Trees (2011) 25:215–229
DOI 10.1007/s00468-010-0499-5

ORIGINAL PAPER

δ^{13}C signature of tree rings and radial increment of *Fagus sylvatica* trees as dependent on tree neighborhood and climate

**Inga Mölder · Christoph Leuschner ·
Hanns Hubert Leuschner**

Received: 9 March 2009 / Revised: 10 September 2010 / Accepted: 21 September 2010 / Published online: 12 October 2010

Abstract We conducted dendroecological analyses in 80-year-long tree ring chronologies to detect neighborhood effects (competition intensity, species identity) on the δ^{13}C signature of tree rings and radial stem increment of *Fagus sylvatica* trees growing either in monospecific or mixed patches of a temperate forest. We hypothesized that tree ring δ^{13}C is a more sensitive indicator of neighborhood effects and the impact of climate variability on growth than is ring width. We found a closer correlation of summer precipitation to δ^{13}C than to ring width. While the ring width showed a decline over the test period (1926–2005), the mean curve of δ^{13}C increased until the mid of the 1970s, remained high until about 1990, and markedly decreased thereafter. Possible explanations related to ontogeny and environmental change ('age effect' due to canopy closure; elevated atmospheric SO_2 concentrations in the 1960s–1980s) are discussed. Beech target trees surrounded by many allospecific trees had a significantly lower mean δ^{13}C in the period 1926–1975 than beech with predominantly or exclusively conspecific neighborhood, possibly indicating a more favorable water supply of beech in diverse stands. Contrary to expectation, trees subject to more intense competition by neighboring trees (measured by Hegyi's competition index) had lower δ^{13}C values in their tree rings, which is thought to reflect denser canopies being linked to increased shading. We conclude that tree ring δ^{13}C time series represent combined archives of climate variability, stand history and neighborhood effects on tree physiology and growth that may add valuable information to that obtained from conventional tree ring analysis.

Keywords Allospecific neighbor · Cambial age · Conspecific neighbor · Dendrochronology · Forest management · Mixed stand

Introduction

One important issue in the biodiversity–ecosystem functioning debate is the dependence of ecosystem stability on diversity (Odum 1953; Loreau et al. 2002; DeClerck et al. 2006). Frequently discussed stability parameters of ecosystems are the resistance to, and the resilience after, disturbances such as drought events or herbivore attack. Most of the relevant research on the relationship between diversity and stability has been conducted in herbaceous plant communities while woody associations have been studied only exceptionally. It is generally accepted that mixed forests show greater resilience with regard to herbivore attack than monospecific stands (Jactel et al. 2005; Pretzsch 2005). However, the relationship between tree species diversity and the resistance to, or the resilience after, drought events in forests is not clear yet (Larsen

Communicated by U. Luettge.

Present Address:
I. Mölder
Northwest German Forest Research Station, Grätzelstr. 2,
37079 Göttingen, Germany

I. Mölder · C. Leuschner (✉)
Plant Ecology, Albrecht von Haller Institute for Plant Sciences,
Georg-August-University of Göttingen, Untere Karspüle 2,
37073 Göttingen, Germany
e-mail: cleusch@gwdg.de

H. H. Leuschner
Palynology and Climate Dynamics, Albrecht von Haller Institute
for Plant Sciences, Georg-August-University of Göttingen,
Untere Karspüle 2, 37073 Göttingen, Germany

1995; DeClerck et al. 2006). This question is of high relevance to forestry because natural forests are widely being replaced by monospecific plantations in temperate and in tropical regions while the consequences for ecosystem functioning and stability are poorly known.

Common reactions of trees to water limitation are reductions in height and diameter growth, which can last for several years or even decades (Peterken and Mountford 1996; Archaux and Wolters 2006; Bréda et al. 2006). Drought effects in forests can be enhanced by intraspecific or interspecific competition for water (Gouveia and Freitas 2008) which may be reflected in the chronology of annual tree rings (Saurer et al. 2008). Another archive of environmental changes is the tree-ring δ^{13}C signature. It can be used as a proxy for stomatal conductance and thus as a tool for obtaining a long-term record of changes in soil moisture and/or the evaporative demand of trees. δ^{13}C values of tree rings have been reported to show drought signals more precisely than tree-ring width does (Andreu et al. 2008). In a similar manner as tree rings, δ^{13}C time series do not represent pure physical archives but may also reflect biological processes such as competition for light or water in the forest stand.

The intensity of interspecific or intraspecific competition in forests is often approximated by indices of stand density such has Hegyi's competition index which is based on stem distance and diameter (Orwig and Abrams 1997; Piutti and Cescatti 1997; Gouveia and Freitas 2008). Like other measures of competition intensity, this index does, however, not take into account that species often differ in their competitive abilities. For most of the investigated mixed forest stands, interspecific competition between different tree species has been reported to be asymmetric (Yoshida and Kamitani 2000; Canham et al. 2004, 2006). Niche complementarity can reduce the intensity of interspecific competition in comparison with intraspecific competition (Kelty 2006). As a consequence, interspecific competition can also lead to positive effects on the growth and water status of one or more partners of the interaction.

Aboveground competition may also result in changes of the canopy structure and the light regime, thereby affecting the δ^{13}C signature of leaf mass (Medina et al. 1991; Buchmann et al. 1997; Hanba et al. 1997; West et al. 2001). Further, competition could affect the water availability for the competing species in a mixed stand. Both mechanisms can have consequences for tree growth and the δ^{13}C signature in the annual rings. Thus, long-term records of these growth and water status proxies can provide valuable insight into a tree's long-term water regime and possibly also into competition-induced changes of the water balance (McNulty and Swank 1995; Buchmann et al. 1997; Skomarkova et al. 2006; Grams et al. 2007; Saurer et al. 2008).

For a time period of 80 years, we analyzed the radial increment and the δ^{13}C signature of tree rings of selected *Fagus sylvatica* trees. These trees were carefully selected for their specific neighborhood constellations and competition intensity in monospecific and mixed patches of a species-rich temperate deciduous forest. Our study tests two hypotheses, (1) the δ^{13}C signature in tree rings is influenced by the competition intensity and the species identity of a tree's neighborhood, and (2) tree ring δ^{13}C signatures are more sensitive indicators of neighborhood effects and climate variation than tree ring series are.

Methods

Study site

Dendrochronological and dendrochemical investigations were conducted in 16 mature *Fagus sylvatica* L. (European beech) trees in the temperate broad-leaved forests of Hainich National Park (western Thuringia, Central Germany) close to the village of Weberstedt (51°05′28″N, 10°31′24″E) at about 350 m elevation. Besides the *Galio–Fagetum* and the *Hordelymo–Fagetum* associations, i.e., beech forests on slightly acidic to basic soils, the *Stellario–Carpinetum* community, a broad-leaved mixed forest rich in hornbeam, linden and ash (Mölder et al. 2008, 2009), is abundant in the study region. The most common tree species are *F. sylvatica*, *Fraxinus excelsior* L. (European ash) and *Tilia cordata* Mill. (little-leaved linden), whereas *T. platyphyllos* Scop. (large-leaved linden), *Carpinus betulus* L. (European hornbeam) and *Acer pseudoplatanus* L. (sycamore maple) are admixed at lower densities.

The trees were chosen at a maximum distance to each other of 4.9 km on eutrophic loess-derived soils with a profile depth of about 60 cm, situated in level or gently sloping terrain on limestone (Triassic Upper Muschelkalk). The soil type of the study sites is (stagnic) Luvisol according to the World Reference Base for Soil Resources (FAO/ISRIC/ISSS 1998). Since the forest exists for at least 200 years, it represents ancient woodland in the definition of Wulf (2003). During the past 40 years, only single stems have been extracted. On the study sites, the last extractions of stems were conducted between 1991 and 1998 (E. Kinne, pers. communication). All trees were selected in stand sections with a closed canopy and a more or less homogeneous stand structure. The recent investigation is part of the Hainich Tree Diversity Matrix Study, which analyzes the functional role of tree diversity in a temperate mixed forest (Leuschner et al. 2009). We conducted soil chemical and physical surveys on all prospective study sites prior to tree selection in order to guarantee sufficient site comparability with respect to edaphic conditions (see Guckland et al. 2009). The study area is characterized by an annual mean temperature of 7.5°C and about 590 mm of precipitation per year (1973–2004, Deutscher Wetterdienst Offenbach, Germany).

Tree selection and neighborhood characterization

For investigating radial increment and the δ^{13}C signature in annual rings of beech in its dependence on variable stem neighborhoods, we selected 16 trees (Table 1) from a pool of 152 adult *Fagus* trees, which had been analyzed for tree ring chronologies in a precedent study (Mölder 2010). The tree selection was based on predefined criteria of the neighborhood constellation, suitable biometric characteristics of the tree and the quality of the extracted core. All target *Fagus* trees were part of the upper canopy, had a diameter at breast height (dbh) of 40–60 cm, and the crown area was at least 30 m^2 large. Another criterion was that the ring series could be successfully cross-dated to stand chronologies and no questionable tree rings occurred, the time period between sample extraction, ring measurement and sample drying did not last longer than one or two days, and the samples were free from signs of injury or infection. This selection procedure reduced the sample size to 16 target trees to be considered. Subsequently, we grouped the target trees according to the importance of *Fagus* and non-*Fagus* trees in the neighborhood (Fagus100 group, all neighbors being *Fagus*; Fagus70-99 group, 70-99% of the competition index (CI) value being contributed by *Fagus–Fagus* interactions; Fagus<70 group, less than 70% of the CI value being due to *Fagus–Fagus* interaction but more than 30% being due to allospecific interactions). Allospecific neighbors belonged to the genera *Tilia*, *Fraxinus*, *Quercus* and *Acer*. The three neighborhood groups contained four Fagus100, five Fagus70-99 and seven Fagus<70 target trees. The 4–7 trees were treated as replicates in the analysis. Even though we ended up with a rather small number of suitable trees in each group, we preferred to apply these strict selection criteria to obtain beech trees with a well-defined neighborhood and to conduct the analysis with rather homogeneous data sets in terms of neighborhood structure, instead of including further target trees with somewhat different neighborhoods which would have increased the data heterogeneity. We accepted that the smallest sample size ($n = 4$) was realized in the group with exclusively intraspecific neighborhood (Fagus100) because these tree clusters were more homogeneous than the Fagus70-99 and Fagus<70 groups with a variable species identity of the neighbors, and thus, a more heterogeneous structure of the neighborhood.

