

# How competitive is the ‘pioneer-climax’ tree species *Nothofagus alpina* in pristine temperate forests of Chile?

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## Abstract

### Aims

*Nothofagus* species are constitutive elements of the temperate forests along the Southern Andes Mountains. The deciduous *Nothofagus alpina* is a fast-growing, but long-lived opportunistic pioneer species (‘pioneer-climax species’) and co-occurs with the evergreen *N. dombeyi*. We tested whether *N. alpina* is competitively superior to *N. dombeyi* in mature stands and whether intra-specific competition in *N. alpina* is stronger than inter-specific competition with *N. dombeyi*.

### Methods

In a pristine old-growth forest in South-Central Chile, we compared the growth of *N. alpina* trees in pure stands and in mixture with *N. dombeyi* to the growth of *N. dombeyi* and calculated competition indices. We related growth variables to climate data and weather extremes.

### Important Findings

In *N. alpina*, juvenile basal area increment was significantly higher in pure than in mixed stands. Contrary to our

hypothesis, *N. dombeyi* exhibited larger radial stem increments than *N. alpina* in the most recent 40 years. In the most recent two decades, this was caused by high growth rates of large *N. dombeyi* trees. In both *Nothofagus* species, stem growth was negatively related to temperature, but *N. dombeyi* responded more sensitively to weather conditions than *N. alpina*. In *N. alpina*, stem increment was negatively related to the intensity of competition, but the size of the competition effects on this species was similar in pure and mixed stands. Thus, compared to *N. alpina*, the ‘pioneer-climax species’ concept is even more appropriate for *N. dombeyi* with its relatively high growth rates even in the early stages of its life.

**Keywords:** competition index, dendroecology, growth–competition relationship, pointer year, productivity, tree-ring analysis

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## INTRODUCTION

Competition within and among plant species belongs to the classic subjects in studies into plant ecology because it ultimately determines species composition, community structure and ecosystem productivity (e.g. Aschehoug *et al.* 2016; Craine and Dybzinski 2013; Grime 2001; Tilman 1997). In forests, intra- and inter-specific competition is particularly complex due to the strong spatial and temporal dynamics during the life histories of forest stands

(Ammer 2016; Forrester 2014). Competition with co-occurring plant species is a pivotal process in the establishment of forest trees from the seedling stage to the stage of (co-)dominance in the canopy layer (e.g. Ammer 2016; Attiwill and Adams 1993; Bazzaz 1979). In temperate forests, secondary forest succession is characterized by ‘gap dynamics’ in which more or less light-demanding woody species benefit from a higher incidence of light in gaps after disturbance (Röhrig 1991). There, secondary succession typically proceeds from pioneer to climax species

(e.g. Barnes 1991; Ellenberg and Leuschner 2010; Röhrig 1991). However, long-lived pioneer species, which are abundant from early stages of succession until the stage of closed canopies in the climax of old-growth forests, may occur in a variety of successional trajectories in various communities (Wirth et al. 2009). In the temperate forests of South America along the southern ranges of the Andes Mountains, the deciduous tree species *Nothofagus alpina* (Poepl. & Endl.) Oerst. (syn. *N. nervosa* [Phil.] Krasser, *N. procera* Oerst.) is considered to be such a long-lived opportunistic pioneer species or ‘pioneer-climax species’: it can efficiently use light in treefall gaps and eventually outgrows previously established juveniles of more shade-tolerant species (Pollmann 2001a, 2005). It is particularly competitive on relatively deep soils such as loose volcanic substrate (Weinberger 1973). Thus, it constitutes a substantial element of those forests from the foothills up to the timberline. In montane regions, it primarily grows at mid-elevations on deep and well-drained soils (Veblen et al. 1996a; Weinberger 1973). Climatic rather than edaphic conditions were assessed to be the principal factors that determine its occurrence and performance (Pollmann 2001b). Its relatively high growth rates (Pollmann 2002) may be related to the species’ low wood density. This implies low ‘construction costs’ of the xylem and results in large conductance to water, allowing higher rates of water flux from the roots to the shoot (Dettmann et al. 2013). A global comparison of several biomes shows that growth rates of trees are related not only to wood density (in a negative manner) but also to the specific leaf area (SLA) (in a positive manner) (Kunstler et al. 2016). Accordingly, we found relatively high SLA values in *N. alpina* (15–35 m<sup>2</sup> kg<sup>-1</sup>) in a preliminary analysis. The occurrence of leaves with a relatively large SLA is also indicative of *N. alpina*’s capability to form shade leaves and is in line with the finding that this species is capable of effectively rejuvenating in the shade (Weinberger 1973).

The evergreen *N. dombeyi* (Mirb.) Oerst., which can reach the tallest tree heights of the South American *Nothofagus* species, also is a long-lived species that can already occur in early stages of secondary succession, but is also capable of forming closed stands for several centuries (Schmaltz 1991). This species is mainly distributed in regions with an oceanic climate and grows nearly from sea level to 2500 m, but can spread out into sporadically warm and dry sites (Donoso 1987). It occurs on habitats that are moister than those of *N. alpina*, but can also grow on a wide range of substrate, from waterlogged soils to shallow soils on recently deposited volcanic debris (Veblen et al. 1996a; Weinberger 1973). According to photosynthetic light-response curves obtained from seedlings (Read and Hill 1985), it is less shade-tolerant than the co-occurring *N. alpina*; this result is in line with *N. dombeyi*’s lower SLA values (7–16 m<sup>2</sup> kg<sup>-1</sup> according to our preliminary measurements). However, *N. dombeyi* displays a larger adaptability to climatic conditions than any other woody species of the southern Andes Mountains and can endure moderate stress resulting from soil drought (Piper et al. 2007). This assessment was corroborated by the finding of xylem cavitation thresholds ( $\psi_{50}$ ; calculated from

features of wood anatomy) that were shifted to lower (more negative) values compared to *N. alpina*, indicating a lower susceptibility to drought-induced cavitation of the xylem (Dettmann et al. 2013). Nevertheless, on the basis of climatic investigations, *N. dombeyi*’s tolerance of xerothermous conditions has been judged to be lower than in *N. alpina* (Weinberger 1973). Accordingly, in a study on old-growth forest stands on volcanic soil in South-Central Chile, Walter et al. (2016) found that the growth of *N. dombeyi* was reduced by high temperature and low precipitation in spring and summer.

In spite of the diverging core areas of their distribution, both species co-occur in the temperate ‘Coihue (*N. dombeyi*)—Raulí (*N. alpina*)—Tepa (*Laureliopsis philippiana*) forest’ along the Andean Cordillera of Chile (S 37°–S 40° 30’, 1000–1300 m a.s.l.; Donoso and Donoso 2010). The plant association *Nothofagetum dombeyi-alpinae* with its elevational extension from ~750 to 1300 m a.s.l. represents the most typical forest type of their co-occurrence (cf. Pollmann 2001a). Considerable insight into the biogeography, ecology and dynamics of *Nothofagus* forests in the southern Andes Mountains has already been achieved on the basis of the fundamental work by, e.g., Schmithüsen (1956), Weinberger (1973), Veblen et al. (1980, 1981), Donoso (1987), Pollmann (2004) and Luebert and Plissock (2006). However, immediate interactions between *N. alpina* and *N. dombeyi*, two of the most important constituents of these montane forests, have rarely been investigated so far. Knowledge on the field performance of these species has mostly been obtained from vegetation relevés and climatic records. In a study including trees up to an age of 250 years, Pollmann (2001a) provided first indications that the stem diameter increment of *N. alpina* can be higher than that of *N. dombeyi*. Thus, in the montane forest of the Western Andes, *N. alpina* may play a role convergent to that of *Fagus sylvatica*, the predominant tree species of Central-European forests from the hill country to sub-montane elevations, which is competitively superior to all the other indigenous forest tree species due to high shade tolerance, effective shading of competing tree species and efficient exploitation of resources in the soil (Ellenberg and Leuschner 2010; Leuschner 1998). To elucidate the competitive ability of *N. alpina* compared to *N. dombeyi*, we studied the intra- and inter-specific competition of *N. alpina* in a region with a climate that should provide optimum growth conditions for both species. Specifically, we tested the following hypotheses:

- (i) In mixture with *N. dombeyi*, *N. alpina* is competitively superior, reflected by consistently larger radial growth increments and a higher productivity;
- (ii) In *N. alpina*, intra-specific competition is stronger than inter-specific competition with *N. dombeyi*;
- (iii) Given the divergent responses of the two species to extreme weather conditions, temporal variation in tree growth will be lower in the species combination of the mixed stands than for individual species.

