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Can trees at high elevations compensate for growth
reductions at low elevations due to climate warming?

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Abstract

Radial tree stem growth of *Picea abies*, *Fagus sylvatica*, *Pinus sylvestris* and *Pinus cembra* was monitored from 2012 until 2015 across sites in Austria with high resolution dendrometers. Seasonal cumulative diameter increment was modeled using a hierarchical nonlinear mixed-effects model framework based on a logistic growth curve. In the dry and warm year 2015 the average annual diameter increment of 0.30 cm decreased by 50% on lower elevation sites and by 10% on higher elevation sites. In the cool and moist year 2014, Norway spruce achieved a higher annual diameter increment than European beech, whereas the opposite occurred in the dry and warm years 2013 and 2015. In the mixed beech-spruce stand, beech's consumptive water-use strategy has obviously caused intensified stress for spruce in these drought periods. On higher elevation sites Norway spruce reacted more sensitively to climate fluctuation compared with stone pine, but overall reactions were only

weak. Productivity varied strongly dependent on the social tree status with dominant and intermediate trees suffering more from drought. As warming and drought lowers increment rates on lower elevation sites and as trees on higher elevation sites react less flexible, productivity losses are expected for Austrian forests due to climate warming.

Keywords

Seasonal growth, dendrometer, nonlinear mixed model, intra-annual growth

Introduction

Recent climate simulations predict a global trend of rising atmospheric temperatures together with seasonal changes of precipitation (IPCC, 2013). Relative to the period 1971–2000, the moderate future climate scenario RCP 4.5 forecasts an average increase of mean annual temperature between 1 °C and 4.5 °C across Europe by the end of 21st century (Jacob *et al.*, 2014). The warming will be especially pronounced in the northeast and south of Europe, the latter subregions comprising the Alps and our study areas in Austria. Additionally, climate projections for Austria suggest a seasonal shift of precipitation totals from summer to winter months, probably resulting in higher frequency and longer duration of drought periods during the growing season (Jacob *et al.*, 2014).

The expected future changes of climate will result in longer growing seasons (Menzel and Fabian, 1999; Badeck *et al.*, 2004; Körner and Basler, 2010) and different rainfall regimes. Predictably, forests will be affected by: modified growth rates (Linares *et al.*, 2009; Pretzsch *et al.*, 2014), changes in site productivity (Albert and Schmidt, 2010; Nothdurft *et al.*, 2012), altered species composition (Rigling *et al.*, 2013; Cavin and Jump, 2017) as well as increased tree mortality rates (Nothdurft, 2013; Rigling *et al.*, 2013; Neuner *et al.*, 2015; Allen *et al.*,

2015).

The relationship between climate and physiological processes impacting tree growth is complex. In general trees respond to meteorological changes during the growing season more noticeably than to changes during the dormant season. In Austria, domestic tree species undergo a winter dormancy period with no cambial activity. The maximum duration of the annual growing season is 180–200 days, whereas a minimum duration of 96 days can be observed on sites close to the tree line (Körner, 2012). Lateral stem growth results from the formation of phloem and xylem, both showing a distinct intra-seasonal pattern. Cambium starts its activity and produces new wood cells in spring only once dormancy has ended. The exact time point of growth onset is mainly triggered by warm spring temperatures as well as by the lengthening of the daily photoperiod (Körner and Basler, 2010). During the subsequent period the predefined wood cells are further expanded and lateral stem growth becomes remarkable. After the cell volume is completely expanded, cell walls are thickened and secondary material is deposited. Cell division and enlargement is already accomplished by late summer. The rest of the growth period is then used for the lignification of cell walls. Finally, the sensitive cambium enters dormancy again well before the winter period in order to prevent potential frost damage. Thus, cell division, cell enlargement as well as lateral stem growth has already stopped when daily temperature still lies in a favorable range. Therefore, it is the length of the photoperiod that is assumed to have major influence on the maximum length of the growth period. For further details on intra-annual xylem and phloem formation the reader is referred to Mäkinen *et al.* (2003), Gruber *et al.* (2009), Prislan *et al.* (2013), Oberhuber *et al.* (2014), Swidrak *et al.* (2014) and Gričar *et al.* (2015).

Austria's topography is highly variable on a small spatial scale, especially in the Alpine region with elevation ranging from 200 m to 3800 m a.s.l. The treeline varies in elevation throughout the Austrian Alps. It has its maximum around 2000 m in the central part and lies at approx.

1600 m at the edges of the Alps (Körner, 2012). On lower elevation sites, tree growth is generally favored by warm spring temperatures, but trees periodically suffer from drought stress during summer months. Often, trees do not benefit from higher summer temperatures on lower elevation sites, because a warm summer often coincides with lower precipitation, and both factors promote severe soil water deficit. Thus, water availability in summer month can be regarded the most limiting factor for tree growth on lower elevation sites (Downes *et al.*, 1999; Gričar *et al.*, 2015). The average air temperature decreases with higher elevation and due to higher precipitation a surplus of water availability is generally present on montane and subalpine sites. Thus, temperature becomes the major limiting factor for tree growth on such sites (Rossi *et al.*, 2008; Gruber *et al.*, 2009; Körner, 2012; Prislán *et al.*, 2013).

Given existing climate projections, we therefore expect two contrasting results for the future growth of Austrian forests. Reduced growth rates are anticipated on sites at lower elevations due to more frequent periods of water shortage in the future. Whereas, increased growth rates are expected on higher elevation sites due to higher temperatures and longer growing seasons (Kindermann *et al.*, 2013). In general, stem growth follows a distinct seasonal pattern and is strongly driven by meteorological variables. Meteorological phenomena also show high intra- as well as inter-annual fluctuation. An in-depth study of climate-related seasonal stem growth patterns is thus required in order to derive a reliable quantification of potential tree growth reactions due to a changing climate.

Besides climate, seasonal tree growth patterns also depend on: tree species (Henhapfl, 1965; Franz *et al.*, 1990; Zweifel *et al.*, 2006; Wipfler *et al.*, 2009; Gruber *et al.*, 2009; Michelot *et al.*, 2012; Cuny *et al.*, 2012; Swidrak *et al.*, 2014; Jyske *et al.*, 2014), applied thinning regimes (Linares *et al.*, 2009; van der Maaten, 2013), social tree position (Kramer, 1982; Franz *et al.*, 1990; Rathgeber *et al.*, 2011; van der Maaten, 2013), neighborhood identity (Metz *et al.*, 2016), ozone concentration (Wipfler *et al.*, 2009), provenance (Kallikowski *et al.*, 2012), fructification

1 (Drobyshev *et al.*, 2010) or needle losses (Franz *et al.*, 1990).

2 In our paper we analyze seasonal growth patterns of 103 trees from 2012 and 2015 at five
3 different sites in Austria. Hereof, two sites are located at lower elevations and three sites at
4 higher elevations. Seasonal growth was monitored in high temporal resolution using dendrom-
5 eters equipped with thermometers. The measurement period comprises contrasting extreme
6 seasonal climate conditions, with a dry and hot growing season in 2015 and rather humid con-
7 ditions in 2014. The dataset encompasses four distinct tree species, namely Scots pine (*Pinus*
8 *sylvestris* L.), Norway spruce (*Picea abies* (L.) H. KARST.), European beech (*Fagus sylvatica*
9 L.) and stone pine (*Pinus cembra* L.). These tree species represent early and late successional
10 species. On each site, sample trees were selected from different social tree classes.