In the direct neighborhood of the target trees, we recorded the species identity, dbh, height and relative position (i.e., distance and angle between neighbor and target tree) of those trees >7 cm dbh whose crowns had direct contact with the beech target tree. The 16 chosen tree groups consisted of 3–5 (in a few cases, up to 8) trees surrounding the beech target tree and covered stand areas of about 100–600 m^2 in size. In winter 2006/2007, dbh, tree height and species composition were recorded in the tree clusters with the aim to characterize the neighborhood of the beech target trees qualitatively and quantitatively. We also quantified the crown dimensions by 8-point crown projections using a sighting tube equipped with a 45° mirror and cross-hairs to ensure the proper view of canopy elements from the ground (Johansson 1985). For approximating the projected crown area by a polygon, eight points along the edge line of the crown were selected in a manner that approximated the estimated crown area best. In summer 2007, hemispheric photos were taken with a digital camera equipped with a fisheye lens, thus providing information on canopy dimensions, gap fraction and canopy openness in the neighborhood of the central beech tree. To calculate canopy openness, we used the software Gap Light Analyzer 2.0 (Simon Fraser University, British Columbia, Canada; Institute of Ecosystem Studies, New York, USA) and restricted the canopy perspective to an opening angle of 30° from the zenith which is in agreement with the protocol for analyzing tree competition in forests applied by Pretzsch (1995). We calculated the coefficient of variation (CV) of tree height in the tree clusters in order to provide a measure of canopy heterogeneity. To estimate the intensity of competition in the tree clusters, we calculated CI after Hegyi (1974) for all those trees in the neighborhood of the target beech tree that were present with a part of their crown in the "influence sphere" of this tree, i.e., a cone with an angle of 60° turned upside down with the apex being positioned at 60% of the target tree's height. The more trees being present in this cone and the smaller the distance to the target tree, the higher is the competition index:

$$\mathrm{CI}_i = \sum_{j=1}^{n} \frac{d_j/d_i}{\mathrm{Dist}_{ij}} \qquad (1)$$

where d_i is the diameter at breast height of the target tree i (cm); d_j is the diameter at breast height of the competitor j (cm); and Dist_{ij} is the distance between target tree and competitor (m). Trees with a competition index larger than 0.9 were classified as trees exposed to higher competition intensity ($n = 8$), target trees with a CI smaller than 0.9 as trees with lower competition intensity ($n = 8$).

We further expressed the tree diversity of the clusters with the Shannon diversity index H' (Magurran 2004):

$$H' = -\sum_{i-1}^{S} p_i \,\mathrm{In}\, p_i \quad \text{with}\, p_i = \frac{n_i}{N} \qquad (2)$$

where S is the species richness of the target tree's neighborhood and p_i is the fraction of trees belonging to species i.

Table 1 Characterization of *Fagus* target trees and their immediate vicinity in the three neighborhood categories from purely intraspecific neighborhoods (Fagus100) to neighborhoods with a contribution of *Fagus* of less than 70% (Fagus<70)

Target tree	Tree height (m)	Tree dbh (cm)	Tree age (year)[a]	Crown area of target tree (m^2)	Rel. contribution of *Fagus* to competition index CI (%)	Clay content (%)	Gap fraction (%)	Mean neighbor height (m)	Variability of tree height in the group (CV in %)	Number of neighbors	Competition index after Hegyi (CI)[b]	Shannon index (H')	Mean neighbor age (year)	Range of neighbor ages (year)	Mean neighbor dbh (cm)	Neighbor species
Fagus100$_1$	36	60	148	87.39	1.00	13.6	24.45	36	20.32	3	0.58	0	150.5	8	55	*Fagus*
Fagus100$_2$	36	58	144	60.29	1.00	14.7	15.76	34	5.39	5	0.59	0	132.5	53	47	*Fagus*
Fagus100$_3$	30	44	127	40.68	1.00	25.2	16.87	30	32.07	3	0.74	0	104.5	26	58	*Fagus*
Fagus100$_4$	33	49	116	50.33	1.00	25.2	19.21	30	6.29	4	0.97	0	82	63	46	*Fagus*
Fagus100	**34**	**53**	**134**	**59.67**	**1.00**	**19.7**	**19.07**	**32**	**16.02**	**4**	**0.72**	**0**	**117**	**38**	**52**	
Fagus70-99$_1$	30	43	108	91.23	0.87	20.3	17.39	29	6.59	5	1.12	0.50	72.5	26	44	*Fagus*, *Tilia*
Fagus70-99$_2$	36	45	97	56.02	0.82	17.5	20.35	35	11.86	8	1.65	0.38	94	13	39	*Fagus*, *Fraxinus*
Fagus70-99$_3$	33	46	85	54.13	0.90	17.5	21.72	32	24.69	8	1.72	0.38	85.5	5	41	*Fagus*, *Fraxinus*
Fagus70-99$_4$	28	50	143	65.64	0.87	32.3	21.17	26	10.67	6	1.00	0.45	129	92	41	*Fagus*, *Acer*
Fagus70-99$_5$	31	48	97	37.69	0.81	31.3	17.54	28	22.32	5	0.65	0.50	100	85	35	*Fagus*, *Fraxinus*
Fagus70-99	**31**	**46**	**106**	**60.94**	**0.86**	**23.8**	**19.63**	**30**	**15.23**	**6**	**1.23**	**0.44**	**96**	**44**	**40**	
p_{Fagus100}	0.674	0.591	0.103	0.704	<0.001	0.613	0.554	0.488	0.698	0.008	0.103	<0.001	0.586	0.750	<0.001	
Fagus<70$_1$	31	42	119	88.52	0.52	13.6	17.62	32	13.73	8	1.30	0.90	143	30	52	*Fagus*, *Quercus*, *Tilia*
Fagus<70$_2$	35	55	156	163.71	0.13	13.6	20.76	34	7.83	5	0.80	0.95	152.5	22	53	*Fagus*, *Quercus*, *Acer*
Fagus<70$_3$	30	58	101	106.52	0.15	22.2	23.32	30	10.93	6	0.74	0.45	75.5	39	32	*Fagus*, *Tilia*
Fagus<70$_4$	34	49	94	41.03	0.49	17.5	14.07	33	28.80	8	1.27	0.66	97	97	44	*Fagus*, *Fraxinus*
Fagus<70$_5$	37	60	138	33.02	0.58	14.7	17.40	32	27.81	5	0.77	0.50	138	24	42	*Fagus*, *Quercus*
Fagus<70$_6$	26	44	146	60.93	0.16	32.3	15.12	26	19.65	5	0.73	0.50	69	106	34	*Fagus*, *Tilia*
Fagus<70$_7$	34	50	92	58.91	0.70	25.2	21.34	33	12.22	6	0.94	0.87	92	106	50	*Fagus*, *Quercus*, *Tilia*
Fagus<70	**32**	**51**	**121**	**78.95**	**0.39**	**19.9**	**18.52**	**31**	**17.28**	**6**	**0.93**	**0.69**	**110**	**61**	**44**	
p_{Fagus100}	0.960	0.961	0.828	0.579	<0.001	0.891	0.945	0.938	0.782	0.006	0.435	<0.001	0.940	0.558	0.286	

Two-sided p values of neighborhood comparisons (Hothorn et al. 2008, Dunnett contrasts) with the Fagus100 category are indicated as p_{Fagus100}. Mean values for each group are printed bold

[a] Trees older than 118 years are considered as 'older trees', those <118 years as 'younger trees'

[b] a CI < 0.9 is considered as 'lower competition intensity', CI > 0.9 as 'higher competition intensity'

The fraction p_i is calculated from the ratio between the number of stems n_i of species i and the total number of neighbors N.

