

# Long-Term Trends in Tree-Ring Width and Isotope Signatures ( $\delta^{13}\text{C}$ , $\delta^{15}\text{N}$ ) of *Fagus sylvatica* L. on Soils with Contrasting Water Supply

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## ABSTRACT

We investigated long-term responses (since 1850) of *Fagus sylvatica* (Luxembourg; central Europe) to shifts in temperature, precipitation, and nitrogen deposition by analyzing diameter at breast height (DBH) increment, basal area increment (BAI), and tree-ring stable isotopes ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ). We compared stands on soils with contrasting water supply (Regosols and Cambisols with an available water capacity of ca. 40 and 170 mm, respectively) and of two different age classes (ca. 60 vs. 200 years). All stands showed a peak in DBH increment in the decade 1978–1987, but a decline in increment

growth in subsequent decades. In addition, BAI declined in mature stands in the last two decades. Decreasing increment rates were attributable to an increasing drought limitation of stands, mainly induced by increasing temperatures in the last two decades. Contrary to our expectations, stands on Cambisols showed a similar susceptibility to shifts in temperature and precipitation as stands on Regosols, suggesting a strong adaptation of the respective ecotypes grown at dryer sites. This result was in line with long-term trends for tree-ring  $\delta^{13}\text{C}$  signatures, which did not differ significantly between stands on Cambisols and Regosols. Climate impacts on tree-ring  $\delta^{15}\text{N}$  signatures were low. High spring precipitation and temperatures caused increasing and decreasing  $\delta^{15}\text{N}$  values, respectively, but only in mature stands on Cambisols. Stands on Regosols tended to have lower  $\delta^{15}\text{N}$  values than stands on Cambisols. Decreasing  $\delta^{15}\text{N}$  values in recent decades suggest an increasing impact of allochthonous N loads with isotopically lighter N.

**Key words:** basal area increment; climate change; dendrochemistry; dendroecology; drought limitation; Luxembourg; nitrogen deposition.

Received 23 March 2012; accepted 28 May 2013;  
published online 12 July 2013

**Author Contributions:** WH, TN, and GvO conceived of the study and study design, performed parts of the research, analyzed data, and wrote the paper. UF, BN, and LP contributed new methods and models, analyzed data, and contributed to writing of the paper. All other authors performed parts of the research, contributed to data analyses, and to writing of the paper.

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## INTRODUCTION

Climate change and atmospheric nitrogen (N) deposition are main drivers of biodiversity loss and impact ecosystem functioning on regional and global scales (Iverson and Prasad 2001; Nordin and others 2005). Effects on forest ecosystems are of particular interest, because forests are important from a socio-economic point of view and provide important ecosystem services such as carbon sequestration (Zerbe 2002; Peñuelas and others 2008). In Europe, temperate forest ecosystems dominated by European beech (*Fagus sylvatica* L.) are considered particularly susceptible to increasing summer temperatures and drought events (Gessler and others 2007; Meier and Leuschner 2008; Friedrichs and others 2009) as currently projected by climatic models (for the study area: annual mean temperature increase about 2°C within the next 40 years; IPCC 2007). Because the morphological and physiological traits typical of European beech constitute its adaptation to an oceanic and semi-oceanic climate, increasing summer temperatures and drought may impose constraints on the competitiveness of *F. sylvatica*, particularly at sites with shallow soils and, thus, low available water capacity (Gessler and others 2007; Scharnweber and others 2011).

Several studies have shown that European beech responded positively to prolonged growing seasons or improved N supply across many sites in NW Europe (Pretzsch 1999; Dittmar and others 2003; Lebourgeois and others 2005). However, these responses may be superimposed by other factors such as environmental pollution (for example, sulfur dioxide immission; Mölder and others 2011) or mediated by site attributes and within-stand genetic variability (Schraml and Rennenberg 2002). To disentangle shifts in growth patterns attributable to different environmental variables, recent studies have complemented dendrochronological approaches with dendrochemical analyses. Stable carbon isotope composition in tree rings can be used as a proxy for the intrinsic water use efficiency (the ratio of net assimilation to stomatal conductance) and thus as a long-term record of a tree's water status and balance (Mölder and others 2011). This in turn may help to assess a tree species' susceptibility to climate change, because long-term chronologies of stable carbon isotope composition provide insight into how trees have responded in the past (Saurer and others 2004a). The N isotope composition of tree rings may record long-term information on the N cycle in forests, which in turn is affected by N emission patterns, climatic condi-

tions, or silvicultural measures (Falkengren-Grerup and others 2004; Bukata and Kyser 2007; Curtis and others 2011).