11 Our study's main aim is to compare intra-annual growth of Norway spruce on low and high
12 elevation sites over a series of consecutive growth periods. We hypothesize that tree growth
13 is mainly influenced by precipitation on lower elevation sites, whereas temperature is more
14 relevant on higher elevation sites. We therefore expect to see reduced growth rates at lower ele-
15 vations and increased growth rates at higher elevations in the dry and hot year 2015. In addition,
16 we provide a comparison of growth reactions among different tree species. We expect that stem
17 growth of Norway spruce is more sensitive to drought and heat than other tree species. Finally,
18 we want to examine whether trees react differently depending on their social tree classes.

19 **Material**

20 **Data**

21 Starting in 2011, dendrometers have been permanently installed at five different sites in Austria
22 (Figure 1). Dendrometers remained fixed at the sample trees during the whole measurement
23 period. In case a dendrometer was installed after April 1, the initial year was discarded from our

data analysis, so that our data set begins with 2012. An overview of the study sites and summary characteristics of the dendrometer measurements is shown in Table 1. Summary characteristics of the climate data given in Table 1 refer to climate conditions at the lower end of the elevational gradients. An average temperature decrease of approximately 0.65°C per 100 m increase in elevation was found in Tyrol and Nasswald. This thermal gradient mainly results from adiabatic processes. Climate data gave no evidence that temperature inversion exists during the growing season.

The original purpose of the experiment in Kreisbach (20 dendrometers) and Rosalia (10 dendrometers) was to study tree growth of European beech and Norway spruce in pure and mixed stands. Kreisbach is a 2.5 ha large triplet study consisting of a stand of pure Norway spruce, pure European beech and a mixture of both tree species. In Rosalia, dendrometers were placed in a 2.9 ha large stand dominated by Norway spruce and European beech. In addition, two Scots pine trees were also sampled. Kreisbach and Rosalia are located at lower elevations of 480 m, and 650 m a.s.l., respectively. The study areas are characterized by a relatively warm climate with frequent summer droughts (Table 1). In Kreisbach and Rosalia dendrometers were installed on dominant, intermediate and suppressed trees. Tree rank was numerically defined in terms of the 90th, 50th and 10th percentile of the empirical distribution of diameter at breast height (dbh), but smaller regeneration trees have been discarded a priori.

Norway spruce and stone pine growth was monitored along elevational transects on silicate bedrock in the Central Alps in Tyrol I and Tyrol II. Tyrol I comprises elevational gradients in Gerlos and Zillertal ranging from 1300 m to 1960 m. In Tyrol I, 39 Norway spruce trees and 11 stone pine trees were measured. Sample plots in Tyrol II were arranged along an elevational gradient in Zillertal ranging from 1660 m to 2070 m. In Tyrol II, only stone pine trees were sampled. Average climate in Tyrol I and II is harsh with relatively low average annual temperature of 4.5°C and 2.5°C together with a relatively high annual precipitation. A broad set

of dendrometric attributes was collected on Tyrolean sites using Bitterlich relascope sampling (Bitterlich, 1952, 1984). Dendrometers in Tyrol I and Tyrol II were only installed on dominant and intermediate trees and not on suppressed trees. In angle count sampling dominant height is often defined as Lorey's mean height of the 3 largest trees. With Bitterlich sampling, Lorey's mean height corresponds well with the height of the 2nd largest tree per sample plot. Thus, in Tyrol dendrometers were installed on the 2nd largest tree on each sample plot to represent dominant trees. Intermediate trees were represented by the median basal area tree per each sample plot.

In order to complement our sample with other relevant montane and subalpine sites in Austria, dendrometers were also placed on Norway spruce trees in Nasswald in the Northern Calcareous Alps. Sample plots in Nasswald were also aligned along elevational gradients ranging from 620 m to 1460 m a.s.l., of which the upper limit is approx. 150 m below the treeline. Stone pine does not occur in the Northern Calcareous Alps and sample trees of the respective species were therefore not available for the Nasswald site. Dendrometers in Nasswald were only placed on dominant trees. Stand attributes were derived from measurements on circular sample plots, each having a fixed area of 300 m². Due to highly contrasting site conditions among the sample plot locations, the complete set of examined tree species could not be sufficiently sampled at each site. Norway spruce was available at all sites except Tyrol II, European beech (*Fagus sylvatica*) existed in Kreisbach and Rosalia, Scots pine (*Pinus sylvestris*) was only present in Rosalia and stone pine (*Pinus cembra*) only in Tyrol II.

We have used automatic band dendrometers, of the type DRL 26 (UGT, Müncheberg, Germany), equipped with thermometers recording changes in stem circumference together with atmospheric temperature in an hourly temporal resolution and with a sensitivity of $< 1 \mu\text{m}$ and $\pm 0.3^\circ\text{C}$, respectively. Hourly dendrometer records were aggregated to daily values of stem circumference and afterwards converted to diameter increments under the assumption of a cir-

cular stem cross-section. We have modeled stem diameter increment, as this measure allows more intuitive interpretation than basal increment. It is noted that both measures have their distinct benefits, but both can be regarded as almost interchangeable when lateral stem growth is analyzed (Weiskittel *et al.*, 2014). Missing data were rare and, mainly, have been caused by the annual servicing of the battery during late autumn. Nevertheless, the few missing values were imputed recursively with preceding existing measurements. The complete data set ranged from one to four growth periods for each of the 103 dendrometers, totalling in 257 annual dbh increment time series. Time-series subsets in terms of annual cumulative diameter increments since April 1 were used for regression modeling. Table 3 shows the average, minimum and maximum diameter increment of the sample trees per site, per tree species and per year as well as indicating the number of dendrometers per tree species and per site.

For each sample tree the dbh, height and crown base height were measured and, subsequently, the crown ratio and height/diameter ratio were calculated. Stand basal area per ha, dominant height and stand age (from increment cores) were assessed at each sample plot and site index was derived from locally valid yield tables (Table 2). Investigated trees were 80–199 years old, with dbh varying between 16 cm and 66 cm and corresponding heights were between 14.3 m and 39.1 m. Basal area varied between 28 m²ha⁻¹ and 96 m²ha⁻¹, and site index at reference age of 100 years varied between 10 m and 38 m. On average, trees were younger in Kreisbach and Rosalia than in Nasswald and Tyrol. The range of the tree diameters was similar in all five study areas. Corresponding heights were also similar, except for stone pine in Tyrol I and Tyrol II. The reduced height growth of stone pine is probably due to the fact that this species rather occupies the highest elevation sites in our study area. Furthermore, generally stone pine is a tree species with very low height growth rates, even when transplanted to lower elevations. Basal area varied considerably between plots and tended to be higher in Tyrol I and II than on the other sites. However, within a given study area, basal area showed no marked

1 trend regarding elevation. Site index was similar for all tree species in Kreisbach and Rosalia,
2 but site index was higher on the latter two sites than in Nasswald and Tyrol. Norway spruce
3 had a similar average site index in Nasswald and Tyrol. On the latter both sites, stone pine had
4 a considerably lower site index than spruce, because stone pine habitat is restricted to higher
5 elevation sites. However, when examined separately for each tree species, site index showed no
6 clear trend with elevation for all tree species, except for Norway spruce, which showed sharply
7 decreasing site indexes towards its distributional limit, where it approaches site indexes of stone
8 pine.