Sample preparation and analysis

In summer 2006, we cored all 16 *Fagus* target trees at 1.3 m height (5 mm corer) on that side of the trunk that showed lowest influence of wood tension or compression. Since we had to meet the conservation regulations of the Hainich National Park, each tree was cored only once. After recutting the surface of the cores with a razor blade, we used titanium dioxide to enhance the visibility of the tree rings before ring analysis. Annual tree-ring width was measured to the nearest 0.01 mm using a LINTAB-5 dendrochronological measuring table (Rinn Tech, Heidelberg, Germany) and TSAP-Software (TSAP-Win Version 0.59 for Microsoft Windows, Rinn Tech, Heidelberg, Germany). In a pre-analysis, we searched for unrecognizable or questionable rings in the cores in order to reconsider them during cross-dating. As quality criteria, we considered the t value (Baillie and Pilcher 1973; Hollstein 1980), the co-linearity of increment (Gleichläufigkeit, Eckstein and Bauch 1969), and the cross-dating index (Grissino-Mayer and Kaennel Dobbertin 2003). Cross-dating of a chronology is accepted as being reliable, if it reaches a minimum t value of 3.5 (Baillie and Pilcher 1973; Hollstein 1980), a minimum co-linearity of 70% for a 50-year overlap (Eckstein and Bauch 1969; Frech 2006), and a minimum cross-dating-index (CDI) >20 (Müller 2007). The tree age at coring height (1.3 m) was calculated as follows: we took pictures from the core centers and determined the distance between the innermost visible tree ring and the point of intersection of the medullary rays. The distance was then divided by the mean ring width of the ten innermost rings to estimate the number of missed tree rings, which were then added to the number of measured tree rings (Schmidt et al. 2009). After the dendrochronological analysis, the samples were dried at 65°C and cut ring by ring for the period 1926–2005. Both the latewood and earlywood of a ring were included in the samples in order to reduce the variation caused by anatomical properties (Smith and Shortle 1996). The wood of a tree ring was cut into small pieces with a razor blade and 1 mg of a ring was weighed out in tin capsules for determination of the δ^{13}C signature. We used samples of 0.4–1 mg of acetanilide as internal standard. The analyses were carried out with a Delta V Advantage isotope ratio mass spectrometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA), which was combined with a Conflo III interface (Thermo Fisher Scientific) and a NA 1500 C/N Elementar Analyzer (Carlo Erba Strumentazione, Milan, Italy). By using the internal standard acetanilide, the ^{13}C/^{12}C isotope ratios were related to the Peedee belemnite limestone standard using the equation $\delta^{13}\mathrm{C}\ (‰) = ([R_{\mathrm{sample}}/R_{\mathrm{standard}}] - 1) \times 1{,}000$, with $R = {}^{13}\mathrm{C}/{}^{12}\mathrm{C}$. Partial stomatal closure may be indicated by an enrichment of ^{13}C, i.e., higher (less negative) values of δ^{13}C.

Statistical methods

Individual ring-width (w) series were standardized following mainly Andreu et al. (2008). After a Box–Cox transformation of the raw width values (in mm) to stabilize the variance, we detrended the series by fitting a linear regression line. Subsequently, standard chronologies were built with robust means. Furthermore, we removed autocorrelation from the single detrended ring series by using an autoregressive model (w_{ac}). δ^{13}C values were first corrected for long-term changes in the atmospheric $^{13}\mathrm{CO}_2$ signal by addition of the difference between modeled atmospheric δ^{13}C and a standard value ($\delta^{13}\mathrm{C}_{\mathrm{cor}}$). As standard we used the “pre-industrial” atmospheric δ^{13}C of −6.4‰ as suggested by McCarroll and Loader (2004). Subsequently, we applied an autoregressive model in order to remove autocorrelation in the $\delta^{13}\mathrm{C}_{\mathrm{cor}}$ time series as was done in the ring-width series (w_{ac}). In the following, the $\delta^{13}\mathrm{C}_{\mathrm{cor}}$ time series corrected for autocorrelation will be referred to as $\delta^{13}\mathrm{C}_{\mathrm{ac}}$.

Descriptive statistics on ring-width series were calculated with the package dplR, yielding mean sensitivity according to Eq. 3 ($\mathrm{MS_I}$) and Eq. 4 ($\mathrm{MS_{II}}$) after Biondi and Qeadan (2008). $\mathrm{MS_{II}}$ takes present trends into account and gives with its absolute value, in a similar way as $\mathrm{MS_I}$, a measure for temporal dissimilarity:

$$\mathrm{MS_I} = \frac{2}{n-1} \sum_{t=2}^{n} \frac{|w_t - w_{t-1}|}{w_t + w_{t-1}} \tag{3}$$

$$\mathrm{MS_{II}} = \frac{n}{n-1} \frac{\sum_{t=2}^{n} w_t - w_{t-1}}{\sum_{t=1}^{n} w_t} \tag{4}$$

with w = width of the tree ring, n = length of the tree-ring series, $t = 1, 2, \ldots, n$ = years in the tree-ring series.

Tests for differences in absolute stem increment and δ^{13}C signatures among beech trees of different neighborhood categories were conducted with a non-parametric multiple comparison procedure after Hothorn et al. (2008), implemented for Dunnett contrasts or, for two groups, with a two-sample test for the non-parametric Behrens–Fisher problem (Brunner and Munzel 2000). Differences between individual tree-ring series were tested for significance with Friedman’s non-parametric test.

For these statistical analyses, we used the software R (version 2.10.1, R Development Core Team, 2009) with the following packages and scripts: sarima, dplR, nparcomp and zoo.

Climate (monthly precipitation and temperature) data were derived from the data set CRU TS 2.1 (Mitchell and Jones 2005) for the coordinates 51.25°N and 10.25°E. The sum of monthly totals of precipitation and averages of temperature for the period between January and December were used to build chronologies of whole-year climate data (hereafter referred to as annual values). We calculated a climate index as the quotient of the precipitation total and the mean temperature of the months April–September (Frech 2006). Bootstrapped Pearson correlations (number of bootstrapped iterations = 1,000) of monthly precipitation and temperature were calculated with the program DendroClim2002 (Biondi and Waikul 2004) for the year of tree-ring formation (current year) and the year prior to ring formation (preceding year). In order to avoid the problem of multi-colinearity, which would occur in data sets on meteorological parameters, we also calculated response functions (Fritts 1976). Correlation coefficients and response function coefficients are only indicated if they were significant at $p < 0.05$.

Results

Beech stem increment and δ^{13}C signatures as dependent on climatic parameters

For our study site, neither annual values (precipitation, temperature and climate index) nor values for the growing season (April–September) revealed significant linear trends with the year as independent variable over the 80-year study period. However, we detected a significant linear increase of temperature in the growing season for the period after 1976 ($R^2_{\text{adj}} = 0.48, p < 0.001, y = 0.087x - 160.183$; x = Gregorian year). In contrast, precipitation and climate index showed no trend for the period 1976–2005.

We detected both negative (July–September, bootstrapped correlation coefficients r between −0.42 and −0.19) and positive (June and October, r values between 0.21 and 0.40) correlations between ring-width chronologies (w_{ac}) and monthly mean temperatures during the growing season of the year prior to the reference year (Fig. 1c). Temperature values of the current year showed exclusively a negative correlation with ring width (June and July, r values between −0.33 and −0.21). Response function coefficients for temperatures of the current year were only significant for June–July and were always negative. In contrast to the correlation analysis, the more rigorous response function coefficients were never significant for a given time period for the sampled trees in all three neighborhood groups (Fagus100, Fagus70-99 and Fagus<70).

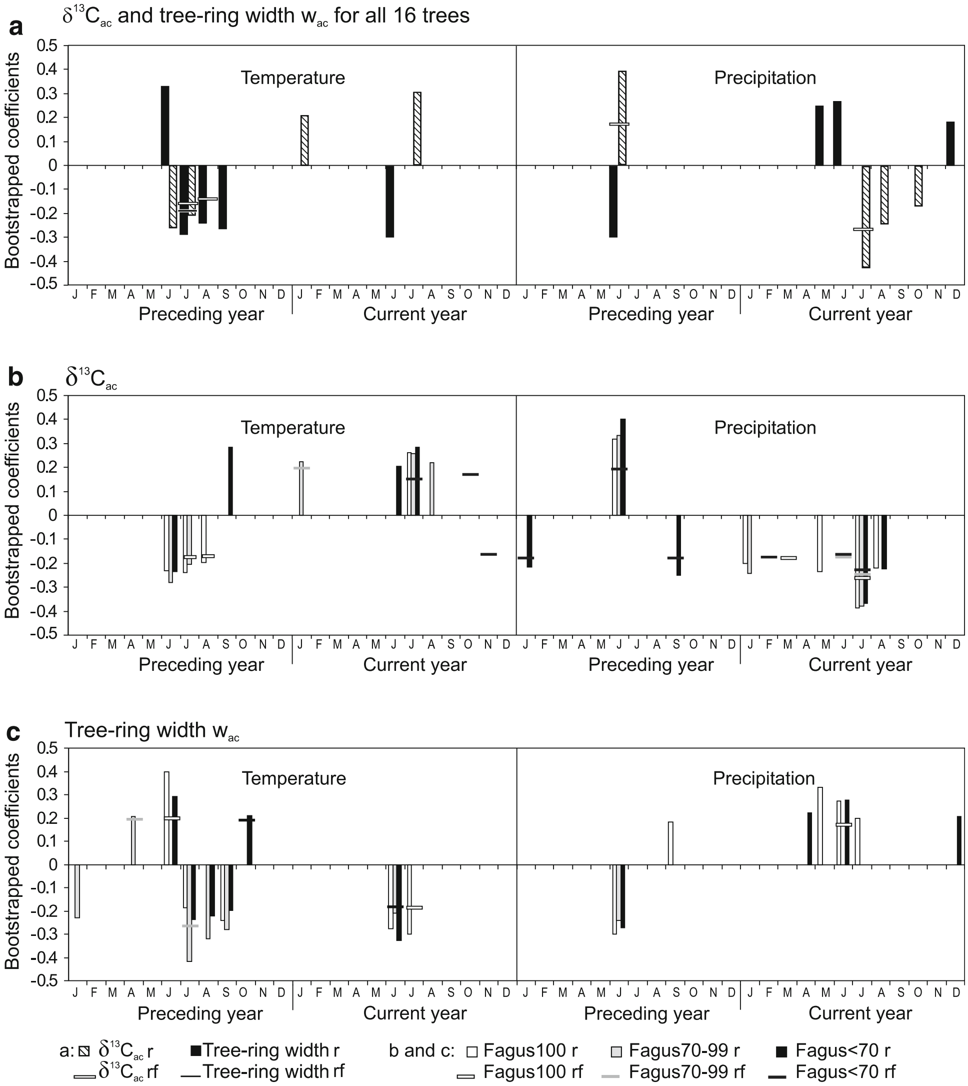
Precipitation in June of the preceding year and ring width (w_{ac}) were negatively correlated (correlation coefficients between −0.30 and −0.24), while precipitation in the growing season of the current year was positively related to w_{ac} (r values ranging from 0.20 to 0.33). The response function coefficient was only significant for the conspecific group Fagus100 in June ($r = 0.17$). Precipitation was a relevant factor for all neighborhoods only in June of the preceding year.