However, it often remains difficult to generalize findings on tree-ring isotope signatures to larger regions, because the spatial and temporal variability of tree response patterns are largely unknown (Saurer and others 2004a). This stresses the importance of site- and region-related analyses (Pretzsch 1999; Peñuelas and others 2008). Moreover, studies have demonstrated that wood isotope composition may vary with tree age (age effect), which in turn emphasizes the need for age-related comparisons (Peñuelas and others 2008).

In the present study we analyzed long-term responses (160 years) of European beech to shifting environmental conditions (climate, N-deposition) in relation to soil properties and tree age using a combined dendrochronological and dendrochemical approach. We focused on beech stands in central Europe (Luxembourg), the core area of the species' European range. In Luxembourg *F. sylvatica* covers a wide range of site conditions, but dendroecological surveys are scarce. We compared growth responses of European beech to climate and N-deposition for stands on soils with contrasting water supply and of two different age classes. In our analyses we considered diameter at breast height (DBH), basal area increment (BAI), and tree-ring isotopic signatures ( $\delta^{13}\text{C}$ ,  $\delta^{15}\text{N}$ ) as dependent variables, soil types with contrasting available water capacity (Cambisols with about 170 mm available water capacity vs. Regosols with about 40 mm available water capacity) and stand age (60 vs. 200 years) as fixed factors, and environmental conditions (temperature, precipitation, N-deposition) as independent variables. We hypothesized that stands on shallow soils (Regosols) would show a more pronounced response pattern (in terms of shifts in DBH, BAI, isotope signatures) to environmental changes compared to stands on Cambisols. Moreover, we expected young and mature stands on corresponding soils to exhibit similar response patterns, but stand age to have a modifying impact on tree responses.

## MATERIALS AND METHODS

### Study Area and Site Selection

The study area is located in the sandstone region of Luxembourg (so-called "Petite-Suisse luxembourgeoise"; 49°45'N–49°51'N and 6°18'E–6°24'E; 255–420 m a.s.l.) and spans an area of about 180 km<sup>2</sup>. The climate is of a sub-oceanic type

(Drogué and others 2005). Precipitation is 750–800 mm  $y^{-1}$  and the annual mean temperature is 8–9°C (Pfister and others 2005). Soils developed from Jura-Sandstone, and prevailing soil types are Regosols, Cambisols, and Luvisols (Krippel 2005; soil types according to the WRB system 2006). Forests cover about 35% of the landscape. Mature beech forests represent “ancient woodlands” (that is, forest sites have not been cleared at least during the last 250 years; Krippel 2005), whereas young forests are reforestations at forest sites that were destroyed during World War Two.

In the study area, a total of 16 forest plots (about 0.25 ha in size) were selected at random. All plots were embedded in discrete larger forests ranging in size from 0.5 to 5 km<sup>2</sup>. Four types of beech forests (differing in age and water supply) were analyzed: (i) mature beech stands on Cambisols, (ii) mature beech stands on Regosols, (iii) young beech stands on Cambisols, and (iv) young beech stands on Regosols (forest types are henceforth referred to as MS<sub>Camb</sub>, MS<sub>Rego</sub>, YS<sub>Camb</sub>, and YS<sub>Rego</sub>, respectively; for stand and soil characteristics see Tables 1 and 2, respectively). Each forest type was represented by 4 plots (that is, 4 replicates per forest type). In all stands, *F. sylvatica* (henceforth referred to as *Fagus*) was the dominant tree species (cover >80%). All stands were nature reserves or “protected forests”, and wood harvest was low over the last 50 years (for data on management history for all 16 plots for the last two decades see Table 3).

### Tree Selection and Sampling Design

The dendrochronological sampling was carried out in May 2008. Each plot was overlaid with a grid and 10 intersections were selected at random. The tallest tree individuals (of the upper canopy) nearest to an intersection were considered for analyses (that is, 10 trees per plot; total n of trees = 160; henceforth referred to as “target trees”; for mean age and age range of target trees see Table 1). Target trees were cored with an increment borer (Suunto 400, Vantaa, Finland), 40 cm in length and 0.5 cm in bit diameter. Two cores per tree were taken at 1.3 m height from two opposite sides.

### Methodological Approach

In our study we combined a “dendroecological approach” (response variable: tree-ring width (TRW)) and a “dendrochemical approach” (response variables: tree-ring isotope signatures, BAI and DBH increment). In the first approach a regression analysis has been used (based on the

analysis of annual ring-width data), and in the second approach a Repeated Measures ANOVA has been applied (based on the analysis of decadal tree-ring isotope signatures and decadal DBH increment and BAI data; for the description of methods and the processing of raw data see sections “Tree-ring analysis” and “Data evaluation and statistics”).