9 In addition to the temperature time-series data from the on site-measurements, further mete-
10 orological data on precipitation and potential evapotranspiration were derived from the INCA-
11 data set (<https://www.zamg.ac.at/incaanalyse/>), providing hourly values as grid-
12 ded data for entire Austria with a spatial resolution of 1 km $\times$ 1 km and a vertical resolution of
13 100–200 m. It combines surface station data, remote sensing data (radar, satellite), forecast
14 fields of numerical weather prediction models and high resolution topographic data. The down-
15 scaling approach is based on inverse distance-weighted interpolations in the geometrical and
16 physical space. The rationale behind this simple approach was that the method should be trans-
17 parent with a minimum of extra climatological assumptions (Kann and Haider, 2011). For our
18 models we used the available on-site data for temperature. Other meteorological variables were
19 derived from the INCA data set, interpolated for each of sample plot locations.

20 Climate showed strong variation across the sample locations and among the different grow-
21 ing seasons (April–October) within our survey period from 2012 until the end of 2015 (Fig-
22 ure 2). In comparison to the long term average atmospheric temperatures, climate was rel-
23 atively warm during the entire survey period. However, the seasonal profile of the average
24 monthly temperatures and the total precipitation per month varied considerably among survey
25 years. Growing season in 2012 started with a cold April. Temperature increased in May and

remained higher than the long-term average throughout the rest of the vegetation period. Growing season in 2013 was characterized by several cold periods between mid-May and mid-June and in September. Summer 2013 was moderately warm. Spring 2014 was warm, followed by a cool summer and a relatively warm autumn. Year 2015 was constantly dry and warm between June and August.

On the higher elevation sites (Nasswald, Tyrol I & II), precipitation totals were relatively high during the four respective growing seasons. On the lower elevation sites Kreisbach and Rosalia precipitation totals were moderate except for 2015 with persistent drought from June to August. However, the intra-seasonal distribution of rainfall varied noticeably in the surveyed growing seasons. Rainfall was evenly distributed throughout 2012 and 2014, whereas 2013 had intense rainfall periods with intermittent dry spells, in particular in July.

Methods

A three-parameter logistic model

$$y(t) = \frac{a}{1 + \exp [(b - t) / c]} \quad (1)$$

was fitted to daily-resolution time-series data of the cumulative dbh increment starting with April 1. Trials with other nonlinear functions were made. However, a two-parameter Weibull function, such as applied in [Wipfler *et al.* \(2009\)](#) and [van der Maaten \(2013\)](#), proved to be less flexible, and model fitting with a Gompertz function, which was formerly used in [Gruber *et al.* \(2009\)](#) and [Linares *et al.* \(2009\)](#), showed serious numerical problems.

The curve of the three-parameter logistic model in Equation 1 has an upper asymptote a , an inflection point at $t = b$ and half asymptote height $y(b) = 0.5 \cdot a$. Scale parameter c represents time point at $b + c$ when approx. 73% of the asymptote is achieved with $y(c) \approx 0.73 \cdot a$. Thus, the asymptote a of our model corresponds to the total annual cumulative dbh increment, the

inflection point at b equals the number of days since April 1 when half of the annual increment is reached and the scale parameter is the time interval between increment culmination until approximately 73% of the total increment is achieved.

A hierarchical nonlinear mixed model approach was applied (Equation 2), because of a hierarchically grouped data structure with correlations among trees from the same sample plot location, several autocorrelated time-series for each tree, and unknown random effects in each measurement period.

Thereby,

$$y_{ijkl} = f(\phi_{ijk}, t_{ijkl}) + \epsilon_{ijkl} \quad (2)$$

gives the cumulative dbh increment for measurement $l = 1, \dots, p_{ijk}$, in season $k = 1, \dots, o_{ij}$, for tree $j = 1, \dots, n_i$ at plot $i = 1, \dots, m$ and with $f(\cdot)$ being the logistic function.

The parameters of the model

$$\begin{aligned} \phi_{ijk} &= (a_{ijk}, b_{ijk}, c_{ijk})' \\ a_{ijk} &= a_0 + x_{ijk}^{(a)'} \beta^{(a)} + z_i^{(a)} + z_{ij}^{(a)} + z_{ijk}^{(a)} \\ b_{ijk} &= b_0 + x_{ijk}^{(b)'} \beta^{(b)} + z_i^{(b)} + z_{ij}^{(b)} + z_{ijk}^{(b)} \\ c_{ijk} &= c_0 + x_{ijk}^{(c)'} \beta^{(c)} + z_i^{(c)} + z_{ij}^{(c)} + z_{ijk}^{(c)} \end{aligned} \quad (3)$$

are composed of fixed-effect parameters $\beta^{(a)}, \beta^{(b)}, \beta^{(c)}$ for the covariates in $x_{ijk}^{(a)}, x_{ijk}^{(b)}, x_{ijk}^{(c)}$ and random parameters $z_i^{(a)}, z_i^{(b)}, z_i^{(c)}$ for plot i , $z_{ij}^{(a)}, z_{ij}^{(b)}, z_{ij}^{(c)}$ for tree j , and $z_{ijk}^{(a)}, z_{ijk}^{(b)}, z_{ijk}^{(c)}$ for measurement period k , respectively. Model fitting was performed using the function `nlme` provided by the same-named R-package (Pinheiro *et al.*, 2016). For numerical reasons, zero-value covariances among the random parameters were assumed on each grouping level.

From a broad set of available covariates several combinations of possible candidates were tested by Wald tests for fixed-effect parameters. At plot level, we tested the effect of: site, aspect, slope, elevation, site index, age and basal area. At tree level, we tested the effect of:

tree species, dbh, tree height, height/diameter ratio and crown ratio. Furthermore, at level of the measurement period, we tested the effect of: different calendar years, length of the vegetation period and of the sum of temperature, precipitation, evapotranspiration and climatic water-balance during the growing season. As definition for the growing season we used the definition of v. Wilpert (1990), except his criterion for soil water tension, because it was unavailable from our dataset. We also plotted each tested variable against the random effect at the respective level to test for possible non-linearities.

Results

In first steps, a restricted nonlinear mixed-effects model was fitted to the data and variances of all curve parameters were modeled via variance components. In this restricted model without further covariates the asymptote parameter was estimated to be 0.296 cm, which represents the average annual diameter increment derived from altogether 257 dendrometer time series. The estimated inflection point, at which half of the asymptotic growth is reached, occurred on average 81 days past April 1 corresponding to the 171th day of the year (DOY). The scale parameter was 21.9 days, which indicates the required time to gain 73% of the asymptotic growth starting from the inflection point. This means that 73% of the total annual increment, on average, was attained on DOY 193.

An analysis of the variance components of the restricted nonlinear mixed-effects model (Table 4) revealed that a negligible small proportion of the asymptote's variance is caused by plot-level random effects and that 65% and 35% are allocated to random-effects on tree-level and measurement period, respectively. That means that total annual stem diameter increment was mainly influenced by tree-level attributes as well as by short-term seasonal climate variation, whereas other site factors besides climate did not play a relevant role. 92% of the total

variance of the inflection point and scale parameter were assigned to seasonal random effects. The latter both parameters determine the shape of the growth curve. This result means that the duration of a growing period is mainly influenced by seasonal climate variation.