We tested these hypotheses in monospecific (*N. alpina* only) and mixed stands (*N. alpina* and *N. dombeyi*) of montane forests in the Conguillío National Park at the western slopes of the Andes Mountains in South-Central Chile. There, pristine *Nothofagus* forests still abound in contrast to large regions outside protected areas, where large-scale clear-cutting and conversion to agricultural or rangeland has taken place. We used tree-ring analyses of stem increment cores and a widely used competition index (CI) to quantify the extent of intra- and inter-specific competition.

## MATERIALS AND METHODS

### Study plots and sampling

Fieldwork and sampling were conducted from 19 to 27 March 2014 in Conguillío National Park, located in the Araucanía Region of South-Central Chile, on plots at elevations of ~1000–1300 m a.s.l. (Table 1). The mean annual temperature of the region is 8.5°C (meteorological station of Lonquimay; 40 km to the northeast of Lake Conguillío, 900 m a.s.l.), and the mean annual precipitation in the park, 2500–3000 mm (Pollmann 2003). In spite of relatively large amounts of precipitation, recurring droughts occur in summer with precipitation rates substantially deviating from long-term averages (Schmaltz 1991). The predominant soil type is Andisol. Syntaxonomically, the investigated forest stands belong to the *Nothofagetum dombeyi-alpinae typicum* (Pollmann 2001a; online supplementary Table S1).

Altogether, nine plots in old-growth forest stands were selected. We restricted the number of plots to nine to ensure (i) comparable conditions of the soil parent material (basaltic lava on all these plots; Table 1) in the geologically heterogeneous National Park (Naranjo and Moreno 2005) and (ii) similar mesoclimatic conditions: all plots were situated along a north-south transect with a length of ~5 km from the eastern shore of Lago Conguillío to the north-western shore of Laguna Verde; north-facing slopes were excluded. Another reason for restricting the number of the plots was their poor accessibility in the remote mountainous National Park. The circular plots had a radius of 13 m around a central tree (area of 531 m<sup>2</sup>). We had to confine sampling and measurements to a relatively small plot size to ensure homogeneous structural (e.g. avoidance of gaps) and edaphic conditions within the plots. Similar plot sizes (500–1260 m<sup>2</sup>) have been used in the relatively rare studies conducted on the structure of pristine temperate forests with old *F. sylvatica* trees (tree age up to 400–500 years) in Central, Eastern and Southern Europe (Glatthorn *et al.* 2017; Hobi *et al.* 2015; Piovesan *et al.* 2005); and with old *N. alpina* and *N. dombeyi* trees (tree age > 200–535 years) in the Conguillío National Park (Pollmann 2003; Walter *et al.* 2016). The plots exhibited a homogeneous stand structure and contained *N. alpina* as the only tree species (four plots) or a mixture of *N. alpina* and *N. dombeyi* (five plots). Pure plots of *N. dombeyi* were not present within the study area and, therefore, were not included in the present study. For

the calculation of the competition indices (see ‘Calculation of competition indices and statistical analyses’), competing trees growing at a distance of up to 6 m beyond the plot boundaries were also considered. This resulted in total numbers of 11–23 trees per plot (Table 1). A comparable number of trees (15–25) per plot has been used for studying the growth or the effects of neighbourhood composition on mature trees (>180 years) in old-growth temperate forests of northern California and south-eastern Australia (Sillett *et al.* 2010) and of Central Europe (Juchheim *et al.* 2017). The stem perimeter at breast height and the distances among all trees on the plot including immediately neighbouring trees beyond the plot limits were determined with a tape measure. The height of the trees used for tree coring (see below) was measured with an ultrasonic hypsometer (Vertex IV, Haglöf Co., Långsele, Sweden).

Using hemispherical photography, we determined the canopy openness (fraction of open sky, i.e. sky area unobstructed by vegetation) as a parameter of stand structure. To the north, south, east and west of the plot’s central tree, at half-distance to the farthest competitor within the plot, we took hemispherical photos using a digital camera (Olympus OM-D E-M1; Olympus, Tokyo, Japan), which was mounted on a tripod and combined with a diagonal fisheye lens (Zuiko Digital ED 8 mm 1:3.5; Olympus). At the Department of Geobotany, the hemispherical photos (four per plot; JPG format) were analysed using WinSCANOPY Pro 2009a software (Regent Instruments, Quebec, Canada) according to Walter *et al.* (2016).

From all trees within the plot boundaries, we took two radial increment cores per tree at breast height of the stems from opposite sides in parallel to the contour line of the slope (length of the increment borer: 400 mm). The increment cores were fixed with adhesive tape on corrugated cardboard for transportation and were allowed to air-dry for 48 h as soon as possible after sampling.

### Tree-ring analyses and climate data

All analyses were conducted at the Department of Geobotany, University of Trier. The increment cores were prepared for tree-ring analyses by cutting the uppermost 0.5 mm with a microtome (Swiss Federal Research Institute WSL, Birmensdorf, Switzerland). The ring widths of the cores were measured with a moveable object table (Lintab 5, Rinntech, Heidelberg, Germany) and a stereo microscope (Carl Zeiss, Jena, Germany) with an accuracy of 10 µm. The tree-ring chronologies of both cores of a given tree were averaged by cross-dating with the TSAP-Win Scientific software (version 4.64; Rinntech). The cambial age of the trees was determined from the number of tree rings. For trees with a stem radius larger than the sampled cores (e.g. due to a stem radius larger than the length of the increment borer or due to rotten heartwood), the age was calculated from the difference between the sampled core and the stem radius without bark, divided by the average tree-ring width (TRW) of the tree according to standard methods (e.g. Norton *et al.* 1987).

