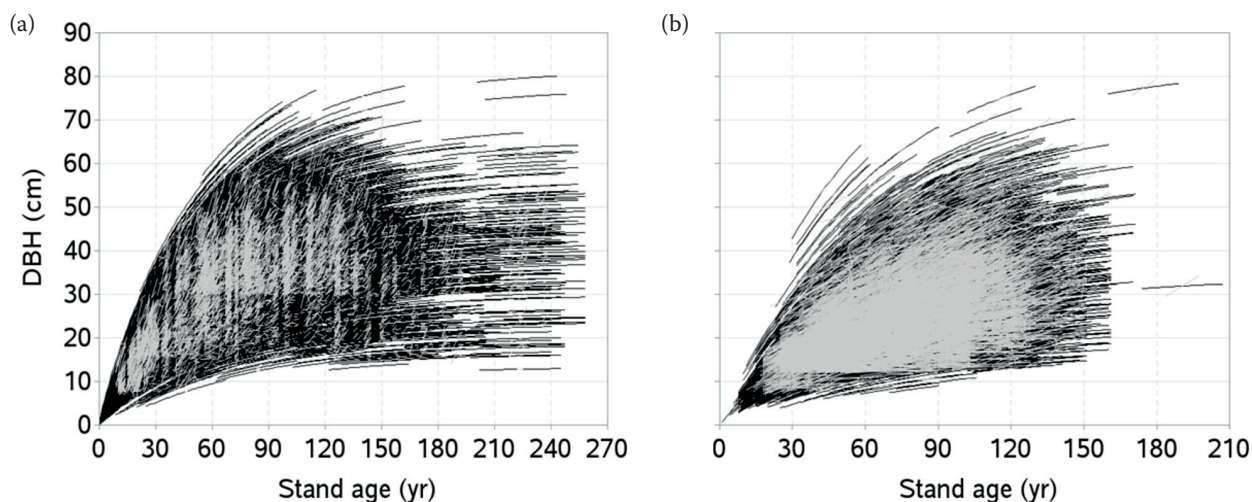


Fig. 5. Simulated curves overlaid on the DBH-age series of model calibration (a), validation (b) data  
grey – observed growth series, black – simulated growth curves

## DISCUSSION

Data used in this study cover a wide variation of site quality, tree size, stand density and age, and management regime. However, measurements were few for the stands aged above 120 years on the higher productive sites. Data were not available from the stands with ages between 190 and 220 years (Fig. 2a) as they were destroyed by heavy industrial pollution during 1979–1995, which caused a destruction of about 7,000 ha of spruce forests in the area. Our data are a short time series and only few measurement or recording errors existed due to which some diameter-age trajectories appear to be steeper, even for very old stands on poorer sites (Fig. 2a). We assumed these errors were random and would not affect the accuracy of the model.

The GADA model was able to describe most of the variations in diameter growth (Table 2), leaving no significant trends in the residuals (Fig. 3). This indicates that tree-specific parameters assumed in the GADA formulation are realistic, and therefore this model was able to describe variations caused by the effects of site quality, stand density or competition, species mixture, and other physical and genetic factors (CIESZEWSKI, BAILEY 2000). This was possible because of using an effective system of the model calibration such as iterative nested regression (CIESZEWSKI 2002; KRUMLAND, ENG 2005; SHARMA et al. 2011; TANG et al. 2017). This system involves the parameter estimation which is based on identifying individual trends of growth represented in the data (BAILEY, CLUTTER 1974; CIESZEWSKI et al. 2000; CIESZEWSKI 2003). This system, where regression assumptions are not violated, is both theoretically and practically desirable (CIESZEWSKI

et al. 2000). The trends of individual tree diameter growth are modelled by considering all individuals' responses in the data that follow similar functional forms with varying parameters of individuals (i.e. tree-specific parameters:  $d_{0i}$ ) and parameters common to all individuals (global parameters in Eq. 6) (CIESZEWSKI 2003; BARRIO ANTA et al. 2006; SHARMA et al. 2011). Although repeated measurements are most accurate for estimating increment, the GADA model developed using stem analysis data may be more efficient and easy to operate (GARCÍA 2005). However, it is noted that the GADA model, which possesses base-invariant properties, is also suitable to the permanent sample plot data as well (NORD-LARSEN 2006; SHARMA et al. 2011). The GADA modelling overcomes the limitations of within-stand competition and limited biometric data and can be applied to study growth and biomass dynamics of the individual trees (CIESZEWSKI, BAILEY 2000; NIGH 2015; TANG et al. 2017).

Generally, self-referencing models are usually estimated using base-age-specific or base-age-invariant approaches. The former approach is more common, which assumes that reference values ( $d_{0i}$ ) are arbitrarily selected as reference points (fixed), and only global parameters are estimated (CIESZEWSKI et al. 2007). However, the base-age invariant approach treats reference points ( $d_{0i}$  in our case) as a tree-specific parameter that varies from tree to tree (BAILEY, CLUTTER 1974; CIESZEWSKI et al. 2000; SHARMA et al. 2011). Unlike the base-age specific model, which needs a common base age of all growth series, fitting of the base-age-invariant model is independent of the length of time series. The short time series (Fig. 2a), which may or may not have a common base age ( $t_{0i}$ ), can be also ef-



ficiently fitted (GARCÍA 2005; SHARMA et al. 2011). Therefore, in recent years, GADA has been used as a standard approach in modelling forest growth and yield, such as modelling dominant height growth (DIÉGUEZ-ARANDA et al. 2005; NORD-LARSEN 2006; CIESZEWSKI et al. 2007; MARTÍN-BENITO et al. 2008; SHARMA et al. 2011; NIGH 2015), stand basal area growth (BARRIO ANTA et al. 2006; CASTEDO DORADO et al. 2007), and tree biomass (TANG et al. 2017).