Additional regressor covariates were selected among all possible candidates guided by visual assessment of diagnostic scatter plots showing predicted random effects against the respective covariate values. A covariate was considered as fixed effect in the nonlinear mixed model, if scatter plots showed at least some signs of a trend. Such hypothesis testing for fixed effects parameters - as is recommended by [Pinheiro and Bates \(2000\)](#), was then performed with Wald tests. The final saturated model included categorical effects for site, tree species and social position as well as a fixed parameter for the continuous variable tree age. In addition, significant interaction effects existed between calendar year and site category, between tree species and calendar year and between the social position and calendar year. The social tree position was coded as a site-specific categorical interaction effect. For each variable the entire set of categories was considered as fixed-effect parameters, if the effect of a single category proved to be significant. A further regrouping among the categories was therefore not accomplished. Hence,

2 the parameters of the final saturated model became:

$$\begin{aligned}
 a_{ijk} &= a_0 + \beta_1^{(a)} \cdot \text{Site}_i + \beta_2^{(a)} \cdot \text{Species}_{ij} + \beta_3^{(a)} \cdot \text{Socialposition}_{ij} \\
 &+ \beta_4^{(a)} \cdot \text{Age}_{ijk} + \beta_5^{(a)} \cdot \text{Site}_i \cdot \text{Year}_{ijk} + \beta_6^{(a)} \cdot \text{Species}_{ij} \cdot \text{Year}_{ijk} \\
 &+ \beta_7^{(a)} \cdot \text{Socialposition}_{ij} \cdot \text{Year}_{ijk} + z_i^{(a)} + z_{ij}^{(a)} + z_{ijk}^{(a)} \\
 b_{ijk} &= b_0 + \beta_1^{(b)} \cdot \text{Site}_i + \beta_2^{(b)} \cdot \text{Species}_{ij} + \beta_3^{(b)} \cdot \text{Socialposition}_{ij} \\
 &+ \beta_4^{(b)} \cdot \text{Age}_{ijk} + \beta_5^{(b)} \cdot \text{Site}_i \cdot \text{Year}_{ijk} + \beta_6^{(b)} \cdot \text{Species}_{ij} \cdot \text{Year}_{ijk} \\
 &+ \beta_7^{(b)} \cdot \text{Socialposition}_{ij} \cdot \text{Year}_{ijk} + z_i^{(b)} + z_{ij}^{(b)} + z_{ijk}^{(b)} \\
 c_{ijk} &= c_0 + \beta_1^{(c)} \cdot \text{Site}_i + \beta_2^{(c)} \cdot \text{Species}_{ij} + \beta_3^{(c)} \cdot \text{Socialposition}_{ij} \\
 &+ \beta_4^{(c)} \cdot \text{Age}_{ijk} + \beta_5^{(c)} \cdot \text{Site}_i \cdot \text{Year}_{ijk} + \beta_6^{(c)} \cdot \text{Species}_{ij} \cdot \text{Year}_{ijk} \\
 &+ \beta_7^{(c)} \cdot \text{Socialposition}_{ij} \cdot \text{Year}_{ijk} + z_i^{(c)} + z_{ij}^{(c)} + z_{ijk}^{(c)}
 \end{aligned} \tag{4}$$

4 Hereof, Site_i is the site location of sample plot i ; the Site variable has five categories.
 5 Species_{ij} means the tree species j on sample plot i and $\text{Socialposition}_{ij}$ the tree's social
 6 position, respectively. Year_{ijk} stands for the calendar year of the k -th measurement period of
 7 tree j on plot i and Age_{ijk} is the corresponding tree age.

8 Tables 5 and 6 show the parameters for the fixed effects. To allow for straightforward inter-
 9 pretations, the respective estimates of the fixed intercept parameters (a_0, b_0, c_0) were added to
 10 each of the dummy categorical effects. Meaningful references were selected for the categorical
 11 parameter effects. Then the estimates of the additive fixed effect parameters could be easily
 12 interpreted in relation to the respective reference category. A dominant (categorical variable
 13 tree class) Norway spruce (tree species category) in year 2013 (measurement period category)
 14 in Kreisbach (study site category) was thus selected as reference. Parameter estimates tested as
 15 significantly different from zero at $\alpha = 0.05$ level are typed in italics in Tables 5 and 6.

1 The final saturated model had a pseudo- R^2 of 0.982 computed according to McKelvey and

Zavoina (1975). Summary diagnostic graphics show standardized residuals versus fitted values and observed versus predicted values (Figure 3). Individual diagnostic plots for each annual dbh increment time series are provided as supplementary material.

Curves of the mean model are shown in Figure 4 for dominant trees and with respect to different study sites, calendar years and tree species. Mean curves were evaluated for a tree age of 80 years. Overall, the highest cumulative diameter increment was measured at the Rosalia site, followed by Kreisbach, Tyrol I, Tyrol II and Nasswald. Furthermore, corresponding information can be obtained from the parameter estimates for the asymptote shown in Tables 5 and 6.

The asymptote parameter, which represents the annual cumulative diameter increment, varies significantly across calendar years. In general, the increment in 2012 (only available for Rosalia) and 2014 was higher than in 2013 and 2015. The effect was more pronounced on lower elevation sites in Rosalia and Kreisbach and became almost negligible on higher elevation sites in Tyrol (Figure 4). At higher elevation sites, growth reactions of stone pine were even more inert than for Norway spruce.

In addition to the lower total increments and as indicated by lower inflection point and scale parameters, radial growth had stopped earlier in the dry and hot year 2015. This effect was more pronounced on lower elevation sites. In particular, in Kreisbach 73% of the annual increment in 2015 was achieved by DOY 158, which is 42 days earlier than in 2014. Similarly, in Rosalia 73% of the annual increment was achieved by DOY 175, which is 35 days earlier than in 2014. In contrast, on the higher elevation sites Tyrol I and Tyrol II 73% of the annual increment in 2015 was realized by DOY 186 and 188, which is only 12 and 6 days earlier than in 2014 (Tables 5 and 6). Most of the possible combinations between calendar year and site location had significant parameter effects, except for Tyrol II, where the mean curve was similar to Kreisbach in 2013 with respect to all model parameters.

Model parameter estimates suggest that, generally, tree species differ in their total annual

diameter increment. On average, the highest annual increment was achieved by European beech, followed by Norway spruce, stone pine and Scots pine. However, the ranking among the tree species was not constant over the survey years (see Figure 5 for a comparison). In the years 2013 and 2015, European beech had higher annual increments than Norway spruce. In contrast, Norway spruce had higher annual increments than European beech in 2012 and 2014. Total annual increment of Norway spruce varied only slightly among different growing seasons on the Tyrolean sites.

Whereas mean model curves for various tree species showed high variation with respect to the asymptote parameter, the other two parameters, inflection point and scale parameter, differed only slightly among the examined tree species. Worth noting, however, is that seasonal growth curves of stone pine and Scots pine had inflection points between 7 and 13 days earlier than Norway spruce and European beech. Furthermore, the scale parameters for both pine species were slightly higher than for the other tree species.

Trees from different social statuses showed more diverse reactions in response to altered seasonal climate conditions on the lower elevation site Kreisbach than on the higher elevation site Tyrol I (Figure 6). Under favorable climate conditions in 2014, dominant Norway spruce trees in Kreisbach had a total diameter increment of 0.52 cm, intermediate trees 0.40 cm, and suppressed trees of only 0.18 cm. Growth of European beech behaved similarly with respect to different social tree classes. In the dry and hot year 2015, the increment of dominant Norway spruce trees was reduced by approx. 50%, whereas the increment reduction for European beech was less pronounced. Furthermore, in 2015, the range of annual diameter increments for trees of a different social status became smaller and dominant trees suffered more regarding relative increment reductions due to a less favorable climate.

In contrast, dominant trees in Tyrol had a diameter increment of approx. 0.40 cm in 2014, which dropped slightly to 0.34 cm in 2015. Increment of intermediate trees was 0.36 cm in

2014, thus differing only slightly from the increment of dominant trees in Tyrol. In addition, annual increment of intermediate trees was reduced by almost the same amount as increment of dominant trees in 2015.