To eliminate age effects, the individual tree-ring chronologies were detrended on the basis of regional curve

**Table 1:** location and features of the pure (*N. alpina*) and mixed (*N. alpina*, *Nothofagetum dombeyi*) stands investigated in the Conguillío National Park of South-Central Chile (means  $\pm$  1 SE, where applicable)

Plot No.	Location	Soil parent material	Elevation (m a.s.l.)	Inclination (°)	Aspect	Canopy openness (%)	Tree species	Number of trees <sup>a</sup>	Tree age (years)	Tree dbh (m)	Tree height (m)
<i>Pure (N. alpina)</i>											
1	S 38°39.016'; W 71°36.818'	Basaltic and dazitic lava	1220	30	ESE	13 $\pm$ 1 ab	<i>N. alpina</i> <i>N. dombeyi</i>	5 + 9 0 + 7	198 $\pm$ 20 B ab	0.52 $\pm$ 0.06 B ab	21.0 $\pm$ 1.7 B ab
3.1	S 38°38.670'; W 71°36.584'	Basaltic and dazitic lava	1303	30	SSE	13 $\pm$ 2 ab	<i>N. alpina</i> <i>N. dombeyi</i>	7 + 10 0 + 1	156 $\pm$ 6 B b	0.40 $\pm$ 0.02 B b	17.4 $\pm$ 1.0 B b
3.2	S 38°38.668'; W 71°36.568'	Basaltic and dazitic lava	1336	40	ESE	16 $\pm$ 3 ab	<i>N. alpina</i> <i>N. dombeyi</i>	7 + 10 0 + 5	166 $\pm$ 18 B b	0.52 $\pm$ 0.07 B ab	22.3 $\pm$ 2.3 B ab
10	S 38°38.783'; W 71°36.600'	Basaltic and dazitic lava	1253	30	ESE	15 $\pm$ 2 ab	<i>N. alpina</i> <i>N. dombeyi</i>	4 + 10 0 + 2	163 $\pm$ 23 B b	0.53 $\pm$ 0.05 B ab	23.9 $\pm$ 0.7 B ab
<i>Mixed (N. alpina, N. dombeyi)</i>											
2.1	S 38°38.845'; W 71°36.664'	Basaltic and dazitic lava	1233	20	SSW	11 $\pm$ 1 b	<i>N. alpina</i> <i>N. dombeyi</i>	4 + 11 2 + 6	193 $\pm$ 28 B ab 242 $\pm$ 18 A	0.54 $\pm$ 0.05 B ab 0.63 $\pm$ 0.19 A	23.6 $\pm$ 0.9 B ab 23.3 $\pm$ 2.5 A
2.2	S 38°38.837'; W 71°36.665'	Basaltic and dazitic lava	1221	30	SE	11 $\pm$ 2 ab	<i>N. alpina</i> <i>N. dombeyi</i>	3 + 7 3 + 3	212 $\pm$ 42 B ab 275 $\pm$ 2 A	0.56 $\pm$ 0.06 B ab 0.50 $\pm$ 0.06 A	21.5 $\pm$ 1.1 B ab 24.2 $\pm$ 3.3 A
5	S 38°41.130'; W 71°36.853'	Monzogranite, granodiorite	1034	5	O	17 $\pm$ 2 ab	<i>N. alpina</i> <i>N. dombeyi</i>	2 + 4 4 + 4	320 $\pm$ 9 B a 535 $\pm$ 59 A	0.64 $\pm$ 0.09 B a 1.01 $\pm$ 0.15 A	32.4 $\pm$ 0.3 B a 31.3 $\pm$ 2.7 A
7	S 38°41.135'; W 71°36.880'	Monzogranite, granodiorite	1030	10	W	22 $\pm$ 3 a	<i>N. alpina</i> <i>N. dombeyi</i>	4 + 0 2 + 5	545 $\pm$ 67 B a 405 $\pm$ 33 A	0.70 $\pm$ 0.13 B ab 0.74 $\pm$ 0.23 A	26.1 $\pm$ 4.1 B ab 21.8 $\pm$ 2.0 A
11	S 38°39.048'; W 71°36.985'	Basaltic and dazitic lava	1192	30	S	19 $\pm$ 3 ab	<i>N. alpina</i> <i>N. dombeyi</i>	3 + 9 3 + 5	164 $\pm$ 12 B ab 293 $\pm$ 19 A	0.50 $\pm$ 0.05 B ab 0.53 $\pm$ 0.07 A	18.4 $\pm$ 0.4 B ab 23.9 $\pm$ 2.8 A

Different lower-case letters indicate significant differences among all plots; and different capitals, significant differences between the tree species across all plots. Across all mixed stands, tree age, dbh and tree height did not differ significantly between species.

<sup>a</sup>Numbers before and after the slash in the 'Number of trees' column represent the number of trees growing on plots and sampled for tree-ring analyses; numbers after '+': trees outside plot boundaries considered in calculating competition indices.

standardization (RCS; Esper *et al.* 2003) with a moving average of 13 years using TSAP-Win. From detrended tree-ring chronologies and from time series of weather data, pointer years were identified by calculating and averaging tree-wise Cropper values ( $C_{jz}$ ;  $z$ -transformed ratios of anomalies in time series to 13-year moving averages; Cropper 1979; cf. Walter *et al.* 2016). Pointer years were defined as significant when the absolute  $C_{jz}$  value exceeded 1.282 (corresponding to  $P < 0.2$ ), and as highly significant when it exceeded 1.645 ( $P < 0.1$ ).

We also calculated the basal area increment (BAI) of the stems as circular rings after subtraction of the bark thickness. For establishing regressions between BAI and weather data, we normalized the BAI values according to Bukata and Kyser (2008) (see Walter *et al.* 2016), yielding values between 0 and 1 for each tree for a time period of 65 years (from 1950 to 2014). These values were averaged to give the normalized BAI chronology for a given *Nothofagus* species and stand type.

The above-ground biomass of the sampled trees was calculated from published allometric regressions (Gonzalez *et al.* 2005):

$$b = 0.175074 \cdot d^{2.30232} \quad (1) \text{ for } N. \textit{alpina} \text{ and}$$

$$b = 0.150381 \cdot d^{2.32103} \quad (2) \text{ for } N. \textit{dombeyi};$$

with  $b$  = biomass in kg and  $d$  = stem diameter in cm. We also calculated the increment in above-ground biomass (i.e. above-ground productivity) using these equations with diameter values obtained from the tree-ring analyses.

We related RCS indices, BAI and biomass production to weather data for the time period with available climate data (i.e. from 1950 onwards). Climate data were derived from the KNMI Climate Explorer (van Oldenborgh 2016). We used the grid data set CRU TS3.24 with a spatial resolution of  $0.5^\circ$  within a minimum grid from S  $38^\circ 00'$ –S  $38^\circ 30'$  to W  $71^\circ 00'$ –W  $71^\circ 30'$ . Weather anomalies were identified using Cropper values (see above) on the basis of averages of temperature and precipitation for individual months, the four seasons, the vegetation period (November–March) and the entire year. Weather of the vegetation period was considered extreme when the respective absolute Cropper values exceeded 1.645 ( $P < 0.1$ ). Cropper values of weather anomalies were used for comparisons with RCS-detrended tree-ring chronologies (see above), and raw climate data, for comparisons with BAI.

### Calculation of competition indices and statistical analyses

Within each plot and for each tree, we calculated the intra- and inter-specific competition among trees using a distance-weighted size-ratio approach according to Hegyi (1974):

$$CI = \sum_{i=1}^n \left( \frac{dbh_i}{dbh_j} \cdot \frac{1}{Dis_{ij}} \right) \quad (3);$$

where CI is the tree-related competition index,  $j$  is the target tree and  $i$  is the competitor with their respective dbh (diameter

at breast height) values and the distance ( $Dis$ ) between them. In their study on competition among deciduous tree species in a temperate forest of the northern US, Cole and Lorimer (1994) found that competitive stress on individual trees is only exerted by trees that immediately surround the crown of the target tree. Accordingly, we considered a tree a competitor if its crown touched the crown of the target tree; or if the distance between the trees was smaller than 6 m. Trees beyond the boundary were also included in calculating CI if they fulfilled the definition of competitors to trees growing on the plot. The precision of CI on the basis of dbh is not lower than that of other indices although its computation is relatively simple; it also is superior to approaches based on basal area (Tomé and Burkhart 1989).