Monthly temperature values in the growing season (June–August) of the year prior to ring formation showed a significant negative correlation with the $\delta^{13}\text{C}_{\text{ac}}$ chronologies (r values between −0.28 and −0.20), while growing season temperature (June–August) of the current year was positively related to the $\delta^{13}\text{C}_{\text{ac}}$ signature (r 0.21–0.29). All three neighborhood groups were similar in showing a relationship of $\delta^{13}\text{C}_{\text{ac}}$ to temperature in July of the current year, while the response function coefficients were not uniformly significant in all three neighborhood groups in a given month. Only July precipitation of the current year was negatively correlated with the $\delta^{13}\text{C}_{\text{ac}}$ signature from all neighborhood groups (r −0.39 to −0.37) and the response function coefficients were significant and negative for all three neighborhoods as well.

Relationship between δ^{13}C signals and annual radial increment

Whereas the $\delta^{13}\text{C}_{\text{cor}}$ mean curve of all 16 sampled trees showed a continuous increase until the mid of the 1970s with a steep decline after about 1990, the increment curve generally declined over the 80 investigated years (Fig. 2). If we assume that increment and $\delta^{13}\text{C}_{\text{cor}}$ signals should be negatively correlated, only 6 of the 16 sampled trees showed the assumed relationship for the period 1926–2005 with correlation coefficients between −0.42 and −0.24 (Table 2). Trees from all neighborhood groups equally showed a negative relationship between ring-width chronologies (w_{ac}) and $\delta^{13}\text{C}_{\text{ac}}$ series. Neither tree height, variability in tree height in the investigated tree cluster, or crown area, nor CI showed significant effects on the direction of the correlation between w_{ac} and $\delta^{13}\text{C}_{\text{ac}}$ chronology (data not shown). In contrast, trees, where $\delta^{13}\text{C}_{\text{ac}}$ and annual increment were negatively correlated, were significantly younger ($p = 0.037$, two-sided) than trees not showing this negative relationship (Table 2, trees with a significant negative relationship in any of the analyzed periods versus trees with no significant or a positive relationship). Moreover, younger trees generally revealed a closer and older trees a less tight $\delta^{13}\text{C}_{\text{ac}}$–$w_{\text{ac}}$ relation. Further, the $\delta^{13}\text{C}_{\text{ac}}$-ring width relationship was different between the 1926–1975 and 1975–2005 periods for most of

Fig. 1 Bootstrapped correlations (*bars*, *r*) of $\delta^{13}C_{ac}$ and radial increment data (w_{ac}) with monthly precipitation and temperature values of the preceding and current year. In addition, the coefficients of response functions are given as *horizontal lines* (*rf*). Only significant correlations and response functions are shown ($p < 0.05$)



the sampled trees with only four trees showing a significant relationship between the two variables in the 1975–2005 period.

Beech stem increment and $\delta^{13}C$ signals influenced by competition intensity and neighborhood diversity

Comparison of w and $\delta^{13}C_{cor}$ in the two allospecific neighborhood categories (Fagus70-99 and Fagus<70) with the purely conspecific group (Fagus100) as control (Table 3) revealed no significant differences for the 80-year period from 1926 to 2005 (w, $p = 0.394$; $\delta^{13}C_{cor}$, $p = 0.138$; one-sided). Further, radial increment w and $\delta^{13}C_{cor}$ were not significantly different between the three categories in the study periods before and after 1975 (w: 1926–1975, $p = 0.408$; 1976–2005, $p = 0.170$; $\delta^{13}C_{cor}$: 1926–1975, $p = 0.113$; 1976–2005, $p = 0.478$), even

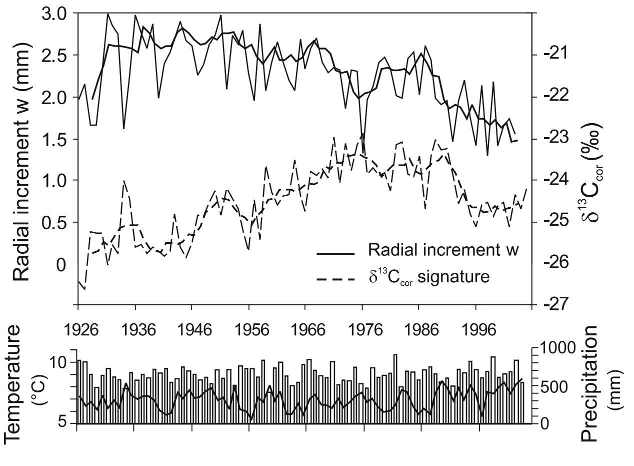


Fig. 2 Chronologies of $\delta^{13}C_{cor}$ and radial increment w for all 16 *Fagus* trees (smoothed with a 5-year running mean). In addition, annual precipitation totals (*bars*) and mean annual temperatures are given

Table 2 Pearson correlation coefficients (r) and p values for relationships between radial increment and $\delta^{13}C_{ac}$

	Tree age (year)	1926–2005		1926–1975		1976–2005	
		p	r	p	r	p	r
Fagus100$_1$	148	0.173	−0.16	0.117	−0.23	0.837	−0.04
Fagus100$_2$	144	0.545	0.07	0.955	−0.01	0.326	0.19
Fagus100$_3$	127	**0.006**	**−0.30**	**0.005**	**−0.39**	0.357	−0.17
Fagus100$_4$	116	**0.008**	**−0.30**	0.091	−0.25	**0.039**	**−0.38**
Fagus70-99$_1$	108	0.083	0.20	0.044	0.29	0.268	0.21
Fagus70-99$_2$	97	0.016	0.29	0.142	0.23	0.048	0.36
Fagus70-99$_3$	85	**0.037**	**−0.24**	**0.005**	**−0.40**	0.529	−0.12
Fagus70-99$_4$	143	0.962	−0.01	0.249	−0.17	0.278	0.20
Fagus70-99$_5$	97	**0.004**	**−0.32**	**<0.001**	**−0.51**	0.947	−0.01
Fagus<70$_1$	119	0.144	0.17	0.007	0.38	0.223	−0.23
Fagus<70$_2$	156	0.470	0.08	0.309	0.15	0.973	−0.01
Fagus<70$_3$	101	**<0.001**	**−0.42**	**0.007**	**−0.41**	**0.005**	**−0.49**
Fagus<70$_4$	94	0.202	−0.15	**0.028**	**−0.31**	0.624	0.09
Fagus<70$_5$	138	0.925	−0.01	0.259	−0.17	0.408	0.16
Fagus<70$_6$	146	0.798	0.03	0.066	0.27	**0.036**	**−0.38**
Fagus<70$_7$	92	**0.015**	**−0.27**	**0.003**	**−0.43**	0.685	−0.08

Tree age has been calculated as described in the text in cases the pith was not hit by coring. Negative correlations between radial increment and $\delta^{13}C_{ac}$ chronology are printed bold

Table 3 Descriptive statistics for the 1926–2005 chronologies of raw ring-width series (w) and $\delta^{13}C_{cor}$ tree-ring chronologies of *Fagus* trees in three different neighborhoods (only conspecific neighbors: Fagus100, few allospecific neighbors, many *Fagus* neighbors: Fagus70-99, many allospecific and also *Fagus* neighbors: Fagus<70)

	Fagus100	Fagus70-99	Fagus<70
Ring-width series			
Mean ring width (1/100 mm)[a]	233	243	236
Standard deviation	89	108	96
Mean sensitivity I (MS$_I$)	0.28	0.30	0.28
Mean sensitivity II (MS$_{II}$)	0.25	0.26	0.25
First order autocorrelation	0.61	0.64	0.63
$\delta^{13}C_{cor}$-chronology			
Mean $\delta^{13}C_{cor}$ (‰)[a]	−24.03	−24.66	−24.92
Standard deviation	1.20	1.33	1.26
First order autocorrelation	0.59	0.58	0.64

[a] Arithmetic mean

though a tendency for a difference in particular between the Fagus100 and the Fagus<70 group was visible (Figs. 3, 4).

When pooling the data of the purely conspecific group (Fagus100) with the Fagus70-99 category and comparing the distribution with that of the allospecific group (Fagus<70), a significantly lower $\delta^{13}C_{cor}$ value is found for the Fagus<70 than for the Fagus70-100 category in the study period from 1926 to 1975 ($p = 0.045$, Fig. 5). This difference was not significant for the period 1976–2005 ($p = 0.475$). The higher radial increment (w) in the Fagus<70 group in 1976–2005 was only significant on a significance level of 10% ($p = 0.076$), and there was no significant difference for the earlier period 1926–1975 ($p = 0.183$). Even though the differences in mean annual growth and $\delta^{13}C_{cor}$ signature between *Fagus* trees with contrasting neighborhood diversity were not significant for the period 1976–2005 (Figs. 3, 4, 5), the plotted mean curves of the ring-width chronologies (w) showed different levels of annual increment indicating a smaller increment since approximately 1976 for beech trees with a predominantly conspecific neighborhood (Fig. 4).