In summary, trees with affiliation to a higher social status had stronger benefit from more favorable climate conditions on lower elevation sites, whereas interaction between social status and calendar year has minor relevance on higher elevation sites. Besides, social status neither noticeably influenced the inflection point nor the scale parameter.

Finally, and as expected, tree age had a negative effect on the asymptote parameter for all study sites, meaning that annual radial increment continuously decreases with increasing age.

When compared with the restricted variance-component model (Table 4), random parameter variances have been significantly reduced by the full saturated mixed-effects model (Table 7). The total variance of the random parameters on the asymptote is reduced by half, most of which (82%) is still allocated to tree-level random effects. The variance of the random parameters on the inflection point is reduced by 60% and the remaining part is almost equally shared by tree-level (43%) and seasonal (57%) random effects. The random parameter variance for the scale parameter in the full saturated model is only 28% of the variance in the restricted model and mainly consists of a seasonal random effect (80%).

Discussion

Tree growth on low elevation sites

Recent phenological studies give evidence that growing season has extended by 2–3 days per decade during the past 50 years (Badeck *et al.*, 2004; Körner and Basler, 2010). In general, annual growth rate would be assumed to correlate positively with the length of the growing season (Prislan *et al.*, 2013). However, higher production rates in spring due to an earlier growth

onset are counterbalanced by subsequent less productive periods due to water shortage during summer droughts (Downes *et al.*, 1999; Gričar *et al.*, 2015). Tree growth at lower elevation sites is therefore fostered by higher precipitation during summer months, whereas drought and heat in summer months may in total cause a significantly reduced diameter increment (e.g. Wenk and Fiedler, 1979; Zweifel *et al.*, 2006; Linares *et al.*, 2009; Zang *et al.*, 2012; van der Maaten, 2013). In this context, climate in 2014 provided highly productive growth conditions with a warm spring and a relatively cool and humid summer. In comparison with 2014, stem diameter increments in 2013 and 2015 were reduced by 40 to 50% in Kreisbach and Rosalia. The lower increments, especially in 2013, might have been caused by dry and warm weather with intermittent cold spells.

Physiological studies (e.g. Zweifel *et al.*, 2001, 2006; Deslauriers *et al.*, 2003; Swidrak *et al.*, 2014) gave evidence that meteorology influences radial stem growth rates on a high temporal resolution. Likewise, our analysis confirms that intra-seasonal stem biomass production underlies high fluctuations and strongly correlates with short-term oscillations of the intra-seasonal climate pattern. Thus, lower resolution climate variables, such as precipitation totals and temperature means per season, often provide little information (Mäkinen *et al.*, 2003) and proved irrelevant for our regression model. Consequently, especially in the context of climate change impact studies, an intra-annual approach is important (Badeck *et al.*, 2004). Recent growth models already include seasonal climatic variables (e.g. Albert and Schmidt, 2010; Seynave *et al.*, 2008). Possibly, this approach will be refined further in the future.

The dry and hot summer 2015 led to an early cessation of annual growth, which is reflected by an early culmination point of the radial increment. Likewise, such an early culmination was reported for the also dry and hot year 2003 (Zweifel *et al.*, 2006; Linares *et al.*, 2009; van der Maaten, 2013). The early culmination point in dry and hot years coincides with a shorter growth period, which can shrink to under two or three month during spring time (Körner, 2003).

If water potential falls below a specific threshold (Zweifel *et al.*, 2001) photosynthesis and structural growth (cell enlargement and cell division) (Larcher, 2003; Oberhuber *et al.*, 2014; Prislan *et al.*, 2013) are sharply constrained. Hereof, the above-ground biomass accumulation is stronger affected (Körner, 2003; Palacio *et al.*, 2014) and photosynthetic activity is usually sustained on a lower level. This conforms with a well-known conservative growth strategy (Palacio *et al.*, 2014) and guarantees survival of the whole organism.

Tree species react differently in their relative response to drought. In the moist years 2012 and 2014 Norway spruce trees had a higher radial increment than equally sized European beech trees, whereas European beech was more productive in 2013 and 2015. This conforms with other comparative studies on growth reactions among Norway spruce and European beech trees (Flury, 1926; Schober, 1951; Pretzsch *et al.*, 2013). During severe summer drought, beech might benefit from deeper fine roots with access to soil layers with higher water content subsequently allowing for sustained stomatal activity and assimilation (Hartl-Meier *et al.*, 2014). This corresponds to a species-specific isohydric and anisohydric behavior (Hartmann, 2011). Isohydric species such as Norway spruce reduce water consumption and growth already in the early phase of drought stress through stomata closure, which reduces the risk of drought stress at the expense of leaving resources to other tree species. Anisohydric species such as beech behave differently, as they sustain transpiration under higher soil moisture tension. Growth reductions are smaller for anisohydric species, but they are more prone to hydraulic failures. In periods with limited water availability, European beech might have a competitive advantage over Norway spruce, but might be more susceptible to risks (Pretzsch *et al.*, 2013). Moreover, some of the differences between European beech and Norway spruce might be alleviated by the shorter recovery time of Norway spruce in comparison to European beech (Scharnweber *et al.*, 2011; Zang *et al.*, 2012). In summary, wood growth is a complex process, that is not only controlled by gross primary production, but also by carbohydrate storage and allocation (e.g.

Hoch, 2003). In consequence, wood growth can also be affected by environmental conditions that occurred several weeks, month or years ago (e.g. Gough *et al.*, 2008; Zweifel *et al.*, 2010).

Trees can also react to drought by adapting their hydraulic characteristics. The wood of tree provenances from dry and warm sites has a higher density and thicker cell walls (Park and Spiecker, 2005; Jyske *et al.*, 2010; Gričar *et al.*, 2015). Such modified vessels enable stronger resistance against mechanical stress caused by enhanced tension, which is accompanied with a low water potential. In response to drought, an increase in cell wall thickness was found in both early wood and late wood cells of Norway spruce, but the increase was much greater in latewood (Jyske *et al.*, 2010). However, changes in wood properties were small in comparison with increment reductions (Jyske *et al.*, 2010).

Tree growth on high elevation sites

Because of Austria's specific orography much rainfall occurs on sites in higher elevations (Table 1). Tree growth is thus limited by the relatively cold temperature on these sites and generally, is fostered by warm temperatures throughout spring and summer months (Körner, 2012; Rossi *et al.*, 2008; Kalliokoski *et al.*, 2012; Prislan *et al.*, 2013; Gričar *et al.*, 2015). Accordingly, drought periods were absent on the high elevation sites. As well as for the low elevation sites, the highest diameter increment on the mountainous sites was achieved in 2014. The warm spring temperatures together with the relatively warm autumn in 2014 obviously provided more favorable growth conditions than the very warm summer temperatures in 2015.

However, the total annual diameter increment on mountainous sites differed only by a maximum of 10% among the four survey years. Our findings conform with those from dendrochronological studies, stating that, generally, tree growth is fostered by warm temperatures, but show that the increase lies below expectations (e.g. Büntgen *et al.*, 2008; D'Arrigo *et al.*, 2008). The phenomenon of such small increases of growth rates in warmer climate periods is

2 termed the “divergence problem” (D’Arrigo *et al.*, 2008). A possible explanation for the “di-
3 vergence problem” and the small growth reactions in our study are the nonlinear relationship
4 between tree growth and altered site conditions (D’Arrigo *et al.*, 2008; Büntgen *et al.*, 2008).
5 This may be due to an adaptation of a species to a particular site (Körner, 2012; Gričar *et al.*,
6 2015).