Means  $\pm$  1 standard error (SE) are presented in the results if not indicated otherwise. Data sets were tested for significant deviations ( $P < 0.05$ ) from a normal distribution according to Shapiro and Wilk (1965); and from homogeneity of variances, with the Brown–Forsythe test. In cases of significant deviations (tree height, tree age), the non-parametric Kruskal–Wallis test, followed by multiple pair-wise Bonferroni-corrected Dunn's tests, or the Mann–Whitney  $U$ -test was applied for comparing independent data sets; in other cases (canopy openness, basal area, CI among plots and between *Nothofagus* species), differences among mean values were tested using  $t$ -tests or analysis of variance with subsequent Holm–Sidak tests. Pearson correlation coefficients were calculated for the relationships between (dependent) growth variables and the predictor variables of climate and competition indices. All these statistical tests were conducted with SigmaStat (version 13.0.0.83; Systat Software, Erkrath, Germany) and with XLSTAT (version 2016.03.31333; Addinsoft, Paris, France). Differences between the tree species in their slopes of the relationships between tree age (predictor variable) and tree height and dbh (dependent variables) were tested with the freeware program SMATR 2.0 (Falster *et al.* 2006; Warton *et al.* 2006) using the OLS method (predicts  $y$  from fixed  $x$  values).

Differences in TRW, BAI and productivity per basal area between *Nothofagus* species as well as between *N. alpina* in pure and mixed stands were tested on the basis of mean annual values of the most recent 20 years to filter out larger year-to-year variations. This is an adequate time span to investigate growth-competition relationships in old-growth forests (Aakala *et al.* 2013). We applied generalized least squares-fitted linear models (GLS) in R (version 3.3.3), using the packages *nlme* and *MuMIn*, in order to evaluate the effects of tree species, tree size, tree age, competition and mixture on annual growth variables. Plot identity was not indicated as a significant random effect by likelihood ratio tests. The explanatory variable 'species' was dummy-coded. The  $z$ -transformed covariates 'starting dbh' and 'starting cambial age' ( $dbh_{1995}$ ,  $age_{1995}$ ), 'competition' (CI), 'mixture' (percentage of *N. alpina* in CI), their interactions with species and the interaction between 'competition' and 'mixture' were considered. Residual error variance was modelled based on the power of the fitted values (Pinheiro and Bates 2000) if indicated by heteroscedastic residuals (this was the case for

BAI). The models with the lowest corrected Akaike Information Criterion (Burnham and Anderson 2002) based on maximum likelihood estimations were selected. Parameter estimates were derived from a model on the basis of residual maximum likelihood, in which the complete effect of the selected covariates was included in their interaction with species and the global intercept was omitted. This does not change model fits but reflects the direct impact of the covariates on the growth variable per species. The species-specific intercept represents the estimated growth variable at the mean value of all included covariates (due to calculations from z-transformed covariates and original growth variables). We checked for normality and homogeneity by diagnostic plots of residuals against fitted values (Zuur et al. 2010).  $R^2_{\text{adj}}$  was calculated from the variation of the dependent variable, the residuals and the degrees of freedom. To address our hypotheses, two models were calculated on subsets of the data set for each growth variable: (i) to identify species differences, only the mixed stand plots were included; (ii) to identify the influence of mixture effects on *N. alpina* only, *N. dombeyi* was omitted from the data set (at our study sites, *N. dombeyi* only occurred in mixed but not in pure stands).

Breakpoint analyses (segmented regression analyses, *R* package segmented; Muggeo 2003) were used to identify changes in the slope of the relationship between BAI and cambial age in the first 160 years of tree growth. The analyses were conducted group-wise with all individual BAI values, and the starting values for breakpoints were set to 50-year intervals. Subsequently, the slopes of the first regression segment were compared between *N. alpina* under pure and mixed conditions as the interaction term in a linear model.

For testing, the effects of extreme weather conditions (temperature or precipitation) in the vegetation period on the productivity, we plot-wise summed up the above-ground biomass produced per species in those extreme years and compared it to the average above-ground biomass production of the preceding 5 years (to filter out larger year-to-year variations) using *t*-tests (for the mixed stands, these comparisons were also made for the combined biomass produced by both *Nothofagus* species). To detect differences in the variation of productivity across the years with climatically extreme vegetation periods, we tested the variances in above-ground biomass production of the four tree sets (*N. alpina* in the pure and in the mixed stands, *N. dombeyi* in the mixed stands, combined production of *N. alpina* and *N. dombeyi* in the mixed stands) on their homogeneity according to Bartlett (Sokal and Rohlf 1995) after having normalized the plot-wise averages according to Bukata and Kyser (2008).

## RESULTS

### Stand structure

The canopy openness was similar across all plots as well as among the pure stands but was significantly lower on mixed plot 2.1 than on mixed plot 7 (Table 1). Across all plots, *N. dombeyi* trees were older ( $367 \pm 36$  years vs  $221 \pm 21$  years;  $P < 0.001$ ), thicker ( $0.70 \pm 0.08$  m vs  $0.53 \pm 0.02$  m;  $P = 0.027$ )

and slightly, yet significantly ( $P = 0.033$ ) higher ( $25.7 \pm 1.5$  m vs  $22.1 \pm 0.8$  m) than the trees of *N. alpina* (Table 1). Across all mixed stands, however, neither tree age nor tree height or dbh differed significantly between species. Differences in tree size and age between *N. alpina* trees in pure and mixed stands were not significant ( $0.57 \leq P \leq 0.75$ ). Across all plots and trees ( $n = 53$ ), tree age was significantly related to dbh (dbh (m) =  $0.0011 \cdot \text{tree age (years)} + 0.2905$ ;  $R^2 = 0.548$ ;  $F = 61.9$ ;  $P < 0.001$ ) and tree height (tree height (m) =  $0.0230 \cdot \text{tree age (years)} + 17.04$ ;  $R^2 = 0.360$ ;  $F = 28.7$ ,  $P < 0.001$ ). These positive relationships between tree age as the predictor variable and dbh and tree height as the dependent variables were also significant when both species were considered separately across the stands (*N. alpina*:  $n = 39$ ,  $R^2 > 0.25$ ,  $F > 12.8$ ,  $P \leq 0.001$ ; *N. dombeyi*:  $n = 14$ ,  $R^2 > 0.43$ ,  $F > 9.1$ ,  $P < 0.011$ ). When comparing the slopes of the age-dependent variables, however, we found that *N. dombeyi* exhibited a steeper slope of the age–dbh relation than *N. alpina* ( $F = 6.822$ ,  $P = 0.011$ ), whereas the slopes of the age–height relationships did not differ significantly between the species ( $F = 0.361$ ,  $P = 0.543$ ).