Analogous to comparisons between mainly conspecific neighborhoods and allospecific neighborhoods (Fig. 5), we grouped beech trees with regard to the competition intensity in the neighborhood according to Hegyi's index CI (Figs. 6, 7), irrespective of con- or allo-specific interactions, and investigated the mean $\delta^{13}C_{cor}$ values and mean radial increment for the two periods 1926–1975 and 1976–2005. Differences between $\delta^{13}C_{cor}$ values of the two competition intensity groups were significant for the period 1976–2005 ($p = 0.014$, one-sided) and existed as a tendency for the earlier period 1926–1975 as well ($p = 0.09$). Radial increment (w) in the period 1926–1975 tended to be higher in the beech trees being subject to a higher competition intensity, but this difference was not significant ($p = 0.176$; 1976–2005: $p = 0.284$).

Effect of age on temporal changes in radial increment and $\delta^{13}C$

Cambium age was negatively correlated with radial increment w ($r^2 = 0.67, p < 0.001, y = -1.62x + 376.61$) regardless of tree age and competition intensity in the neighborhood. The correlation of cambial age with the $\delta^{13}C_{cor}$ signature was significant and positive when the entire period (1926–2005) was considered ($r^2 = 0.43$, $p < 0.001$, $y = 0.007x - 25.18$).

Discussion

Correlation of climate parameters with tree ring $\delta^{13}C$ signatures and radial increment

Often, $\delta^{13}C_{cor}$ and ring-width data (w) reveal a negative correlation because wet conditions in summer lead to better growth (wider tree rings) and a stronger discrimination against ^{13}C (lower $\delta^{13}C_{cor}$ values) under the condition of higher leaf conductance. However, in our sample the two parameters frequently did not show this relationship. *Fagus* trees lacking a correlation between $\delta^{13}C$ and ring width

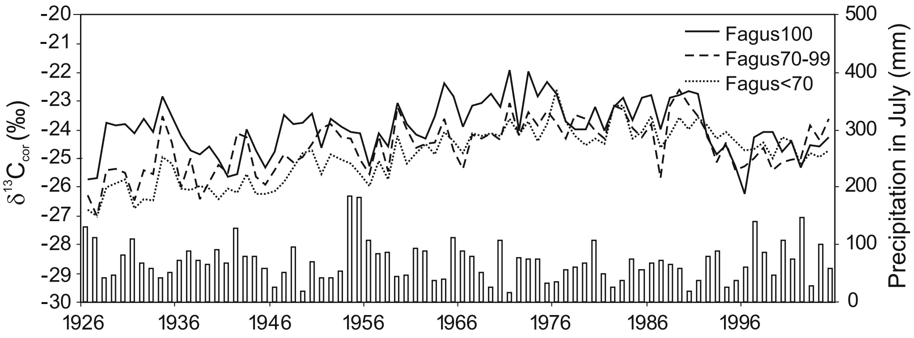


Fig. 3 $\delta^{13}C_{cor}$ chronologies of beech (period 1926–2005) corrected for changes in atmospheric $\delta^{13}C$ (*lines*) in three different neighborhood categories (only conspecific neighbors: Fagus100, few allospecific neighbor and many *Fagus* neighbors: Fagus70-99, many allospecific and also *Fagus* neighbors: Fagus<70) and corresponding precipitation in July (*bars*)

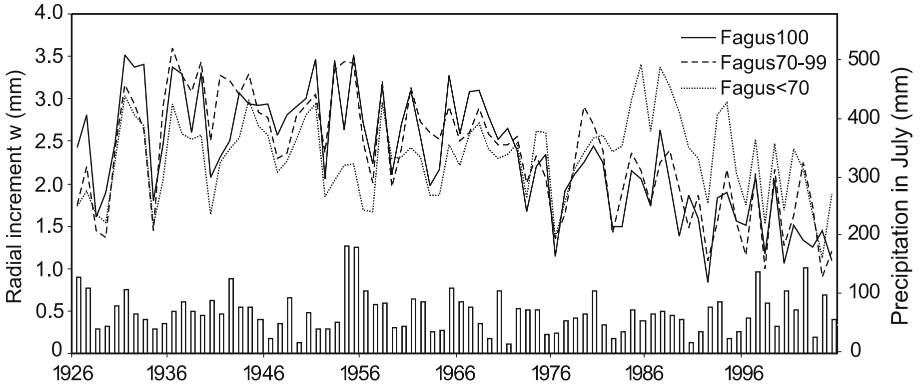


Fig. 4 Ring-width chronologies (*w*) in three different neighborhood categories (only conspecific neighbors: Fagus100, few allospecific neighbors, many *Fagus* neighbors: Fagus70-99, many allospecific and also *Fagus* neighbors: Fagus<70) and corresponding precipitation in July (*bars*)

tended to be older than those showing a significant negative correlation and were exposed to a relatively high competition intensity (CI, 1.12–1.65). One explanation of this mismatch is that ring width and the $\delta^{13}C$ signature of tree rings at least partly depend on different environmental factors. While both parameters were influenced by precipitation and temperature in our study, the months with a significant effect were different between the two signals (see Fig. 1). In addition, other factors than climate may also affect the $\delta^{13}C$ signature including stand thinning (McDowell et al. 2003; Skomarkova et al. 2006) and changes in atmospheric $\delta^{13}C$ (McCarroll and Loader 2004). Skomarkova et al. (2006) explain the partial mismatch between $\delta^{13}C$ signal, ring width and climate with the remobilization of carbohydrates stored in the earlier growing season. In their study, only the mid-season $\delta^{13}C$ value of wood tissue was related to the season's actual climate and associated climatic constraints on the assimilation rate. Beech wood isotope ratios matched modeled isotope ratios in the assimilates only in the mid-part of the growing season while wood growth was found to be disconnected from carbon assimilation during the early and late part of the year (Skomarkova et al. 2006). Contrasting carbon allocation patterns between younger and older trees may also be an explanation for our observation that a significant ring width-$\delta^{13}C_{ac}$ relation existed only in younger beeches. When trees reach maturity, additional C sinks (such as masting events) compete with wood growth, and existing C sinks (as the root system) may operate more independently from climate signals as the organs reach a larger size than early in life, thus decoupling $\delta^{13}C$ and w to a certain degree.

Only for the $\delta^{13}C_{ac}$ signal, all three neighborhood categories showed a uniform response to current year precipitation (in particular that of July). This influence was less clear for ring width (w_{ac}) which seems to support our second hypothesis that the isotope signal is more sensitive to climate variation than is ring width, at least with respect to precipitation. Similarly, Robertson et al. (1997) reported that significant components of a climate signal may be included in $\delta^{13}C$ values even if ring width is only poorly correlated with climate fluctuation. Other authors also found a closer dependence of the $\delta^{13}C$ signal on precipitation, compared to the precipitation dependence of ring width, in particular at drought-influenced sites, what matches with the findings in the Hainich stand (Saurer et al. 1995; Gagen et al. 2004; Andreu et al. 2008).

For temperature variation, the situation was different with a closer relation to ring width than to $\delta^{13}C_{ac}$ in annual rings. Particularly influential was the temperature of the

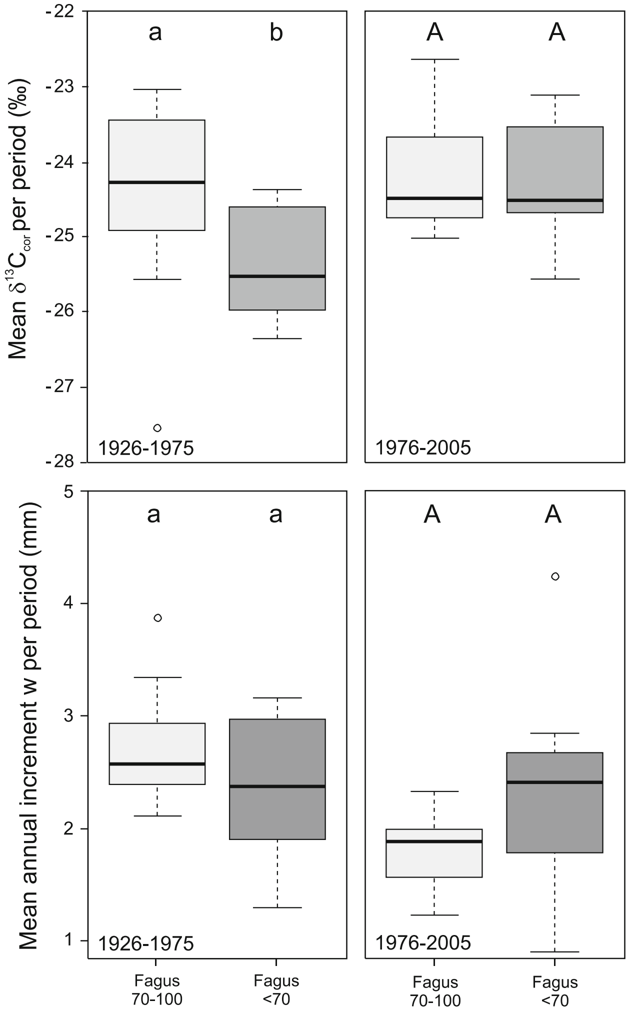


Fig. 5 Mean annual radial increment (*w*) and $\delta^{13}C_{cor}$ in annual rings of *Fagus* trees in the periods 1926–1975 and 1976–2005 in aggregated neighborhood categories (relative contribution of *Fagus* to competition index (CI) 70-100%: Fagus70-100, $n = 9$; relative contribution of *Fagus* to competition index CI $< 70\%$: Fagus<70, $n = 7$). *Different letters* indicate significant differences at $p < 0.05$ (one-sided, non-parametric two-sample test after Hothorn et al. 2008)