7 Norway spruce is considered to have a high adaptation potential (Skrøppa, 2003). The
8 distribution of Norway spruce in Austria covers diverse site conditions and ranges from lower
9 elevation sites up to sites on the tree line. On higher elevation sites spruce trees show a later
10 flushing and lower growth rates (Körner, 2012) compared with spruces on lower elevation sites.
11 Experiments have shown that the typical phenology of a certain provenance is conserved, even
12 if trees from sub-alpine sites are transplanted onto lower elevation sites with more favorable
13 growth conditions (Körner, 2012, and references therein). This is because specific traits have
14 been established during a long evolutionary history and remain relatively fixed.

15 Trees’ adaptation to the harsh site conditions at high elevations can be interpreted as a life
16 assurance against the likely occurring risk of extreme events on such sites (Körner, 2003, 2012;
17 Badeck *et al.*, 2004). Trees have developed a photo-sensitivity and other physiological control
18 mechanisms to prevent themselves from “falling into a trap”, if their phenology would simply
19 follow the course of short-term changes in atmospheric temperatures (Körner and Basler, 2010).

20 Our results demonstrate that it seems hard to project possible future growth trends in con-
21 text of a changing climate from short-term increment series and climate data, if results were
22 evaluated undifferentiatedly and without acknowledging specific site conditions.

23 Successional status of tree species

24 Usually, the characteristical intra-seasonal pattern of increment allocation of a certain tree
1 species is accompanied by a characteristic growth pattern over the whole lifetime and can be

interpreted as specific “successional strategy” (Körner and Basler, 2010; Cuny *et al.*, 2012). According to generally accepted theory, early-successional species have a distinct risk-taking affinity, whereas late-successional species follow a risk-averse strategy (Körner and Basler, 2010; Cuny *et al.*, 2012). Pioneer tree species from early succession stages behave relatively inert against photo stimulation in spring and stem growth tends to be initiated by a favorable temperature. In contrast, stem growth of species from later succession stages is strongly controlled by the photoperiod in spring and temperature has a modulating effect, only, which should prevent trees from an early vegetation start during spring frost periods (Körner and Basler, 2010).

A literature review revealed that theory-confirming results have been found also in other existing studies. Thereby, an early starting and culmination point was found for Scots pine as an early successional species (Henhappl, 1965; Zweifel *et al.*, 2006; Cuny *et al.*, 2012; Michelot *et al.*, 2012; Jyske *et al.*, 2014; Swidrak *et al.*, 2014), whereas a later onset and culmination point was found for Norway spruce (Franz *et al.*, 1990; Zweifel *et al.*, 2006; Wipfler *et al.*, 2009; Cuny *et al.*, 2012; Jyske *et al.*, 2014; Swidrak *et al.*, 2014) as well as for European beech (Henhappl, 1965; Wipfler *et al.*, 2009; Michelot *et al.*, 2012), both similarly dominating in late succession stages. Contrary to our expectations, our analysis revealed an early growth onset for stone pine although considered a late successional tree species. Similar results have been reported in existing literature (Rossi *et al.*, 2008; Gruber *et al.*, 2009). The early vegetation start of stone pine, presumably, result from successfully adapting to cold climates on sup-alpine sites. However, the seasonal growth of stone pine culminates and stops relatively late as is characteristic for a late-successional tree species (Gruber *et al.*, 2009).

Empirical results from our dendrometer data analysis conform with the above outlined hypotheses. However, the ranking between Norway spruce and European beech may vary among subsequent growing seasons (with the growing season defined as the 95-th percentile from the logistic model). Beech stopped radial increment earlier than spruce, but only in warmer weather

periods in 2014. The opposite occurred in the dry and hot year 2015.

For a given site and under same climate conditions, intra-seasonal allocation patterns of Norway spruce, European beech, Scots pine and stone pine show some signs of general synchronism. Stem biomass accumulation is produced within a restricted sub-period of the entire growing season. Generally, culmination of tree growth occurs around summer solstice (e.g. [Seo et al., 2008](#); [Jyske et al., 2014](#)), irrespective of the tree species. However, [Gruber et al. \(2010\)](#) reported a culmination of tree growth for stone pine as early as in May.

Tree-level effects

From the entire set of possible candidates, fixed-effect parameters proved to be significant only for social position and tree age, which, finally, were both considered as regressor covariates. In addition, Gaussian random parameters within a nonlinear mixed model framework accounted for other unknown effects and correlations among several time series of each single tree.

With respect to social position, existing studies showed that dominant trees achieve higher annual increment rates than intermediate or suppressed individuals ([Kramer and Kätsch, 1982](#); [Linares et al., 2009](#); [Rathgeber et al., 2011](#)). Differences between dominant and intermediate trees are often small, whereas differences between dominant and suppressed trees can be very pronounced ([Kramer and Kätsch, 1982](#); [Rathgeber et al., 2011](#); [Franz et al., 1990](#); [van der Maaten, 2013](#)). In comparison with suppressed trees, the higher increment of dominant trees is usually associated with a longer growth period ([Rathgeber et al., 2011](#)). Our results confirm the findings from previous studies, but provide extra information insofar that we have detected a varying effect of social position depending on calendar years. Our analysis indicated that differences in productivity with respect to social tree position were more pronounced in 2014 than in 2013 or 2015. In particular, predominant trees in Kreisbach showed excessive growth depressions and suffered more than other social statuses from drought and heat in 2015. Drought

and heat have therefore an equalizing effect for the productivity of trees from different social classes. Similar findings were made by Pretzsch and Dieler (2011), who found that in the warm and dry year 1976, all trees showed increment proportional to their size irrespective of social tree position, whereas the dominant trees' increment was overproportional in 1978.

We have found a constant and linearly decreasing effect for tree age on the asymptote parameter, but no significant effect of age on the duration of the growth period. Presumably, this is due to our limited data covering a relatively narrow span of older ages from 80 to 139 years. However, Rossi *et al.* (2008) found shorter growth periods for older trees (approx. 200–350 years) compared with younger trees (approx. 50–80 years).

Statistical experimental design

Observations from a single dendrometer could be correlated among the different measurement periods. Such a possible between-year correlation in conjunction with time-lagged effects of climate covariates is not problematic with our model formulation, because climate covariates themselves were not included as fixed-effects in the final saturated model. Thus, statistical inference (parameter estimation) and statistical hypothesis testing for the fixed-effects parameters is not influenced by a between-year correlation. Because the complete monitoring period was rather short, with four consecutive growing seasons, the variance between the growth periods was taken into account by categorical fixed-effects parameters for the measurement periods and was not modeled by fixed-effects parameters for climate variables, which would likely act in time-lagged manner on the radial increment in a specific growing season. Finally, when compared with other existing dendrometer studies our dendrometer time series can be regarded as a rather comprehensive survey with a relatively large sample size and a long observation period.

The sample design was unbalanced with respect to the number of sample plots, the observed species and the social position per site. The unbalanced design was addressed by taking into

account (i) fixed-effects parameters for categorical variables, such as tree species and site location, as well as by including interaction terms hereof, and (ii) by a hierarchical structure of random effects on the sample plot level, the tree level, and the measurement-period level.

In our modelling approach a 3-parameter logistic model was selected, which fitted the data well. McMahon and Parker (2015) applied an extended logistic model formulation, corresponding to a Richards-type representation providing additional flexibility. Because the Richards model has “very poor” statistical properties (Ratkowsky, 1989) much effort was necessary in McMahon and Parker (2015) to overcome these problems in terms of numerical optimization even when this curve type was applied to single trajectories without further regressor covariates and random effects. However, this approach was not applicable in our non-linear hierarchical mixed-model context.