### Tree-Ring Analysis

Cores were air dried, fixed to a core-mounting, and the surface was leveled with a core-microtome (WSL Birmsdorf, Switzerland). Subsequently, the TRW was measured using a measuring table with 0.01 mm resolution (Instrumenta Mechanik Labor IML, Wiesloch, Germany) combined with a binocular (Wild, Heerbrugg, Switzerland) and recorded by the IML software T-Tools pro (Wiesloch, Germany). The data were then imported and further processed by the software TSAP-Win (Version 0.53, Rinntech, Heidelberg, Germany). All TRW series were cross-dated following the procedure described by Yamaguchi (1991; using chronologies of Friedrichs and others (2009) as reference). The TRW series of the two cores per tree were averaged to tree mean curves. The analyses for MS were confined to the period 1848–2007, and for YS<sub>Camb</sub> and YS<sub>Rego</sub> to the periods 1948–2007 and 1958–2007, respectively. In addition to DBH increment, we calculated the mean BAI of the trees analyzed as a variable describing the trees’ growth rates and vitality as related to environmental changes (Peñuelas and others 2008; Sun and others 2010).

Descriptive statistics on ring-width series (standard deviation, first-order autocorrelation, and mean sensitivity) were calculated using TSAP-Win (Table 1). Climate impacts on TRW were analyzed by means of multiple linear regressions (for two chronologies: from 1850–2007 (MS) and 1958–2007 (MS and YS); to detect time-related shifts in the relative importance of climate variables). To this end, we detrended raw ring-width data of single trees (using residuals from 5-year moving averages; TSAP-Win) and then averaged the single-tree chronologies to site-specific chronologies. Regression analyses were based on these site chronologies. We used 5-year moving averages as a detrending method, because this procedure removes long-term trends such as age effects but keeps the high-frequency (that is, inter-annual) signals typical of a respective chronology (Stan and Daniels 2010; Trouet and others 2010; Dittmar and others 2012). In the regression analyses, TRW was considered as the dependent variable. Monthly precipitation and temperature from July to December of the previous

**Table 1.** Stand Characteristics and Descriptive Statistics

| Forest type        | Mean altitude a.s.l. (m) | Mean age of trees (years) | Age range of trees (years) | Mean DBH (cm) | Mean cover <i>F. syl.</i> (%) | SD               | AC                | MeS (%)          | DBH increment (mean, mm y <sup>-1</sup> ) | BAI (mean, cm <sup>2</sup> y <sup>-1</sup> ) |
|--------------------|--------------------------|---------------------------|----------------------------|---------------|-------------------------------|------------------|-------------------|------------------|---|--|
| MS <sub>Camb</sub> | 377                      | 191                       | 160–254                    | 65            | 92                            | 61 <sup>ab</sup> | 0.78 <sup>a</sup> | 20 <sup>a</sup>  | 3.32 <sup>a</sup>                         | 23.6 <sup>a</sup>                            |
| MS <sub>Rego</sub> | 341                      | 202                       | 160–265                    | 56            | 86                            | 47 <sup>a</sup>  | 0.74 <sup>a</sup> | 18 <sup>ab</sup> | 2.82 <sup>b</sup>                         | 15.9 <sup>b</sup>                            |
| YS <sub>Camb</sub> | 344                      | 63                        | 60–83                      | 28            | 91                            | 74 <sup>b</sup>  | 0.71 <sup>a</sup> | 20 <sup>a</sup>  | 4.50 <sup>c</sup>                         | 10.2 <sup>c</sup>                            |
| YS <sub>Rego</sub> | 335                      | 52                        | 50–62                      | 23            | 91                            | 77 <sup>b</sup>  | 0.79 <sup>a</sup> | 16 <sup>b</sup>  | 5.04 <sup>d</sup>                         | 8.7 <sup>c</sup>                             |

Calculation based on raw ring-width data. MS<sub>Camb</sub> and MS<sub>Rego</sub> = mature stands on Cambisols and Regosols, respectively; YS<sub>Camb</sub> and YS<sub>Rego</sub> = young stands on Cambisols and Regosols, respectively; *F. syl.* = *Fagus sylvatica*; SD = standard deviation (0.01 mm); AC = first-order autocorrelation; MeS = mean sensitivity; DBH = diameter at breast height; BAI = basal area increment.

All data refer to the target trees analyzed (only data on "mean cover of *Fagus sylvatica*" are stand-related). Superscript letters within the same column indicate significant differences with  $P < 0.05$  (Tukey test).