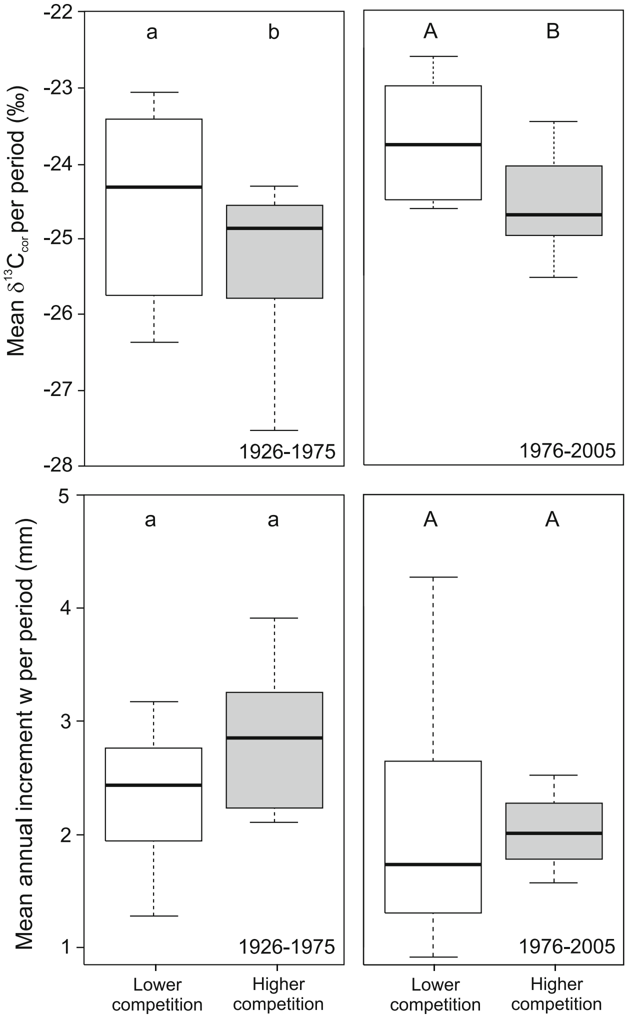


Fig. 6 Mean annual radial increment (*w*) and $\delta^{13}C_{cor}$ in annual rings of *Fagus* trees in the periods 1926–1975 and 1976–2005 in two categories of competition intensity. *Different letters* indicate significant differences at $p < 0.05$ (one-sided, non-parametric two-sample test after Hothorn et al. 2008)

previous year. For this variable, we found a larger number of significant correlation and response function coefficients than for other temperature parameters. The significance of the temperature of the previous year for current wood growth has been linked to carbohydrates stored in the previous year that support radial growth in the following year (Hoshino et al. 2008; Lo et al. 2010). Carbohydrate storage and associated carry-over effects are likely causes not only for the frequently observed correlation of $\delta^{13}C_{ac}$ signals with climate parameters of the previous year, but also for the autocorrelation in tree ring width (Skomarkova et al. 2006; Vaganov et al. 2009).

Since our study sites are characterized by pronounced summer droughts (Frech 2006; Guckland et al. 2009), the strong relationship between summer (July) precipitation and $\delta^{13}C_{ac}$ in tree rings makes it likely that the variation in $\delta^{13}C_{ac}$ values in the Hainich forest is a reflection of interannual variation in mean stomatal conductance in the growing season. Drought-induced stomatal closure has been found to significantly reduce the canopy carbon gain of temperate broad-leaved trees in drier summers even in the mostly humid climates of Central and Northern Europe (Gagen et al. 2004; Granier et al. 2007).

$\delta^{13}C$ in tree rings is dependent on competition intensity

Competition can change the intensity of mutual shading among neighboring crowns (Canham et al. 2004) which could influence the $\delta^{13}C$ signature of tree rings. Indeed, various studies revealed an increase of $\delta^{13}C$ in tree biomass with increasing irradiance (e.g., Hanba et al. 1997). The

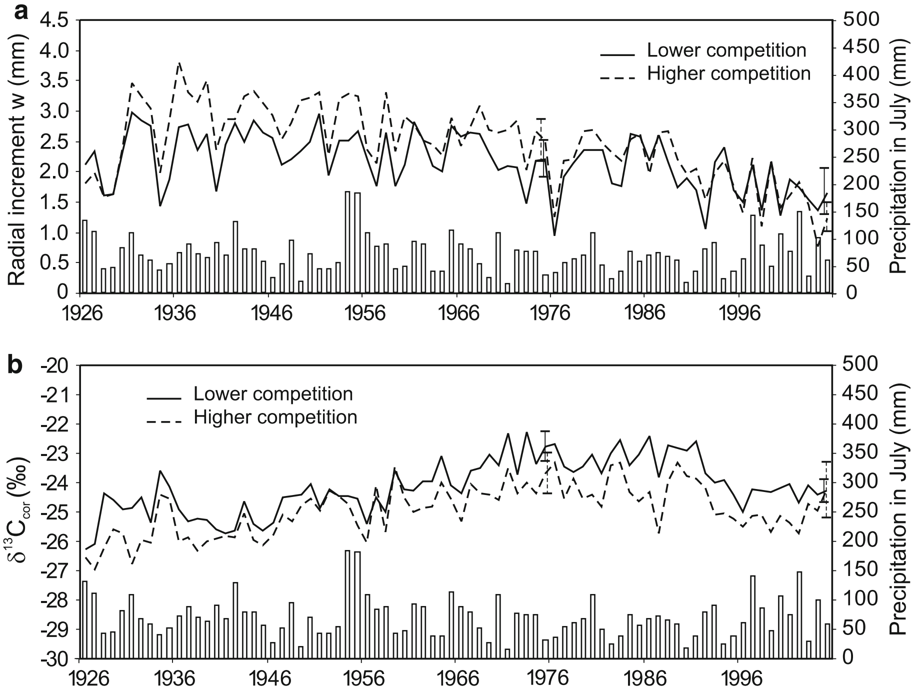


Fig. 7 Chronologies of radial increment *w* (**a**) and $\delta^{13}C$ (**b**) in two different classes of competition intensity in the neighborhood of the target trees ($n = 8$). 'Lower competition intensity' stands for Hegyi competition indices <0.9, 'higher competition' for CI values >0.9. Standard errors of the means associated with the period 1926–1975 and 1976–2005 are shown for the lower competition group (*solid lines*) and the higher competition group (*dotted lines*)

structure of tree canopies is influenced by the stem density in the neighborhood and may also depend on the functional traits of neighboring trees (Jack and Long 1991). Therefore, the neighborhood could leave traces in the $\delta^{13}C$ signature of tree rings. In our study, trees subject to more intense competition by neighboring trees (measured by Hegyi's CI) had lower $\delta^{13}C_{cor}$ values in their rings, on average by about 0.8‰ for CI values between 0.94 and 1.72 versus CI values between 0.58 and 0.90 (Fig. 7b, $p = 0.057$ for the comparison of intercepts). If competition for water were a key factor, one would expect the opposite, i.e., reduced discrimination of ^{13}C due to lowered stomatal conductance. In a water-limited oak forest, Gouveia and Freitas (2008) found stand density-dependent differences in leaf carbon isotope discrimination and were able to define an optimal stand density from comparisons of $\delta^{13}C$ signatures in stands differing in stem density. They argued that higher tree densities would lead to increased competition for water resources while lower densities were associated with lower water retention in the ecosystem, since trees in this forest type improve the water storage capacity, resulting in the lowest $\delta^{13}C$ values at moderate tree densities. Thus, a simple positive relationship between competition intensity and $\delta^{13}C$ is unlikely. Water limitation, as reported for the forests studied by Gouveia and Freitas (2008), is also characteristic of our study site, which is located close to the eastern drought-induced range limit of *Fagus* in Central Europe (Mölder et al. 2009). We hypothesize that mechanisms leading to reduced drought stress of beech such as self-shading of leaves and shading by other trees (West et al. 2001) may facilitate the existence of *Fagus* at this site. This effect may mask the expected positive effect of competition intensity on the $\delta^{13}C$ signature of beech leaf and wood tissue and may result in lowered stomatal limitation. However, it is important to mention that trees exposed to lower competition intensity were on average older than trees with a higher competition index ($p = 0.01$). Competition intensity and tree age were in fact negatively correlated in our data set, which may have influenced any relationship between CI and $\delta^{13}C$. Studies with a more complete control of influencing factors are needed to disentangle this relationship.

Another mechanism, which could contribute to the observed pattern in $\delta^{13}C$ among trees differing in their exposure to competition intensity, is that leaves within the canopy may assimilate CO_2 released from respiration of lower canopy strata. Respiration leads to discrimination of ^{13}C (see Berry et al. 1997), thus reducing the abundance of $^{13}CO_2$ in the air and resulting in more negative $\delta^{13}C$ values in the lower canopy where heterotrophic processes dominate. The lower and upper canopies of forests have been found to differ in atmospheric $\delta^{13}C$ by 1.7–5.5‰ (Sternberg et al. 1989; Knohl et al. 2005). Thus, in denser stands with higher CI, the closer packing of crown elements could lead to an intensified assimilation of ^{13}C-depleted CO_2. In spite of carry-over effects due to carbon storage, the signal is likely to be manifested in the corresponding tree rings.

Competition with conspecific versus competition with allospecific neighbor trees

In predominantly allospecific neighborhoods competition intensity appeared to be higher than in conspecific ones (Table 1, differences not significant). In order to separate diversity effects from competition intensity effects, we pooled all trees that were exposed to mainly intraspecific competition (Fagus70-100). This led to a harmonization of competition intensity in the neighborhood categories to be compared (average CI, Fagus 100 = 0.72; Fagus70-99 = 1.23; Fagus<70 = 0.93; Fagus70-100 = 1.00). Since competition intensity was not significantly different between the Fagus<70 and Fagus70-100 categories, the specific properties of the neighbors (tree identity) or tree diversity must have been influential and not competition intensity itself.