Conclusions

We can conclude from our dendrometer-data analysis that warming in conjunction with drought leads to reduced increment rates on lower elevation sites, whereas trees on higher elevation sites react less noticeably and clearly, have adapted well to harsh environmental conditions with a persistent but conservative assimilation strategy. In consequence, we expect that minor productivity gains on higher elevation sites insufficiently compensate for severe productivity losses on lower elevation sites when calculating on a larger spatial scale for entire Austria. However, further research is needed to verify that increasing temperatures are associated with increasing growth rates on montane and sub-alpine sites. Future research must therefore consider seasonal growth patterns as well as possible adaptation mechanisms to specific site conditions before the growth of complete forest stands is projected in response to future climate warming.

Our analysis clearly demonstrates that altered climate conditions strongly affect produc-

tivity rates of various tree species coexisting in the same habitat. Norway spruce on lower elevation sites is at its lower distributional limit and European beech was clearly less affected by longer dry spells during summer months. Thus, future climate warming may lead to a higher domination of European beech on lower elevation sites. However, some of the effects might be mitigated through various recovery strategies of the tree species (Scharnweber *et al.*, 2011; Zang *et al.*, 2012).

Finally, we can conclude that our hierarchical nonlinear mixed model proves an appropriate model framework that can handle complex dendrometer time-series data by accounting for autocorrelations on varying hierarchical grouping levels.

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Study area	Year	No. Plots	Species	Elevation [m]	Annual Mean Temperature [°C]	Annual Precipitation Sum [mm]
Kreisbach	2013 – 2015	1	<i>Picea abies</i> , <i>Fagus sylvatica</i>	480	9.2	659
Rosalia	2012 – 2015	6	<i>Picea abies</i> , <i>Fagus sylvatica</i> , <i>Pinus silvestris</i>	650	6.5	796
Nasswald	2015	6	<i>Picea abies</i>	620 – 1460	6.6	866
Tyrol I (Gerlos, Zillertal)	2013 – 2015	22	<i>Picea abies</i> , <i>Pinus cembra</i>	1300 – 1960	4.5	975
Tyrol II (Schlegeis, Zillertal)	2013 – 2015	6	<i>Pinus cembra</i>	1660 – 2070	2.5	1162

Table 1: Summary description of the study sites. Summary characteristics of the climate data refer to climate conditions at the lower end of the elevational gradients.

Site	Species	Age	Dbh cm	Height m	Basal area m ² ha ⁻¹	Site index m
Kreischbach	<i>Fagus sylvatica</i>	80	37.2	31.4	45.3	36.3
		80 - 80	20.2 - 58	25.1 - 36.6	41.7 - 47.1	36.3 - 36.3
	<i>Picea abies</i>	80	37.4	29.5	46.2	36.5
		80 - 80	20.5 - 56.9	24.1 - 33.8	41.7 - 50.7	36.5 - 36.5
Rosalia	<i>Fagus sylvatica</i>	105	37.6	27	34.7	34.3
		105 - 105	20.2 - 56.3	18.6 - 33.3	26.1 - 50.2	31.9 - 38.1
	<i>Picea abies</i>	105	34	27.3	37.7	36.1
		105 - 105	16.3 - 58.2	14.5 - 39.1	27.9 - 50.2	34.1 - 38.1
	<i>Pinus sylvestris</i>	105	48	33.5	27.9	35.6
		105 - 105	36.7 - 59.4	30.1 - 36.9	27.9 - 27.9	35.6 - 35.6
Nasswald	<i>Picea abies</i>	115.8	40.7	26.2	42.6	25.3
		78 - 170	32 - 62	21 - 35	23.2 - 66.7	16.5 - 37.7
Tyrol I	<i>Picea abies</i>	134	47.7	31.9	62.7	25.4
		81 - 199	34.9 - 64.9	21.3 - 43.3	20 - 88	13.2 - 33.7
	<i>Pinus cembra</i>	125	52.1	20.6	68	19.3
		77 - 188	44.5 - 66.1	16.1 - 25.6	36 - 96	13.2 - 25.5
Tyrol II	<i>Pinus cembra</i>	136.8	50.1	17.6	66	13.7
		106 - 194	39.4 - 62.9	14.3 - 21.5	32 - 92	10.1 - 16.6

Table 2: Mean, minimum and maximum age (years), dbh (cm) and height (m) of dendrometer trees and mean, minimum and maximum stand basal area (m²ha⁻¹) and site index (m) at the base age of 100 years.

Site	Species	Year				Dendrometers
		2012	2013	2014	2015	
Kreischbach	<i>Fagus sylvatica</i>		0.38	0.46	0.29	12
			0.02 - 0.60	0.02 - 0.77	0.01 - 0.39	
	<i>Picea abies</i>		0.29	0.43	0.17	8
			0.09 - 0.49	0.04 - 0.83	0.01 - 0.26	
Rosalia	<i>Fagus sylvatica</i>	0.46	0.47	0.48	0.47	4
		0.31 - 0.67	0.33 - 0.57	0.29 - 0.64	0.28 - 0.57	
	<i>Picea abies</i>	0.5	0.37	0.58	0.33	4
		0.22 - 0.82	0.13 - 0.62	0.21 - 0.9	0.15 - 0.44	
	<i>Pinus sylvestris</i>	0.51	0.25	0.57	0.37	2
		0.36 - 0.65	0.16 - 0.35	0.42 - 0.72	0.24 - 0.49	
Nasswald	<i>Picea abies</i>				0.14	18
					0.04 - 0.31	
Tyrol I	<i>Picea abies</i>		0.3	0.34	0.3	9
			0.14 - 0.76	0.16 - 0.72	0.13 - 0.71	
	<i>Pinus cembra</i>		0.3	0.32	0.32	11
			0.14 - 0.43	0.19 - 0.42	0.15 - 0.43	
Tyrol II	<i>Pinus cembra</i>		0.33	0.3	0.3	35
			0.22 - 0.54	0.21 - 0.50	0.2 - 0.44	

Table 3: Average, minimum and maximum diameter increment (cm/year) of dendrometer trees by site, tree species and year. The last column indicates the number of dendrometers per species and year.

Parameter	Site	Tree	Measurement period	Sum
a	0.00022 ²	0.13604 ²	0.10031 ²	0.16902 ²
b	0.00627 ²	0.00141 ²	13.32858 ²	13.32858 ²
c	2.01011 ²	0.00278 ²	7.16062 ²	7.43741 ²
Residual	0.02111 ²			

Table 4: Estimated random effect variances (reported as squared standard deviations) of the restricted non-linear mixed-effects model.