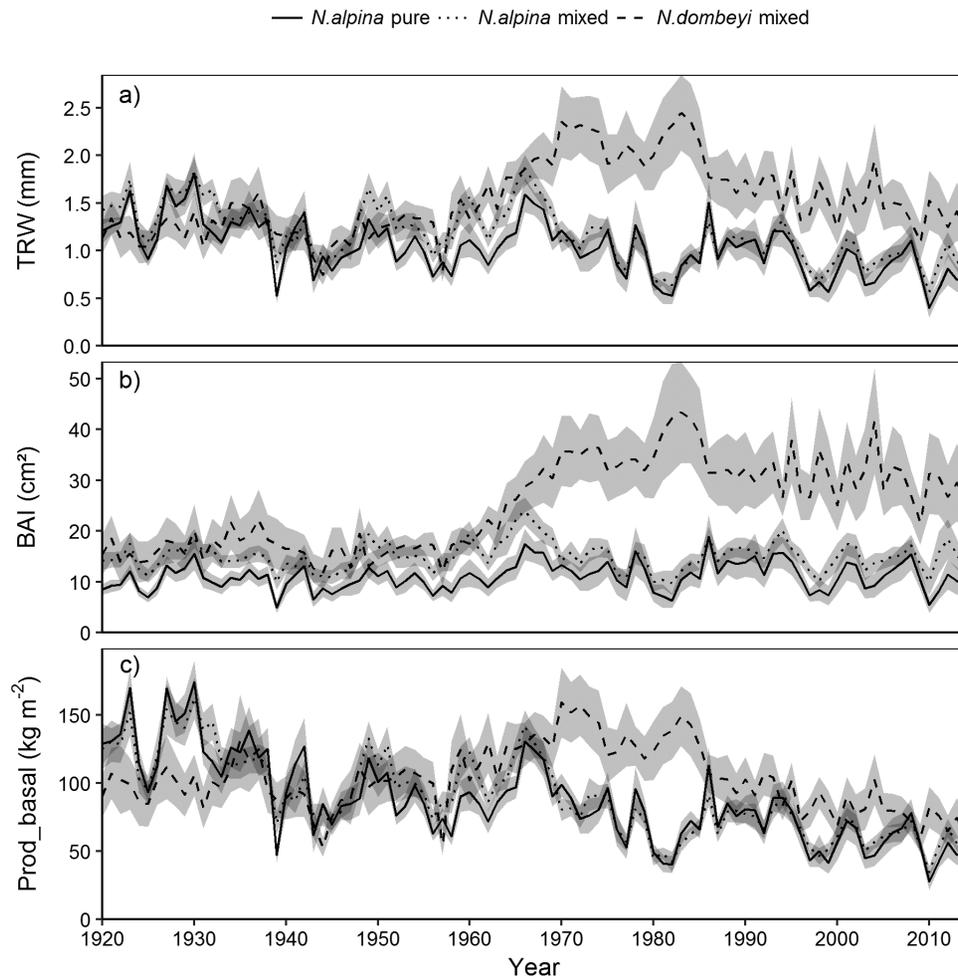
### Stem growth and biomass production

For the past 100 years, general growth patterns remained constant for *N. alpina*, but *N. dombeyi* showed a distinct increase in increment during the 1960s, which lasted until recent years albeit in an attenuated form (Fig. 1). We concentrated our analysis on the more recent decades because changing conditions such as stand structure cannot be reconstructed for longer time scales. In the most recent 40 years, *N. dombeyi* on average exhibited larger increments than *N. alpina* (Fig. 1). The GLS analyses of mean annual growth variables for the most recent 20 years in the mixed stands revealed that the ‘Marginal Effect’ of species (i.e. the difference of intercepts) on growth (at mean dbh<sub>1995</sub> and age<sub>1995</sub>) was only marginally significant for the basal area-related productivity and non-significant for TRW and BAI (Table 2). Larger TRW and BAI of *N. dombeyi* compared to *N. alpina* was due to significantly (in TRW, only marginally significant) (in TRW, only marginally significant) larger positive effects of dbh<sub>1995</sub> on growth. This interaction between species and dbh<sub>1995</sub> reflects particularly high growth rates of large *N. dombeyi* trees. In contrast, tree age exerted a negative effect on the growth of *N. dombeyi*. The CI and the fraction of *N. alpina* in CI were not included in the models for the mixed stand.

Juvenile increase in annual BAI lasted to a cambial age of 33 years in *N. alpina* pure stands, 63 years for *N. alpina* in mixed stands and 48 years in *N. dombeyi* (Fig. 2). In *N. alpina*, the initial slope of BAI vs cambial age was significantly higher under intra-specific competition than under combined intra- and inter-specific competition (Table 3).

### Climate effects on growth

Positive and negative deviations (pointer years) from standardized growth trends were mainly detected for *N. alpina* in both the pure and the mixed stands, but only in a few cases (for the years 1957, 2004 and 2009) for *N. dombeyi* (Fig. 3). In

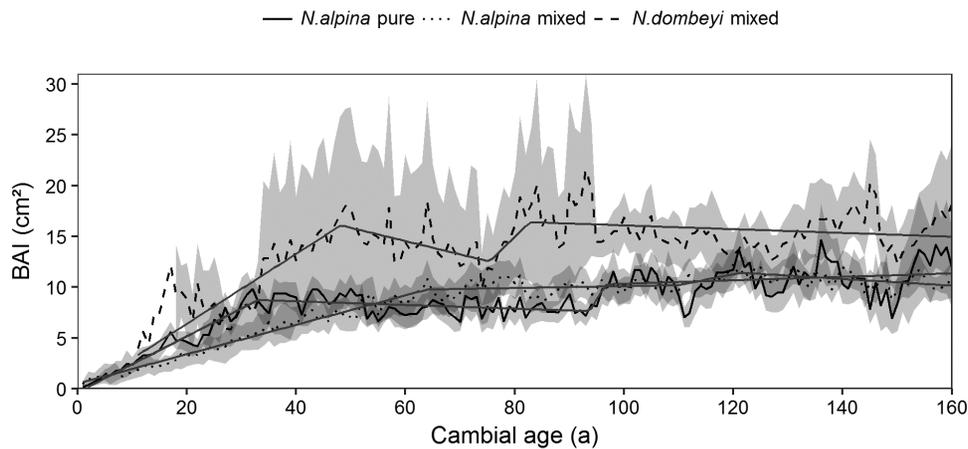


**Figure 1:** tree-ring width (TRW; **a**), basal area increment (BAI; **b**) and basal area-related productivity (Prod\_basal; **c**) since 1920 for *Nothofagus alpina* under intra-specific competition (pure) and combined intra- and inter-specific competition (mixed) and *N. dombeyi*. Lines and ribbons represent mean values  $\pm 1$  SE.

**Table 2:** effects of species identity, tree size (dbh) and cambial age on the mean annual growth increment (means  $\pm 1$  SE) of *Nothofagus alpina* ( $n = 16$ ) and *N. dombeyi* ( $n = 14$ ) in the mixed stands for the most recent 20 years of the study (1995–2014)

		TRW	BAI	Prod_basal
Intercept	<i>N. alpina</i>	$0.8 \pm 0.1^{***}$ a	$13.1 \pm 1.6^{***}$ a	$52.8 \pm 7.0^{***}$ (b)
	<i>N. dombeyi</i>	$1.1 \pm 0.2^{***}$ a	$16.5 \pm 2.1^{***}$ a	$72.8 \pm 7.8^{***}$ a
dbh <sub>1995</sub>	<i>N. alpina</i>	$0.4 \pm 0.2$ (b)	$8.4 \pm 2.5^{**}$ b	$19.4 \pm 8.2^*$
	<i>N. dombeyi</i>	$0.9 \pm 0.2^{***}$ a	$32.7 \pm 6.5^{***}$ a	
age <sub>1995</sub>	<i>N. alpina</i>	$-0.1 \pm 0.1$ a	$-0.7 \pm 1.0$ a	$-8.7 \pm 5.9$ a
	<i>N. dombeyi</i>	$-1.3 \pm 0.3^{***}$ b	$-33.7 \pm 7.3^{***}$ b	$-48.1 \pm 12.1^{***}$ b
$R^2_{adj}$		0.56	0.56	0.47

Growth is represented by tree-ring width (TRW;  $\text{mm a}^{-1}$ ), basal area increment (BAI;  $\text{cm}^2 \text{a}^{-1}$ ) and basal area-related productivity (Prod\_basal;  $\text{kg m}^{-2} \text{a}^{-1}$ ). Indicators of competition and mixture were not included in the best-fitting model. Parameters and SE are estimated with GLS analyses of the mixed plots and shown if included in the best-fitting model. Different letters indicate significant differences ( $P < 0.05$ ) of parameter estimates between the two species; brackets indicate marginal significance ( $P < 0.10$ ). Significance levels of the parameter estimates are  $P < 0.001$  (\*\*\*),  $P < 0.01$  (\*\*) and  $P < 0.05$  (\*).