For the period 1926–1975, the δ^{13}C values of beeches from primarily conspecific neighborhoods were found to be higher than corresponding values of trees in the neighborhood of allospecific competitors. Since intraspecific competition for water between beech trees is likely to be an important factor, allospecific neighbors may facilitate better growth of beech indirectly through reduced water consumption if the neighbors use water more conservatively than beech (Köcher et al. 2009). In fact, xylem flux measurements in the stem and measurement of leaf conductance in the dominant tree species of the Hainich mixed forest revealed that beech coexists with species that generally use less water than *Fagus* when soil moisture content is moderate to high (Hölscher et al. 2005). A higher water availability in more diverse stands should be associated with higher stem increment rates of beech. This, however, was only observed as a tendency in the more recent period 1976–2005 but not in the 1926–1976 period. Moreover, the δ^{13}C values of the recent period do not show a significant effect of neighborhood diversity. Thus, another factor than neighborhood patterns must have influenced δ^{13}C additionally that was active only for the past 30 years.

Long-term trends in δ^{13}C and stem increment

A conspicuous result is the characteristic optimum curve of $\delta^{13}C_{cor}$ values since 1926. The 80-year $\delta^{13}C_{cor}$ record revealed a period of elevated values between 1965 and 1990, when the signature was about 1‰ higher than before and after this period. The ascending curve might be explained by the 'age effect' when $\delta^{13}C_{cor}$ increases in ageing trees with increasing irradiance due to crowns reaching higher canopy strata (Francey and Farquhar 1982; Saurer et al. 1997). Another cause underlying the curve pattern could be changes in atmospheric chemistry over the past decades. We speculate that elevated SO_2 concentrations in the atmosphere of Central Europe from the 1960s to the late 1980s may have resulted in partial stomatal closure of sensitive trees, thus decreasing ^{13}C discrimination during photosynthesis (Savard et al. 2004; McNulty and Swank 1995; Sakata et al. 2001). The drop in δ^{13}C from 1990 to 1995 coincides with a sharp decrease in SO_2 concentrations due to strict emission reduction measures in the European Community and especially in the former German Democratic Republic (Thüringer Landesanstalt für Umwelt und Geologie 2002) in that time. Another reason could be the development of denser canopies in the past two decades after selective cutting ceased. A denser canopy is typically linked to reduced δ^{13}C values due to lower radiation penetration (Francey and Farquhar 1982) and less stomatal limitation (Farquhar et al. 1989).

In a period when many Central European forests on poorly buffered soils suffered from acid rain, annual stem increment in the beeches of our stand showed a lasting reduction from about 1985 onwards, and $\delta^{13}C_{cor}$ decreased as well. For the Hainich forests on limestone, however, anthropogenic acidification is not a likely cause of this change in growth patterns. We rather suggest that forest management practices may have had a substantial influence on both radial growth patterns and the δ^{13}C signal. With the cessation of selective cutting in the 1990s (E. Kinne, pers. communication), competition between beech and the other species has most likely increased. Beech trees growing in a species-rich neighborhood (Fagus<70 group) had been favored in the past by an extensive selection cutting regime. Now, these trees face a more closed and darker stand which simultaneously reduces radial growth and leads to lower δ^{13}C values (see also Duquesnay et al. 1998). In turn, selective cutting in earlier decades may have increased soil moisture availability due to reduced stand water use (Sucoff and Hong 1974; McDowell et al. 2003) which might have caused reduced δ^{13}C signatures in the period before 1975.

Another reason for the simultaneous decrease in ring width and δ^{13}C since 1990 could have been elevated summer temperatures since the 1990s accompanied by an increasing number of masting events in beech (Schmidt 2006). Frequent masting depletes the carbohydrate resources and leads to reduced radial growth as does the more frequent occurrence of extreme summer heat waves as they happened in 2003 (Granier et al. 2007).

Finally, a possible explanation is also offered by the age effect with a decelerating height and diameter growth in maturing forests. Since competition intensity and tree age were negatively correlated in our data set, age could have confounded an assumed effect of CI on ring width and δ^{13}C.

We conclude that chronologies of width and δ^{13}C in annual rings of beech can be significantly influenced by the structure of the tree's neighborhood. However, this signal is typically weaker than the influence of climate variation, tree age and effects of forest management. Current neighborhood constellations are only a snapshot of the community structure, which change substantially over the lifetime of a tree. Nevertheless, for parts of the chronology we obtained evidence of lowered $\delta^{13}C$ signatures (significant) or elevated radial growth (non-significant tendency) in beeches growing in mainly allospecific neighborhoods as compared to trees in a predominantly conspecific neighborhood. This indicates, at least for certain periods, that beech grew better in a mixed than in a monospecific neighborhood in this broad-leaved forest. Our study is probably the first to investigate dendrochronological climate archives in their dependence on the simultaneous action of climate, tree age, neighborhood structure, and management effects in a species-rich mixed forest. Further studies in other mixed forest types are needed to substantiate the effects of neighborhood identity and diversity on tree growth using larger sample sizes and by proving the effect to be independent from species and forest management. We suggest that the synchronous analysis of ring width and $\delta^{13}C$ chronologies for target trees with contrasting neighborhoods may be a promising tool for improving our understanding of the mechanisms of negative and positive interactions between trees in mixed stands.

Acknowledgments We would like to thank the two reviewers for their valuable comments on the first versions of the manuscript. We are grateful to Philippe Marchand for taking hemispheric photos, Laura Rose for support in cross-dating tree-ring series, Erika Müller and Gabriele Krisinger for their help in sample preparation and various helpers for stem coring. We thank Astrid Rodriguez for language correction. The study was funded by the German Research Foundation (DFG) within the Research Training Group 1086.

References

Andreu L, Planells O, Gutiérrez E, Helle G, Schleser GH (2008) Climatic significance of tree-ring width and $\delta^{13}C$ in a Spanish pine forest network. Tellus B 60:771–781

Archaux F, Wolters V (2006) Impact of summer drought on forest biodiversity: what do we know? Ann Forest Sci 63:645–652

Baillie MGL, Pilcher JR (1973) A simple cross-dating program for tree-ring research. Tree-ring Bull 33:7–14

Berry SC, Varney GT, Flanagan LB (1997) Leaf $\delta^{13}C$ in *Pinus resinosa* trees and understory plants: variation associated with light and CO_2 gradients. Oecologia 109:499–506

Biondi F, Qeadan F (2008) Inequality in paleorecords. Ecology 89:1056–1067

Biondi F, Waikul K (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. Comput Geosci 30:303–311

Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann Forest Sci 63:625–644

Brunner E, Munzel U (2000) The nonparametric Behrens–Fisher problem: asymptotic theory and a small-sample approximation. Biom J 42:17–25

Buchmann N, Kao W, Ehleringer J (1997) Influence of stand structure on carbon-13 of vegetation, soils, and canopy air within deciduous and evergreen forests in Utah, United States. Oecologia 110:109–119

Canham CD, LePage PT, Coates KD (2004) A neighborhood analysis of canopy tree competition: effects of shading versus crowding. Can J For Res 34:778–787

Canham CD, Papaik MJ, Uriarte M, McWilliams WH, Jenkins JC, Twery MJ (2006) Neighborhood analyses of canopy tree competition along environmental gradients in New England forests. Ecol Appl 16:540–554

DeClerck FAJ, Barbour MG, Sawyer JO (2006) Species richness and stand stability in conifer forests of the Sierra Nevada. Ecology 87:2787–2799

Duquesnay A, Bréda N, Stievenard M, Dupouey JL (1998) Changes of tree-ring $\delta^{13}C$ and water-use efficiency of beech (*Fagus sylvatica* L.) in north-eastern France during the past century. Plant Cell Environ 21:565–572

Eckstein D, Bauch J (1969) Beitrag zur Rationalisierung eines dendrochronologischen Verfahrens und zur Analyse seiner Aussagesicherheit. Forstwiss Cent bl 88:230–250

FAO/ISRIC/ISSS (1998) World reference base for soil resources. World Soil Resources Rep. 84. FAO, Rome

Farquhar GD, Ehleringer JR, Hubick KT (1989) Carbon isotope discrimination and photosynthesis. Annu Rev Plant Physiol Plant Mol Biol 40:503–537

Francey RJ, Farquhar GD (1982) An explanation of $^{13}C/^{12}C$ variations in tree rings. Nature 297:28–31

Frech A (2006) Walddynamik in Mischwäldern des Nationalparks Hainich - Untersuchung der Mechanismen und Prognose der Waldentwicklung. Ber Forsch zent Waldökosyst (Reihe A) 196:1–120

Fritts HC (1976) Tree rings and climate. Academic press, London

Gagen M, McCarroll D, Edouard J (2004) Latewood width, maximum density, and stable carbon isotope ratios of pine as climate indicators in a dry subalpine environment, French Alps. Arct Antarct Alp Res 36:166–171

Gouveia AC, Freitas H (2008) Intraspecific competition and water use efficiency in *Quercus suber*: evidence of an optimum tree density? Trees 22:521–530

Grams TEE, Kozovits AR, Häberle K, Matyssek R, Dawson TE (2007) Combining $\delta^{13}C$ and $\delta^{18}O$ analyses to unravel competition, CO_2 and O_3 effects on the physiological performance of different-aged trees. Plant Cell Environ 30:1023–1034