Parameter		Kreisbach			Rosalia			
		2013	2014	2015	2012	2013	2014	2015
Asymp-tote	a0	<i>0.3694</i>	<i>0.6084</i>	0.3126	<i>0.6992</i>	<i>0.5069</i>	<i>0.8391</i>	<i>0.5289</i>
	a1×Fs	<i>0.1329</i>	<i>-0.0352</i>	0.1511	<i>-0.0337</i>	<i>0.1329</i>	<i>-0.0352</i>	0.1511
	a2×Ps				<i>-0.0940</i>	<i>-0.0940</i>	<i>-0.0940</i>	<i>-0.0940</i>
	a3×Pc							
	a4×Pred	0.0772	<i>0.2016</i>	<i>-0.0669</i>				
	a5×P50B							
	a6×P50	-0.0544	<i>-0.1209</i>	-0.0968	-0.0429	-0.0544	<i>-0.1209</i>	-0.0968
	a7×P10	<i>-0.2119</i>	<i>-0.3421</i>	<i>-0.2084</i>	<i>-0.2388</i>	<i>-0.2119</i>	<i>-0.3421</i>	<i>-0.2084</i>
	a8×age	<i>-0.0011</i>	<i>-0.0011</i>	<i>-0.0011</i>	<i>-0.0011</i>	<i>-0.0011</i>	<i>-0.0011</i>	<i>-0.0011</i>
Inflection point	b0	<i>94.1970</i>	<i>79.9663</i>	<i>57.9952</i>	<i>82.8652</i>	<i>79.1085</i>	<i>87.8835</i>	<i>70.9968</i>
	b1×Fs	-5.1310	<i>3.1107</i>	0.8479	1.2390	-5.1310	<i>3.1107</i>	0.8479
	b2×Ps				<i>-13.0605</i>	<i>-13.0605</i>	<i>-13.0605</i>	<i>-13.0605</i>
	b3×Pc							
	b4×Pred	-0.8435	1.0374	-8.6301				
	b5×P50B							
	b6×P50	-2.3901	-5.0862	2.8372	-4.2961	-2.3901	-5.0862	2.8372
	b7×P10	-3.7897	<i>-2.9887</i>	-0.1405	-11.2285	-3.7897	<i>-2.9887</i>	-0.1405
	b8×age	0.0196	<i>0.0196</i>	0.0196	0.0196	0.0196	0.0196	0.0196
Scale	c0	<i>20.2426</i>	<i>27.0297</i>	<i>6.9953</i>	<i>24.4919</i>	<i>13.6340</i>	<i>29.1969</i>	<i>11.5362</i>
	c1×Fs	-0.8552	<i>-5.8737</i>	<i>4.6835</i>	<i>-5.7470</i>	<i>-0.8552</i>	<i>-5.8737</i>	<i>4.6835</i>
	c2×Ps				1.7811	1.7811	1.7811	1.7811
	c3×Pc							
	c4×Pred	-1.0755	1.8749	-3.1349				
	c5×P50B							
	c6×P50	-1.0620	-0.8561	-0.1320	-0.9490	-1.0620	-0.8561	-0.1320
	c7×P10	0.2846	-1.7773	1.9818	-1.7062	0.2846	-1.7773	1.9818
	c8×age	0.0206	0.0206	0.0206	0.0206	0.0206	0.0206	0.0206

Table 5: Estimates of fixed parameters for the final saturated nonlinear mixed model with respect to Kreisbach and Rosalia sites. Dummy-categorical fixed-effects with regard to different tree species are abbreviated as Fs (European beech), Ps (Scots pine) and Pc (stone pine). Categories of varying social statuses are named as Pred (Predominant, higher than 90th percentile of diameter distribution), P50B (50th percentile of diameter distribution by basal area), P50 (50th percentile of diameter distribution), P10 (10th percentile of diameter distribution). Significant parameter estimates according to Wald tests using $\alpha = 5\%$ level are indicated by italic typeface.

Parameter		Nasswald	Tyrol I			Tyrol II		
		2015	2013	2014	2015	2013	2014	2015
Asymp- tote	a0	0.2387	0.4598	0.4874	0.4324	0.4902	0.4983	0.4806
	a1×Fs							
	a2×Ps							
	a3×Pc		-0.0294	-0.0376	-0.0057	-0.0294	-0.0376	-0.0057
	a4×Pred							
	a5×P50B	-0.0457	-0.0507	-0.0417	-0.0457	-0.0507	-0.0417	-0.0457
	a6×P50							
	a7×P10							
	a8×age	-0.0011	-0.0011	-0.0011	-0.0011	-0.0011	-0.0011	-0.0011
Inflection point	b0	64.0159	91.8914	88.4060	78.6690	87.0894	87.0426	76.5471
	b1×Fs							
	b2×Ps							
	b3×Pc		-6.5964	-9.4994	-5.4747	-6.5964	-9.4994	-5.4747
	b4×Pred							
	b5×P50B	-2.0426	-7.9526	-0.5008	-2.0426	-7.9526	-0.5008	-2.0426
	b6×P50							
	b7×P10							
	b8×age	0.0196	0.0196	0.0196	0.0196	0.0196	0.0196	0.0196
Scale	c0	10.7696	28.2675	16.1062	14.5778	25.4242	13.5969	18.0214
	c1×Fs							
	c2×Ps							
	c3×Pc		-0.6038	10.3269	2.7451	-0.6038	10.3269	2.7451
	c4×Pred							
	c5×P50B	0.6509	-0.5712	0.8753	0.6509	-0.5712	0.8753	0.6509
	c6×P50							
	c7×P10							
	c8×age	0.0206	0.0206	0.0206	0.0206	0.0206	0.0206	0.0206

Table 6: Estimates of fixed parameters for the final saturated nonlinear mixed model with respect to Nasswald and both Tyrolean sites. Dummy-categorical fixed-effects with regard to different tree species are abbreviated as Fs (European beech), Ps (Scots pine) and Pc (stone pine). Categories of varying social statuses are named as Pred (Predominant, higher than 90th percentile of the diameter distribution), P50B (50th percentile of the diameter distribution by basal area), P50 (50th percentile of the diameter distribution), P10 (10th percentile of the diameter distribution). Significant parameter estimates according to Wald tests using $\alpha = 5\%$ level are indicated by italic typeface.

Parameter	Site	Tree	Measurement period	Sum
a	0.00001 ²	0.10131 ²	0.04721 ²	0.11177 ²
b	0.00748 ²	5.52420 ²	6.34167 ²	8.41033 ²
c	1.32223 ²	1.12125 ²	3.50230 ²	3.90788 ²
Residual	0.02112 ²			

Table 7: Estimated random effect variances of the final saturated nonlinear mixed effects model, reported as squared standard deviations.

Figure 1: Location of study areas in Austria, Central Europe.

Figure 2: Average monthly temperatures (T) ($^{\circ}\text{C}$) and total monthly precipitation (mm) per site and year. Note that the diagram shows the average for elevational gradients in Tyrol and Nasswald. A temperature decrease of approximately 0.65°C with an increase in elevation of 100 m was found for both sites. This corresponds to the adiabatic decrease in temperature. During the growing season (April–October), climate data did not show any evidence of temperature inversion. Note also that climate diagrams were prepared according to the suggestions of [Walter and Lieth \(1960\)](#) who suggest that monthly precipitation of more than 100 mm should be represented by 100 mm steps.

Figure 3: Diagnostic plots: Standardized residuals versus fitted values (left), observed versus fitted values (right).

Figure 4: Mean curves for the cumulative diameter increment of dominant trees in Kreisbach, Rosalia, Tyrol I and Tyrol II for the growth periods between 2012 and 2015 for various tree species.

Figure 5: Total annual diameter increment and DOY for inflection point and scale parameter of varying tree species on available study sites and across different calendar years according to parameter estimates from the final saturated model and evaluated for a fixed tree age of 80 years. K=Kreibach, R=Rosalia, T1=Tyrol I, T2=Tyrol II, N=Nasswald.

Figure 6: Cumulative diameter increment for Norway spruce in Kreisbach (left panel) and in Tyrol I (right panel) dependent on varying categories of social tree statuses. Categories are named as Pred (Predominant, above the 90th percentile of the diameter distribution), P90 (90th percentile of the diameter distribution), P50B (50th percentile of the diameter distribution by basal area), P50 (50th percentile of the diameter distribution), P10 (10th percentile of the diameter distribution).