**Figure 2:** basal area increment (BAI) in the first 160 years of tree cambial age for *Nothofagus alpina* under intra-specific competition (pure) and combined intra- and inter-specific competition (mixed), and for *N. dombeyi*. Lines and ribbons represent mean values  $\pm 1$  SE; straight grey lines are segmented regression lines.

**Table 3:** cambial age of the first change of slope in the relationship of BAI vs cambial age and the initial slopes according to the segmented regression analyses for *Nothofagus alpina* under intra-specific competition (pure) and combined intra- and inter-specific competition (mixed), and for *N. dombeyi*

	First breakpoint cambial age (years)	Initial slope	$R^2_{adj}$
<i>N. alp.</i> pure	33 $\pm$ 3	0.27 $\pm$ 0.02***	0.43 a
<i>N. alp.</i> mixed	63 $\pm$ 4	0.14 $\pm$ 0.01***	0.14 b
<i>N. dom.</i> mixed	48 $\pm$ 6	0.34 $\pm$ 0.13*	0.03

$R^2_{adj}$  refers to the first regression segment. See Table 1 for the number of trees considered. Number of trees available at juvenile age: *N. alpina* pure: 7; *N. alpina* mixed: 21; *N. dombeyi*: 8.

\*Statistically significant at  $P < 0.05$ ; \*\*\*Statistically significant at  $P < 0.001$  (difference in slopes was only tested between *N. alpina* pure and *N. alpina* mixed).

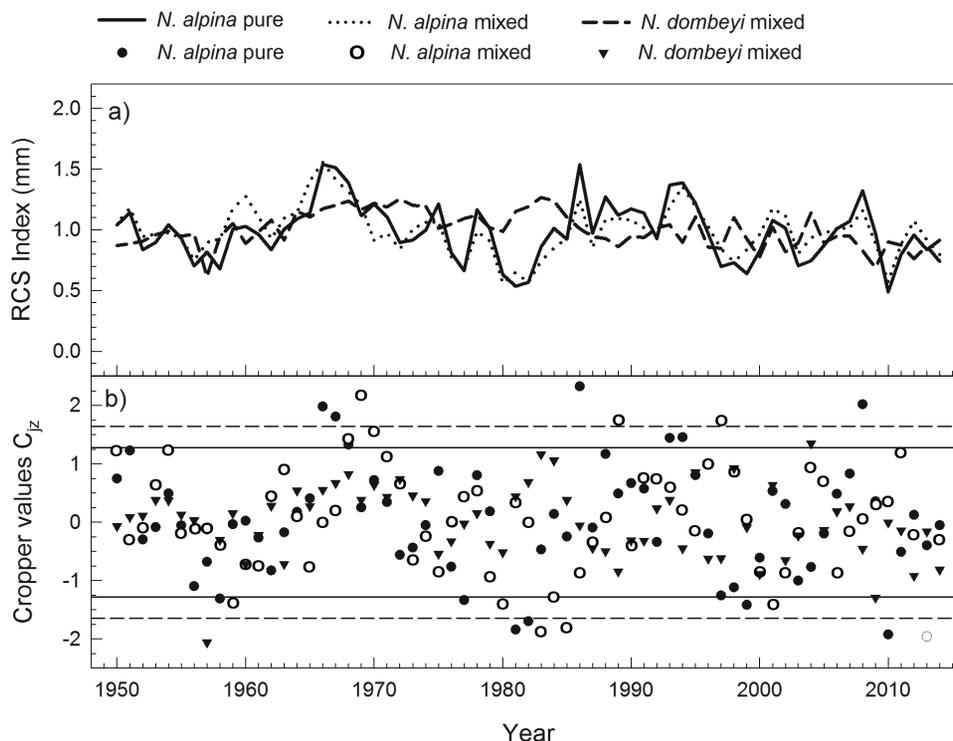
both *Nothofagus* species, stem growth (RCS indices and BAI) exhibited negative correlations with temperature (Table 4). In *N. dombeyi*, stem growth correlated negatively with summer temperatures (December, February and entire summer months) and with the average temperatures of the vegetation period. In *N. alpina*, such negative correlations were only found for individual months in autumn (May of the preceding year) and winter (August), whereas positive responses of RCS indices and BAI to the average temperature of the preceding June were detected. Precipitation of the current vegetation period (sums of individual months, of the spring or the entire summer) had a positive effect on growth in *N. dombeyi* only, whereas in *N. alpina*, the preceding June (a winter month) was the only period with a positive effect of precipitation on stem growth (Table 4).

In the time period 1950–2014, we found 15 ‘extreme’ pointer years for climate, in which temperature or precipitation deviated significantly (absolute Cropper values  $> 1.645$ ) from the average values of that period (online

supplementary Table S2). However, the above-ground productivity of the *Nothofagus* trees was reduced in those ‘extreme’ years in two instances only: in *N. alpina* in a year with a dry (1976, mixed stand) or cool vegetation period (2010, pure stand; online supplementary Table S2). All the other significant responses of *N. alpina*’s productivity were positive, irrespective of warm (1965, 1980) or cool (1960) vegetation periods. In *N. dombeyi*, the productivity exhibited a significant response in only one instance: it was higher in 1967, a year with a warm vegetation period. Across those 15 climate pointer years, the variances of above-ground productivity did not differ significantly among the four tree groups (*N. alpina* in pure and in mixed stands, *N. dombeyi* in mixed stands, combination of both species in the mixed stand;  $X^2 = 0.223$ ,  $df = 3$ ,  $P > 0.99$ ), although the variance of the combined productivity of *N. alpina* and *N. dombeyi* in the mixed stand was lowest, and variance was highest for the productivity of *N. dombeyi* in the mixed stands.

### Intra- and inter-specific competition

The strength of competition on *N. alpina*, exerted by conspecific trees on the *N. alpina* plots and by a combination of intra- and inter-specific competition (*N. alpina* + *N. dombeyi*) on the mixed plots, did not differ significantly (Table 5). The analyses of the  $dbh_{1995}$  and  $age_{1995}$  effects on mean annual tree growth gave similar results for all *N. alpina* trees (Table 6) and for the *N. alpina* trees in the mixed stands only (cf. Table 2). Additionally, we detected a significantly negative effect of competition on TRW; it was marginally significant for BAI. This effect was not influenced by mixture. Accordingly, TRW (for the pure *N. alpina* stands) and BAI of *N. alpina* (for the pure and the mixed stands) correlated negatively with CI, with correlation coefficients of CI with TRW and BAI being higher under intra-specific competition than in the mixed stands (Fig. 4). The productivity of above-ground biomass was not related to CI.



**Figure 3:** RCS-indexed tree-ring increments (a) and Cropper values for the identification of pointer years (b) calculated for *Nothofagus alpina* trees in the pure and the mixed stands and for *N. dombeyi* trees in the mixed stand. Solid lines in (b) mark significance thresholds for  $P = 0.20$  ( $C_{jz} = +1.282$  and  $-1.282$ ); and dashed lines, significance thresholds for  $P = 0.10$  ( $C_{jz} = +1.645$  and  $-1.645$ ).