Granier A, Reichstein M, Bréda N, Janssens I, Falge E, Ciais P, Grünwald T, Aubinet M, Berbigier P, Bernhofer C, Buchmann N, Facini O, Grassi G, Heinesch B, Ilvesniemi H, Keronen P, Knohl A, Köstner B, Lagergren F, Lindroth A, Longdoz B, Loustau D, Mateus J, Montagnani L, Nys C, Moors E, Papale D, Peiffer M, Pilegaard K, Pita G, Pumpanen J, Rambal S, Rebmann C, Rodrigues A, Seufert G, Tenhunen J, Vesala T, Wang Q (2007) Evidence for soil water control on carbon and water dynamics in European forests during the extremely dry year: 2003. Agric For Meteorol 143:123–145

Grissino-Mayer HD, Kaennel Dobbertin M (2003) Dendrochronology species database. Names of tree and shrub species for which tree rings have been analysed in the published literature. Eidg. Forschungsanstalt WSL, Birmensdorf

Guckland A, Jacob M, Flessa H, Thomas FM, Leuschner C (2009) Acidity, nutrient stocks, and organic-matter content in soils of a temperate deciduous forest with different abundance of European beech (*Fagus sylvatica* L.). J Plant Nutr Soil Sci 172:500–511

Hanba YT, Mori S, Lei TT, Koike T, Wada E (1997) Variations in leaf δ^{13}C along a vertical profile of irradiance in a temperate Japanese forest. Oecologia 110:253–261

Hegyi F (1974) A simulation model for managing jack-pine stands. In: Fries J (ed) Growth models for tree and stand simulation. Royal College of Forestry, Stockholm, pp 74–90

Hollstein E (1980) Mitteleuropäische Eichenchronologie: Trierer dendrochronologische Forschungen zur Archäologie und Kunstgeschichte. von Zabern, Mainz

Hölscher D, Koch O, Korn S, Leuschner C (2005) Sap flux of five co-occurring tree species in a temperate broad-leaved forest during seasonal soil drought. Trees 19:628–637

Hoshino Y, Yonenobu H, Yasue K, Nobori Y, Mitsutani T (2008) On the radial-growth variations of Japanese beech (*Fagus crenata*) on the northernmost part of Honshu Island, Japan. J Wood Sci 54:183–188

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biom J 50:346–363

Jack SB, Long JN (1991) Analysis of stand density effects on canopy structure: a conceptual approach. Trees 5:44–49

Jactel H, Brockerhoff E, Duelli P (2005) A test of the biodiversity-stability theory: meta-analysis of tree species diversity effects on insect pest infestations and re-examination of responsible factors. In: Scherer-Lorenzen M, Körner C, Schulze E (eds) Forest diversity and function - temperate and boreal systems, Ecological studies, Springer, Berlin, pp 235–262

Johansson T (1985) Estimating canopy density by the vertical tube method. For Ecol Manag 11:139–144

Kelty MJ (2006) The role of species mixtures in plantation forestry. For Ecol Manag 233:195–204

Knohl A, Werner RA, Brand WA, Buchmann N (2005) Short-term variations in δ^{13}C of ecosystem respiration reveals link between assimilation and respiration in a deciduous forest. Oecologia 142:70–82

Köcher P, Gebauer T, Horna V, Leuschner C (2009) Leaf water status and stem xylem flux in relation to soil drought in five temperate broad-leaved tree species with contrasting water use strategies. Ann For Sci 66:101

Larsen J (1995) Ecological stability of forests and sustainable silviculture. For Ecol Manag 73:85–96

Leuschner C, Jungkunst HF, Fleck S (2009) Functional role of forest diversity: pros and cons of synthetic stands and across-site comparisons in established forests. Basic Appl Ecol 10:1–9

Lo Y, Blanco JA, Seely B, Welham C, Kimmins J (2010) Relationships between climate and tree radial growth in interior British Columbia, Canada. For Ecol Manag 259:932–942

Loreau M, Naeem S, Inchausti P (2002) Biodiversity and ecosystem functioning: synthesis and perspectives. Oxford University Press, New York

Magurran AE (2004) Measuring biological diversity. Blackwell Science, Oxford

McCarroll D, Loader NJ (2004) Stable isotopes in tree rings. Quat Sci Rev 23:771–801

McDowell N, Brooks JR, Fitzgerald SA, Bond BJ (2003) Carbon isotope discrimination and growth response of old *Pinus ponderosa* trees to stand density reductions. Plant Cell Environ 26:631–644

McNulty SG, Swank WT (1995) Wood δ^{13}C as a measure of annual basal area growth and soil water stress in a *Pinus strobus* forest. Ecology 76:1581–1586

Medina E, Sternberg L, Cuevas E (1991) Vertical stratification of δ^{13}C values in closed natural and plantation forests in the Luquillo mountains, Puerto Rico. Oecologia 87:369–372

Mitchell TD, Jones PD (2005) An improved method of constructing a database of monthly climate observations and associated high-resolution grids. Int J Climatol 25:693–712

Mölder I (2010) Diversity and tree neighborhood effects on the growth dynamics of European beech and the stand seed bank in temperate broad-leaved forests of variable tree diversity. Dissertation, University of Göttingen

Mölder A, Bernhardt-Römermann M, Schmidt W (2008) Herb-layer diversity in deciduous forests: raised by tree richness or beaten by beech? For Ecol Manag 256:272–281

Mölder A, Bernhardt-Römermann M, Leuschner C, Schmidt W (2009) Zur Bedeutung der Winterlinde (*Tilia cordata* Mill.) in mittel- und nordwestdeutschen Eichen-Hainbuchen-Wäldern. Tuexenia 29:9–23

Müller A (2007) Jahrringanalytische Untersuchungen zum Informationsgehalt von Holzkohle-Rückständen der historischen Meilerköhlerei. Dissertation, University of Freiburg, Breisgau

Odum EP (1953) Fundamentals of ecology. Saunders, Philadelphia

Orwig DA, Abrams MD (1997) Variation in radial growth responses to drought among species, site, and canopy strata. Trees 11:474–484

Peterken GF, Mountford EP (1996) Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. Forestry 69:125–136

Piutti E, Cescatti A (1997) A quantitative analysis of the interactions between climatic response and intraspecific competition in European beech. Can J For Res 27:277–284

Pretzsch H (1995) Zum Einfluss der Baumverteilungsmusters auf den Bestandeszuwachs. Allg Forst Jagdztg 166:190–201

Pretzsch H (2005) Diversity and productivity in forests: evidence from long-term experimental plots. In: Scherer-Lorenzen M, Körner C, Schulze E (eds) Forest diversity and function - temperate and boreal systems, Ecological studies, Springer, Berlin, pp 41–64

Robertson I, Rolfe J, Switsur VR, Carter AHC, Hall MA, Barker AC, Waterhouse JS (1997) Signal strength and climate relationships in ^{13}C/^{12}C ratios of tree ring cellulose from oak in Southwest Finland. J Geophys Res 102:19507–19516

Sakata M, Suzuki K, Koshiji T (2001) Variations of wood δ^{13}C for the past 50 years in declining Siebold's beech (*Fagus crenata*) forests. Environ Exp Bot 45:33–41

Saurer M, Siegenthaler U, Schweingruber F (1995) The climate–carbon isotope relationship in tree rings and the significance of site conditions. Tellus B 47:320–330

Saurer M, Borella S, Schweingruber F, Siegwolf R (1997) Stable carbon isotopes in tree rings of beech: climatic versus site-related influences. Trees 11:291–297

Saurer M, Cherubini P, Reynolds-Henne CE, Treydte KS, Anderson WT, Siegwolf RTW (2008) An investigation of the common signal in tree ring stable isotope chronologies at temperate sites. J Geophys Res 113:G04035

Savard MM, Begin C, Parent M, Smirnoff A, Marion J (2004) Effects of smelter sulfur dioxide emissions: a spatiotemporal perspective using carbon isotopes in tree rings. J Environ Qual 33:13–26

Schmidt W (2006) Temporal variation in beech masting (*Fagus sylvatica* L.) in a limestone beech forest (1981–2004). Allg Forst Jagdztg 177:9–19

Schmidt I, Leuschner C, Mölder A, Schmidt W (2009) Structure and composition of the seed bank in monospecific and tree species-rich temperate broad-leaved forests. For Ecol Manag 257:695–702

Skomarkova M, Vaganov E, Mund M, Knohl A, Linke P, Boerner A, Schulze E-D (2006) Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. Trees 20:571–586

Smith KT, Shortle WC (1996) Tree biology and dendrochemistry. In: Dean JS, Meko DM, Swetnam TW (eds) Tree rings, environment and humanity. Proceedings of an international conference. Radiocarbon, Tucson, AZ, pp 629–635

Sternberg LDSL, Mulkey SS, Wright SJ (1989) Ecological interpretation of leaf carbon isotope ratios: influence of respired carbon dioxide. Ecology 70:1317–1324

Sucoff E, Hong SG (1974) Effects of thinning on needle water potential in red pine. For Sci 20:25–29

Thüringer Landesanstalt für Umwelt und Geologie (ed) (2002) Lufthygienischer Jahresbericht 2000. Thüringer Landesanstalt für Umwelt und Geologie, Jena

Vaganov EA, Schulze E, Skomarkova MV, Knohl A, Brand WA, Roscher C (2009) Intra-annual variability of anatomical structure and δ^{13}C values within tree rings of spruce and pine in alpine, temperate and boreal Europe. Oecologia 161:729–745

West AG, Midgley JJ, Bond WJ (2001) The evaluation of δ^{13}C isotopes of trees to determine past regeneration environments. For Ecol Manag 147:139–149

Wulf M (2003) Preference of plant species for woodlands with differing habitat continuities. Flora 198:444–460

Yoshida T, Kamitani T (2000) Interspecific competition among three canopy-tree species in a mixed-species even-aged forest of central Japan. For Ecol Manag 137:221–230