**Table 2.** Summary of Soil Characteristics

| Forest type        | Soil type | Soil profile      | Depth of soil horizons (cm) | Soil pH (H <sub>2</sub> O) | S value (mval 100 g <sup>-1</sup> ) | Base saturation (%) | CN ratio   | Available water capacity (mm) |
|--------------------|-----------|-------------------|-----------------------------|----------------------------|-------------------------------------|---------------------|------------|-------------------------------|
| MS <sub>Camb</sub> | Cambisol  | O                 | 0–8                         | 3.9 (0.2)                  | 5.8 (0.9)                           | 46.4 (6.5)          | 16.5 (1.5) | 176                           |
|                    |           | A <sub>h</sub>    | 9–17                        |                            |                                     |                     |            |                               |
| MS <sub>Rego</sub> | Regosol   | (S)B <sub>v</sub> | 18 to >100                  | 3.8 (0.2)                  | 5.3 (1.1)                           | 43.3 (8.5)          | 18.2 (2.9) | 41                            |
|                    |           | O                 | 0–10                        |                            |                                     |                     |            |                               |
|                    |           | A <sub>h</sub>    | 11–19                       |                            |                                     |                     |            |                               |
| YS <sub>Camb</sub> | Cambisol  | C                 | Below 20                    | 4.4 (0.2)                  | 7.3 (1.2)                           | 54.4 (6.2)          | 14.1 (1.6) | 164                           |
|                    |           | O                 | 0–5                         |                            |                                     |                     |            |                               |
|                    |           | A <sub>h</sub>    | 6–11                        |                            |                                     |                     |            |                               |
| YS <sub>Rego</sub> | Regosol   | (S)B <sub>v</sub> | 12 to >100                  | 3.7 (0.1)                  | 5.0 (0.6)                           | 54.7 (7.2)          | 20.3 (3.9) | 35                            |
|                    |           | O                 | 0–6                         |                            |                                     |                     |            |                               |
|                    |           | A <sub>h</sub>    | 7–13                        |                            |                                     |                     |            |                               |
|                    |           | C                 | Below 14                    |                            |                                     |                     |            |                               |

Soil chemical measurements (means and SD in brackets of  $n = 4$  plots) refer to the upper mineral horizon (A-horizon). MS<sub>Camb</sub> and MS<sub>Rego</sub> = mature stands on Cambisols and Regosols, respectively; YS<sub>Camb</sub> and YS<sub>Rego</sub> = young stands on Cambisols and Regosols, respectively.