## DISCUSSION

### Inter-specific differences in growth

Contrary to our first hypothesis, the increments of stem diameter and basal area as well as of above-ground productivity were not higher but, at least in tendency for BAI and productivity, even smaller in *N. alpina* than in *N. dombeyi*. This result indicates that the negative effect of age on the growth of *N. dombeyi*, which was larger than in *N. alpina*, was outweighed by the positive effect of stem size (larger dbh) in the former species. Against the conventional assumption of a decrease in growth increment in old and tall trees, enhanced biomass production in large trees has been found in 13 out of 14 investigated tropical species (Sheil *et al.* 2017), in giant (>100 m tall, >1000 years old) specimens of *Sequoia sempervirens* in a temperate lowland forest (Sillett *et al.* 2010) and in a mountain forest dominated by the evergreen *N. solandri* in New Zealand (Coomes *et al.* 2012). In primeval *F. sylvatica* forests of Central Europe, the above-ground net primary production was not lower than in nearby managed production forests and did not decrease in the forests' terminal stage (Glatthorn *et al.* 2017). The exact mechanisms underlying this phenomenon are unclear. It has been assumed that the lack of decrease in productivity with increasing tree and stand age is due to a higher structural diversity of old-growth forests (Glatthorn *et al.* 2017). Alternatively, it could be caused by adjusting the positioning, nutrient content and angles of leaves within the

canopies (Coomes *et al.* 2012). Such an adjustment could result in a 'compound interest' effect through increasing space occupation in the canopy; however, such effects seem to be species-specific (cf. Reiter *et al.* 2005; Seidel *et al.* 2013).

In our present study, we found larger BAI increments in *N. dombeyi* than in *N. alpina* already in the first decades of the trees' lives. Such growth advantage has also been described for seedlings of these tree species in nurseries (cf. Veblen *et al.* 1996a), but might have been insufficiently considered in field studies so far. It may have provided the basis for the superiority of the former species over *N. alpina* in the later stages of growth. All these findings and their interpretation would imply that in the temperate *N. dombeyi*-*N. alpina* forests in the Southern Andes, the previously observed advantage of *N. alpina* in growth and competition—according to its pioneer character—is restricted to early phases of establishment in gaps under conditions of low or intermediate irradiance, when the growth of *N. dombeyi* is hampered by the lack of light (cf. Veblen *et al.* 1996a), whereas *N. dombeyi* dominates in the later stages of the stand development and, thus, displays an even higher 'climax' potential than *N. alpina*.

### Competition and growth

Competition by neighbouring trees had a negative effect on the growth of *N. alpina*, but not of *N. dombeyi*. Contrary to our second hypothesis, the effects of intra- and inter-specific competition on the radial stem growth of *N. alpina* did not differ

**Table 4:** statistically significant (two-sided;  $P < 0.05$ , or  $P \leq 0.01$  when marked with an asterisk) Pearson correlation coefficients between RCS-indexed tree-ring widths and Cropper values of climate data (air temperature, precipitation), and between normalized values of the basal area increment (BAI) and raw climate data for different time periods in the tree species *Nothofagus alpina* growing in monospecific ('mono') or in mixed stands and *N. dombeyi* in mixed stands

Temperature								
	Indexed tree-ring width							
	Year	Aug	Dec	Feb	Veg.per	Summer	May <sub>prec</sub>	Jun <sub>prec</sub>
<i>N. alpina</i> , mono		-0.256					-0.252	0.284
<i>N. alpina</i> , mixed		-0.296					-0.318*	0.285
<i>N. dombeyi</i> , mixed	-0.327*		-0.310	-0.264	-0.362*	0.365*		
BAI								
<i>N. alpina</i> , mono								-0.261
<i>N. alpina</i> , mixed		-0.279					-0.279	
<i>N. dombeyi</i> , mixed			-0.295	-0.261	-0.341*	-0.334*		

Precipitation							
	Indexed tree-ring width						
	Jul	Oct	Dec	Jan	Spring	Summer	Jun <sub>prec</sub>
<i>N. alpina</i> , mono							
<i>N. alpina</i> , mixed							0.245
<i>N. dombeyi</i> , mixed			0.321*	0.263		0.359*	0.390*
BAI							
<i>N. alpina</i> , mono							0.345
<i>N. alpina</i> , mixed							
<i>N. dombeyi</i> , mixed	0.248	0.326*			0.269	0.285	

The indexed tree-ring widths and BAI values are averaged over all the respective stands (four monospecific stands of *N. alpina* and five mixed stands with *N. alpina* and *N. dombeyi*).  $n = 65$  years. Veg.per., entire vegetation period (November–March). The index 'prec' refers to the respective month of the preceding vegetation period.

**Table 5:** means  $\pm$  1 SE of plot-wise competition indices (CI;  $m^{-1}$ ) according to Hegyi (1974)

Plot type	Competing species		
	<i>Nothofagus alpina</i>	<i>N. dombeyi</i>	<i>N. alpina</i> + <i>N. dombeyi</i>
Pure ( <i>N. alpina</i> )	0.91 $\pm$ 0.13 ( $n_{tot} = 62$ )	0.16 $\pm$ 0.06 ( $n_{tot} = 15$ )	1.08 $\pm$ 0.09 ( $n_{tot} = 77$ )
Mixed ( <i>N. alpina</i> , <i>N. dombeyi</i> )	0.53 $\pm$ 0.11 ( $n_{tot} = 47$ )	0.38 $\pm$ 0.06 ( $n_{tot} = 37$ )	0.91 $\pm$ 0.13 ( $n_{tot} = 84$ )

The values indicate the extent of competition exerted on *N. alpina* trees on pure *N. alpina* plots and on mixed plots with both *N. alpina* and *N. dombeyi* by competing trees of *N. alpina* (intra-specific competition) and of *N. dombeyi* (inter-specific competition), and the combined competition effect by *N. alpina* and *N. dombeyi* (additive CI values of both species). On the *N. alpina* plots, competition by *N. dombeyi* was exerted in some instances by some trees growing just beyond the plot boundary next to *N. alpina* trees. The differences between the CI values are non-significant in all cases (analysis of variance for all plots:  $F = 2.07$ ,  $P = 0.06$ ; comparison between competition effects of *N. alpina* and *N. dombeyi* on mixed plots:  $t = 1.223$ , two-tailed  $P = 0.256$ ; comparison of additive CI values between pure and mixed plots:  $t = 0.964$ , two-tailed  $P = 0.367$ ).  $n_{tot}$ , number of trees considered for each type of plot and competition in calculating CI (including trees growing beyond the plot boundaries; cf. Table 1).

significantly. In the juvenile stages, growth of *N. alpina* in the mixed stands was even slower than in the pure stands and was distinctly slower than the growth of *N. dombeyi*. Therefore, the characterization of *N. alpina* as a 'pioneer-climax species' in *N. alpina*-*N. dombeyi* forests cannot be interpreted towards a strong competitive ability of this species from its establishment in gaps until its mature stage, but only as the capability to keep pace with the competitively superior *N. dombeyi* and

to form the canopy layer together with the latter. Thus, the term 'opportunistic' (Pollmann 2001a, 2005) with regard to *N. alpina*'s capability of rapidly colonizing gaps under low to intermediate light conditions fits the growth dynamics of this species better. On the other hand, under ample light supply at exposed sites, *N. dombeyi* is also capable of establishing as one of the first tree species in the succession towards old-growth forest stands (Schmaltz 1991; Weinberger 1973).