The curves produced by the GADA model pass through each of the measured diameter-age trajectories in both data sets (Fig. 5), suggesting that individual tree-based GADA models are almost similar to properly localized tree-level mixed effect models. The latter model produces the curves that pass through the measured diameter-age trajectories when both sample-plot and tree-level random effect parameters were estimated using the empirical best linear unbiased prediction theory (VONESH, CHINCHILLI 1996; PINHEIRO, BATES 2000) and adjusted them to fixed parts of the mixed effect model, i.e. making a tree-specific model (YANG, HUANG 2011a, b). However, application of the two-level mixed effect model is more cumbersome and costly than the GADA model, because the former model requires measurements of a response variable (i.e. diameter in our case) for a number of new sample trees on each sample plot to localize the mixed effect model. Furthermore, calibration of a nonlinear mixed effect model is rather complex as it requires non-standard software and optimization methods (CIESZEWSKI, BAILEY 2000; CIESZEWSKI 2003; NIGH 2015). On the other hand, calibration of the GADA model can be done easily using simpler software (e.g. spreadsheet software, custom software) without the need of complex nonlinear optimization code (NIGH 2015). The application of GADA model requires measurement of diameter  $d_0$  at age  $t_0$  to make a precise prediction of diameter for age  $t_1$ . Both calibration and application of GADA model is therefore easier and prediction accuracy can be reasonably high as well. We dealt with a potential problem of autocorrelations because it was extremely important to secure unbiased estimates of the model parameters and variances. When autocorrelations are not effectively accounted for, they cause statistical complication and invalidate the hypothesis tests (HUANG, TITUS 1995; VONESH, CHINCHILLI 1996; PINHEIRO, BATES 2000; CIESZEWSKI 2003).

The GADA model fits the data adequately well, taking into account most of the tree-specific and global effects, and is also able to produce biologi-

cally desirable curves (CIESZEWSKI 2001, 2002, 2003). However, the choice of the functional forms that establish relationships between tree-specific parameters and theoretical variable  $X$  in Eqs 2–5 can affect the accuracy and behaviour of the GADA model (CIESZEWSKI, BAILEY 2000; CIESZEWSKI 2003; NIGH 2015). Some GADA models that we evaluated were difficult to fit and did not produce any biologically sensible asymptotes. The Chapman-Richards model did not exhibit any calibration problems and resulted in biologically more sensible asymptotes (Fig. 5). In general, if the model is calibrated using short time-series data, predictions might be largely biased when the model is applied for longer time steps. However, our model can be suitable to predict future diameter growth for longer time steps (i.e., up to 10 years) because this was confirmed by testing our model against NFI data, which have ten year's growth period. Nevertheless, longer time-series data are needed to develop growth models to include stand dynamics and development histories. In a couple of growth modelling studies, advantages and disadvantages of using sample plot inventory and long-term experimental plot data or stem analysis data or combination of both have been discussed (VON GADOW, HUI 1999; PRETZSCH 2009; CRECENTE-CAMPO et al. 2010). Furthermore, the effects of competition and facilitation, and abiotic stress on tree growth have also been analysed and described in various studies (HASENAUER 2006; PRETZSCH 2009).

It would be interesting to test the growth models against longer time-series data that originate either from stem analysis or long-term research sample plots, which show clear growth trends caused by long-term changes in environmental conditions (MARTÍN-BENITO et al. 2008; SHARMA et al. 2011; YUE et al. 2014). However, we could not do this because of unavailability of such data. Since the thinning effect on diameter growth can be substantial (MÄKINEN, ISOMÄKI 2004; VOSPERNIK et al. 2015), we could not evaluate this either due to the lack of a variable describing thinning response in our data. The test against NFI data confirmed that our model is precise enough to predict diameter growth for different conditions from those represented by model calibration data. The proposed model is path-invariant, and therefore applicable for both forward and backward predictions (i.e.  $t_0 \rightarrow t_1$  or  $t_1 \rightarrow t_0$ ), meaning that the model can precisely predict diameters at any past age. The model also possesses biologically desirable properties, because it produces polymorphic curves with multiple asymptotes (Fig. 5).

## CONCLUSIONS

Given the data limitations (e.g. short time series), the model derived by GADA described most of the variations in diameter growth, leaving no significant trends in the residual errors in either model calibration or validation data sets. This suggests that GADA is also applicable to develop an individual tree growth model that successfully accounts for all potential effects (tree-specific and global effects) and variations (random and deterministic variations). Diameter growth of individual trees largely varies with site quality and stand age, which is clearly exhibited by simulated curves (polymorphic curves with multiple asymptotes) produced by our GADA model. This model is thus able to describe the variations caused by the effects of site quality, stand density or competition, species mixture, and other environmental and genetic factors on diameter growth. The test against NFI data confirms that our model is precise enough for ensuring a high accuracy in the prediction. Our model is path-invariant, and therefore applicable for both forward and backward predictions (i.e.  $t_0 \rightarrow t_1$  and  $t_1 \rightarrow t_0$ ), meaning that the model can precisely predict diameters at any past age of the trees. The proposed model can be used for the precise prediction of future diameter growth that, in turn, can be useful for estimating volume growth, and biomass and carbon amounts of Norway spruce forests in the Czech Republic.

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