**Table 3.** Data on Stand and Management History

| Forest type        | Stand volume (m <sup>3</sup> ha <sup>-1</sup> ) |      | Tree density, DBH > 7 cm, (n ha <sup>-1</sup> ) |      | Wood harvest (m <sup>3</sup> ha <sup>-1</sup> y <sup>-1</sup> ) |      | Basal area (m <sup>2</sup> ha <sup>-1</sup> ) |           | DBH increment in recent decades <sup>1</sup> (0.01 mm y <sup>-1</sup> ) |          | DBH increment decline <sup>1</sup> (0.01 mm y <sup>-1</sup> ) |      | Competition index <sup>1</sup> |               | Shifts in competition indices <sup>1</sup> |  |
|--------------------|---|------|---|------|---|------|---|-----------|---|----------|---|------|--------------------------------|---------------|--|--|
|                    | 1987  | 2007 | 1987  | 2007 | 1987–2007   | 2007 | 1978–1987                                     | 1998–2007 | 1978–1987 vs. 1998–2007   | 1987     | 2007  | 1987 | 2007                           | 2007 vs. 1987 |  |  |
| MS <sub>Camb</sub> | 619   | 732  | 148   | 139  | <2  | 32.7 | 366 (38)                                      | 290 (14)  | -76*  | 65 (4.4) | 64 (4.3)  | -1   |                                |               |  |  |
|                    | 519   | 652  | 146   | 142  | <3  | 28.4 | 418 (34)                                      | 364 (32)  | -54*  | 59 (6.6) | 62 (6.4)  | 3    |                                |               |  |  |
|                    | 536   | 702  | 129   | 124  | <3  | 29.9 | 586 (38)                                      | 402 (54)  | -184*   | 75 (7.0) | 77 (7.1)  | 2    |                                |               |  |  |
| MS <sub>Rego</sub> | 465   | 603  | 204   | 191  | <2  | 26.7 | 436 (38)                                      | 430 (26)  | -6  | 34 (6.3) | 43 (4.7)  | 9    |                                |               |  |  |
|                    | 523   | 635  | 154   | 143  | <3  | 28.9 | 384 (24)                                      | 304 (20)  | -80*  | 73 (6.2) | 73 (6.1)  | 0    |                                |               |  |  |
|                    | 531   | 627  | 172   | 162  | <2  | 28.8 | 300 (40)                                      | 242 (36)  | -58*  | 49 (5.3) | 51 (5.2)  | 2    |                                |               |  |  |
| YS <sub>Camb</sub> | 687   | 798  | 332   | 324  | <2  | 40.4 | 262 (30)                                      | 196 (34)  | -66*  | 43 (3.2) | 46 (3.4)  | 3    |                                |               |  |  |
|                    | 550   | 690  | 278   | 268  | <2  | 33.8 | 442 (58)                                      | 306 (20)  | -136*   | 60 (7.7) | 63 (7.8)  | 3    |                                |               |  |  |
|                    | 292   | 356  | 618   | 593  | <2  | 22.1 | 550 (44)                                      | 416 (36)  | -134*   | 53 (4.6) | 61 (4.9)  | 8    |                                |               |  |  |
| YS <sub>Rego</sub> | 210   | 282  | 739   | 707  | <2  | 20.7 | 594 (30)                                      | 564 (52)  | -30   | 56 (5.5) | 67 (5.2)  | 11   |                                |               |  |  |
|                    | 470   | 580  | 755   | 742  | <0.5  | 38.4 | 482 (30)                                      | 414 (26)  | -68*  | 30 (3.8) | 32 (3.5)  | 2    |                                |               |  |  |
|                    | 405   | 517  | 1115  | 1091 | <0.5  | 38.3 | 618 (46)                                      | 522 (68)  | -96*  | 60 (8.1) | 67 (8.3)  | 7    |                                |               |  |  |
| YS <sub>Rego</sub> | 145   | 296  | 1650  | 1605 | <1  | 26.8 | 558 (28)                                      | 614 (72)  | 56  | 29 (6.0) | 43 (7.1)  | 14   |                                |               |  |  |
|                    | 186   | 355  | 1243  | 1226 | <1  | 28.5 | 616 (56)                                      | 556 (46)  | -60*  | 36 (4.8) | 53 (5.1)  | 17   |                                |               |  |  |
|                    | 281   | 390  | 633   | 615  | <2  | 23.2 | 520 (38)                                      | 474 (28)  | -46*  | 62 (7.0) | 72 (8.4)  | 10   |                                |               |  |  |
|                    | 101   | 155  | 244   | 231  | <0.3  | 10.3 | 436 (40)                                      | 298 (48)  | -138*   | 53 (5.5) | 59 (6.0)  | 6    |                                |               |  |  |

Values are given for the last two decades, for which growth decline in diameter at breast height (all forest types) and basal area increment (mature stands) has been proven.

<sup>1</sup>These data refer to the 10 target trees analyzed per plot; MS<sub>Camb</sub> and MS<sub>Rego</sub> = mature stands on Cambisols and Regosols, respectively; YS<sub>Camb</sub> and YS<sub>Rego</sub> = young stands on Cambisols and Regosols, respectively; BAI = basal area increment; DBH = diameter at breast height. Competition indices for target trees (means of 10 target trees per plot, n of plots: 16) were calculated according to Biging and Dobbertin (1995).

Asterisks (\*) indicate significant differences ( $P < 0.05$ ) in declining DBH increments between the decades 1978–1987 and 1998–2007 (ANOVA). Values in brackets give the standard error for DBH increment and competition indices.

year and from January to August of the year of tree-ring formation were used as predictors (following Dittmar and others 2003). In addition, we included precipitation values for the growing season (previous and current year's data; April–October), the annual mean temperature (previous and current year's data), and previous year's increment as predictors. Climate variables (used as predictors in the model) were detrended in the same way as ring-width data. Model selection was based on identifying significant ( $\alpha = 0.05$ ) predictor variables. A correction of the degrees of freedom was applied due to lag-1 autocorrelation  $r_1$  (effective sampling size  $N' = N(1 - r_1) / (1 + r_1)^{-1}$ ; Dawdy and Matalas 1964).

### Measurement of Wood $N_{\text{tot}}$ Concentrations, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ Signatures

For stable isotope composition of C and N a subsample of five trees (randomly selected out of the 10 trees) per plot was used. Chronologies of MS and YS were divided into 10-year intervals and the wood material of cores was assigned to these intervals (beginning in 2007–1998, 1997–1988 and so on, for MS until 1857–1848, for  $YS_{\text{Camb}}$  until 1957–1948, and for  $YS_{\text{Rego}}$  until 1967–1958). Wood sampling from tree cores followed the method described by Nock and others (2011), using whole wood material of two cores per tree and five trees per plot (advantages of the use of whole wood samples see Sun and others 2010). According to the 'pool method' after Treydte and others (2001) the rings corresponding to the same time interval and the same plots were combined in one sample, thus providing decadal averages. Decadal averages of isotope signatures are appropriate to reflect long-term trends in the trees' environmental conditions and minimize noise from short-term variations (Hietz and others 2010; Nock and others 2011). Moreover, decadal averages partly remove the randomness that radial migration of N introduces to the distribution of N throughout the cross section. The pool method was applied to obtain enough material for  $N_{\text{tot}}$  analyses as some of the tree rings were very narrow and had low wood N concentrations. The interpretation of N concentrations considered the border between sapwood and heartwood. We expected wood N concentrations to support the interpretation of  $\delta^{15}\text{N}$  signatures (Hart and Classen 2003).