## Climate effects on growth

Our finding that *N. alpina* responds even less sensitive to weather conditions during the vegetation period than *N. dombeyi* (Table 4) contradicts assumptions of an increased susceptibility of *N. alpina* to climatic extremes as the cause of the observed lower growth rates. It also contradicts earlier implications on the basis of vegetation relevés that cold and dry climate conditions may be the reason of a reduced competitive power of *N. alpina* vs *N. dombeyi* (cf. Pollmann 2001a). Thus, the higher variability in stem diameter increment (as evidenced by the distinctly larger amount of positive and negative pointer years) in *N. alpina* compared to its sister species should be due to non-climatic factors, for instance, to light conditions upon alterations in the size and amount of gaps in the stands during the years. In *N. dombeyi*, however, the negative correlation of

**Table 6:** effects of diameter at breast height (dbh) and competition index (CI) on the mean annual tree growth (represented by tree-ring width TRW,  $\text{mm a}^{-1}$ ; basal area increment BAI,  $\text{cm}^2 \text{a}^{-1}$ ; and basal area-related productivity Prod\_basal,  $\text{kg m}^{-2} \text{a}^{-1}$ ; means  $\pm 1$  SE) of *Nothofagus alpina* in pure and mixed stands (in total,  $n = 39$ ) in the most recent 20 years of the study (age<sub>1995</sub>)

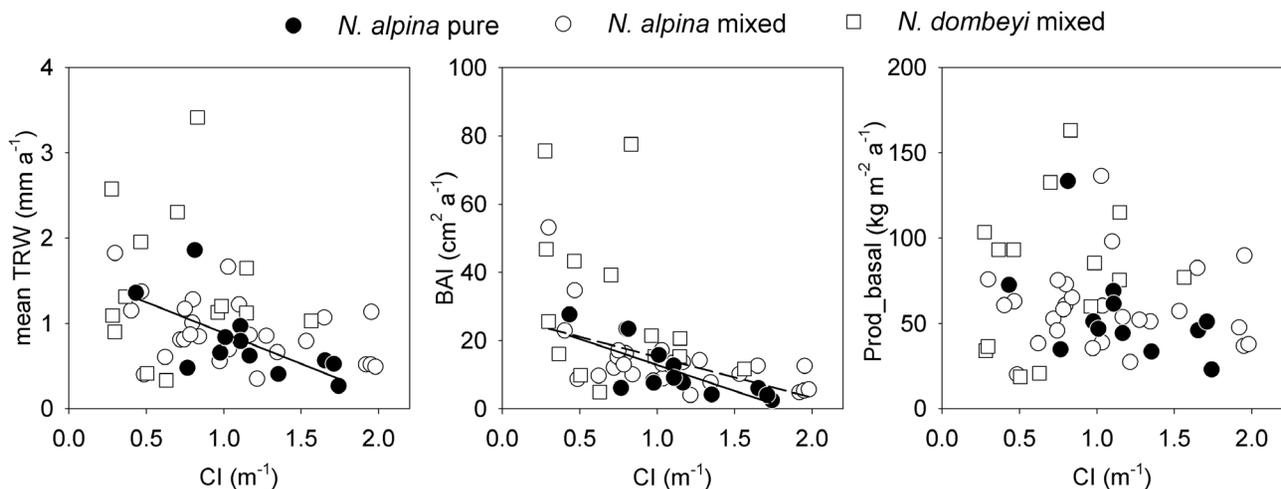
	TRW	BAI	Prod_basal
Intercept	$0.9 \pm 0.1^{***}$	$14.7 \pm 1.1^{***}$	$57.9 \pm 4.0^{***}$
dbh <sub>1995</sub>		$6.4 \pm 1.9^{**}$	
CI	$-0.2 \pm 0.1^{**}$	$-1.7 \pm 1.0^{\circ}$	
$R^2_{\text{adj}}$	0.15	0.52	0.00

Cambial age and mixture (percentage of *N. alpina* in CI) were not included in the best-fitting models. Parameters and SE are estimated with GLS analyses and shown if included in the best-fitting model. Significance levels of the parameter estimates are  $P < 0.001$  (\*\*\*),  $P < 0.05$  (\*) and  $P < 0.1$  (°).

stem diameter increment with summer temperatures (in particular, when accompanied by low amounts of precipitation) could be expected on the basis of earlier investigations (Suarez 2010; Suarez and Kitzberger 2010; Walter *et al.* 2016): upon analyses of stable carbon and oxygen isotope ratios, a reduction in the photosynthetic capacity was assumed as a cause for the reduced growth (Walter *et al.* 2016). This sensitivity against high summer temperatures also is in line with *N. dombeyi*'s lower tolerance of a xerothermous climate (Weinberger 1973) and fits to the assessment of this species as a floral element of the Antarctic (Breckle 2002). On the other hand, extreme (relative to the site) weather conditions during the vegetation period did not result in significant decreases in above-ground biomass production in either species. This finding, however, might have been unavoidably influenced by the method of data evaluation as some of the respective 5-year reference periods inevitably also comprised years with weather extremes. The different responses of the species to weather conditions had prompted us to formulate our third hypothesis postulating that the temporal variation in tree growth should be lower in the species combination of the mixed stands than in the individual species. However, our results do not confirm our expectation but concur with outcomes of a Central-European study on temperate forests with mixtures of *F. sylvatica* and *Picea abies*. In this study, no straightforward interaction effects of species composition and weather conditions on productivity have been found (Pretzsch *et al.* 2012).

## CONCLUSION

For *N. alpina*, the 'pioneer-climax species' concept is valid in the modified sense that in the late stage of stand development in *N. alpina*-*N. dombeyi* forests, *N. alpina* is co-dominant with



**Figure 4:** relationship between the mean annual growth variables tree-ring width (TRW; **a**), basal area increment (BAI; **b**) and basal area-related productivity (Prod\_basal; **c**) in the most recent 20 years and the competition index (CI) for *Nothofagus alpina* under intra-specific competition (pure), combined intra- and inter-specific competition (mixed) and for *N. dombeyi*. Significant negative correlations exist with TRW for *N. alpina* pure ( $R^2 = 0.43$ ,  $P < 0.05$ ; **a**) and with BAI for *N. alpina* pure (solid line,  $R^2 = 0.59$ ,  $P < 0.01$ ; **b**) and *N. alpina* mixed (dashed line,  $R^2 = 0.33$ ,  $P < 0.01$ ; **b**). Both regressions with BAI share a common slope ( $-12.9$ ).

*N. dombeyi*, but inferior in radial stem growth due to competition. The ‘pioneer-climax species’ concept is even more appropriate for *N. dombeyi* with its relatively high rates of radial stem increment not only in the late but also in the early stages of its life, even under competition with *N. alpina*. Thus, the development of the stands towards old-growth forests might be more variable than previously thought, in dependence on the frequency and intensity of gap-creating disturbance (cf. Veblen *et al.* 1996b) and the subsequent small-scale dynamics of light conditions. On the other hand, growth and competitive ability of *N. alpina* are not equivalent with the respective characteristics of *F. sylvatica* in the temperate forests of Central Europe’s low mountain to sub-montane regions, where the latter species is relatively slow in colonizing gaps and exhibits relatively low growth rates in the earliest stages of its life, but outgrows all the other indigenous forest tree species in the course of stand development and forest succession.

## SUPPLEMENTARY DATA

Supplementary material is available at *Journal of Plant Ecology* online.

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