Wood samples were dried and ground with a mill (MM 400, Retsch, Haan, Germany), and re-dried at 40°C and weighed prior to analyses.  $N_{\text{tot}}$ ,  $\delta^{15}\text{N}$ , and  $\delta^{13}\text{C}$  were determined using a continuous flow

elemental analyzer (Vario El cube, Elementar, Haan, Germany) coupled to an isotope ratio mass spectrometer (Isoprime IRMS, Isoprime Ltd., Cheadle Hulme, UK). Each sample was measured threefold, and the mean was used for further calculations. Isotope values were presented in the  $\delta$  notation (in per mil; ‰) as a relative deviation from the international standard (atmospheric  $\text{N}_2$  for  $\delta^{15}\text{N}$ , V-PDB for  $\delta^{13}\text{C}$ ). The relative precision of repeated analyses of IAEA standards (IAEA-N-1 for N, IAEA-CH-3 for C) was  $\pm 0.3\text{‰}$  for  $\delta^{15}\text{N}$  and  $\pm 0.1\text{‰}$  for  $\delta^{13}\text{C}$ .

### Soil, Meteorological and N Deposition Data

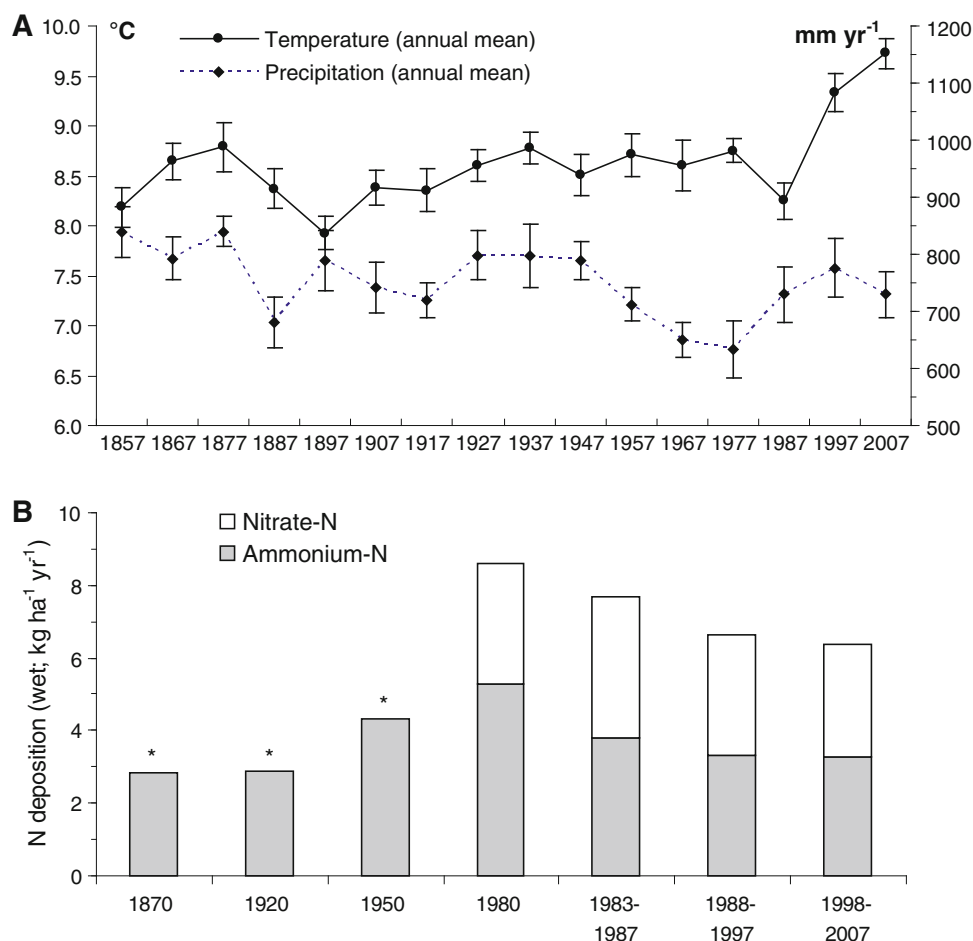
In each plot the soil profile (thickness of soil horizons) was recorded at three randomly chosen spots using a soil auger (Pürckhauer, ecoTech, Bonn, Germany). For the A-horizon, soil chemical properties were analyzed ( $\text{pH}_{\text{H}_2\text{O}}$ ,  $S$ -value, base saturation, CN ratio) following standard sampling and analytical procedures as described by Steubing and Fangmeier (1992). The "available water capacity" of soils was calculated according to AG Boden (1994; approximate calculation based on the thickness, the bulk density, and the soil classes of all soil horizons that characterize a soil profile). Soil ecological characteristics are summarized in Table 2.

Meteorological data (monthly precipitation and monthly temperature, documented from 1850 onwards) were obtained from Freyermuth and Pfister (2010). Long-term shifts in annual mean temperatures and precipitation (calculated as decadal means) are shown in Figure 1A. Data on airborne N loads (wet deposition of ammonium and nitrate) in Luxembourg were taken from Asman and others (1988) and Matthias and others (2007; modeled data from 1870 onwards), and deposition measurements (since 1983) from the European Monitoring and Evaluation Programme EMEP/CCC Report (Hjellbrekke and Fjæraa 2010; Figure 1B).

### Data Evaluation and Statistics

For an assessment of possible management impacts on growth responses of target trees, we evaluated management history data of stands and shifts of the competitive relationships between target trees and surrounding neighbors (that is, competitors) by means of an analysis of shifts in competition indices (also known as distance-dependent competition indices (CIs), in which competition effects are accounted for by the distance between a target tree

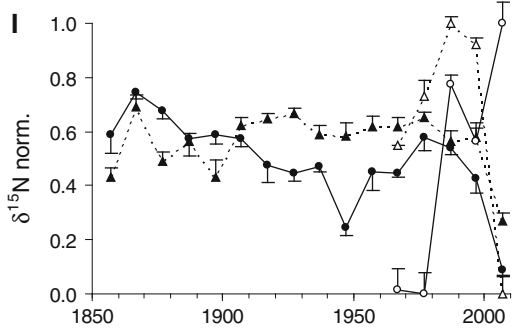
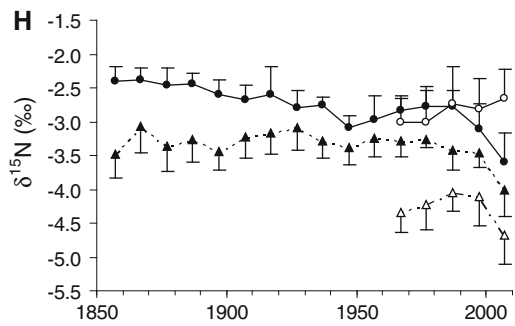
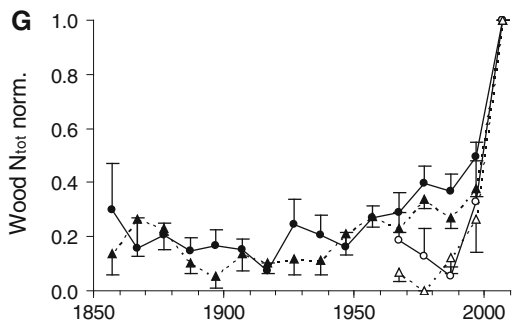
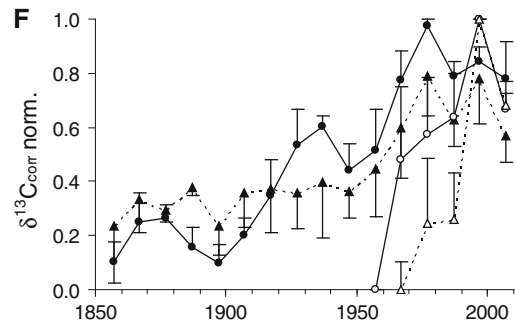
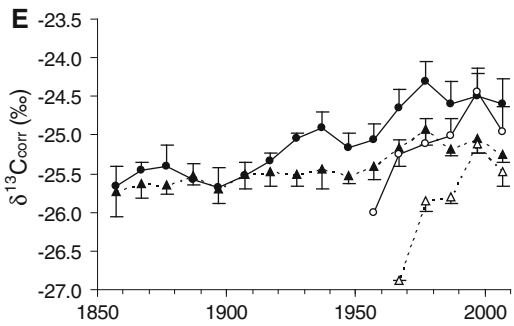
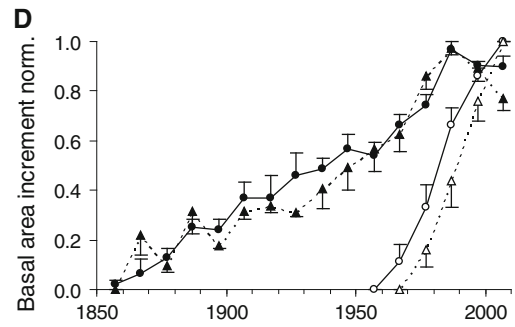
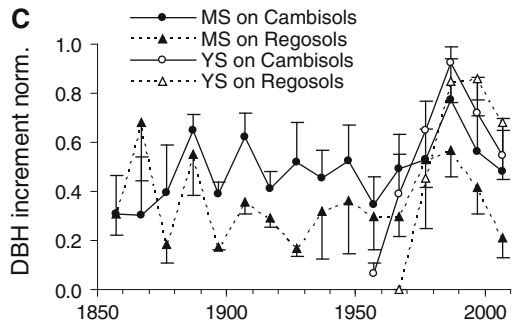
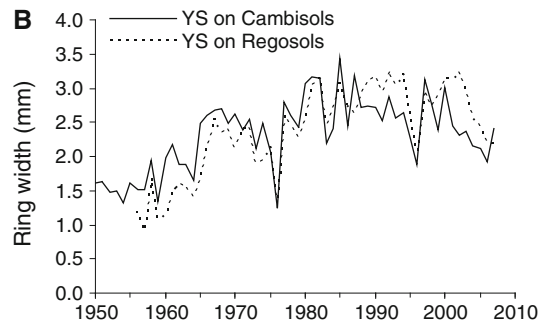
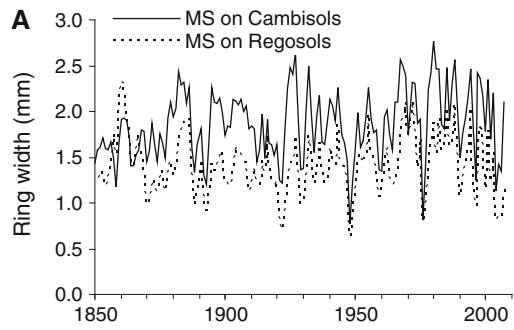




**Figure 1.** Time series in **A** annual mean temperatures (decadal averages,  $\pm 1$  SE) and precipitation (decadal averages,  $\pm 1$  SE), and **B** wet deposition of nitrogen in the study area. N deposition data for the years 1870, 1920, 1950, and 1980 are based on modeling studies and presented as annual values (wet deposition; from Asman and others (1988), and Matthias and others (2007); \* = nitrate deposition data for 1870, 1920, and 1950 not available for Luxembourg). N deposition data from 1983 onwards are based on deposition measurements (wet deposition; European Monitoring and Evaluation Programme EMEP/CCC Report, Hjellbrekke and Fjæraa 2010) and presented as annual means calculated for the time spans 1983–1987, 1988–1997, 1998–2007 (in correspondence with decadal values for temperature and precipitation).

and its neighbors, and their relative sizes). CI was calculated according to Biging and Dobbertin (1995), using tree DBH as an expression of a tree's size ( $CI_i = \sum DBH_j (DBH_i * Dist_{ij})^{-1}$ ), where  $CI_i$  is the competition index calculated for the target tree  $i$ ,  $DBH_i$  is the diameter at breast height of the target tree  $i$ ,  $DBH_j$  is the diameter at breast height of the competitor  $j$ , and  $Dist_{ij}$  is the distance between target tree and competitor; results for CI are presented in Table 3). To test for both possible crowding (increasing competition) and age effects on growth responses of target trees, shifts in DBH increment (as far as identified) were related to CI and the age of tree individuals (by means of a linear regression).

$\delta^{13}C$  data were corrected for the decline of  $\delta^{13}C$  in atmospheric  $CO_2$  due to fossil fuel emissions following the method of McCarroll and Loader (2004; henceforth referred to as  $\delta^{13}C_{corr}$ ). To compare isotope signatures between forest types,  $\delta^{15}N$  and  $\delta^{13}C$  values were normalized following the technique of Bukata and Kyser (2008;  $X_{norm,i} = (X_i - X_{lowest}) / (X_{highest} - X_{lowest})$ , where  $X_{norm,i}$  is the normalized value for the year  $i$ , and  $X_{lowest}$  and  $X_{highest}$  are the lowest and highest values, respectively, in the measurement series considered). This normalization procedure was also applied to DBH increment, BAI, and wood  $N_{tot}$  concentrations (Figure 2; due to the calculation of averages of





◀ **Figure 2.** Time series in **A** tree-ring width of MS (raw ring-width data; means of, respectively, 40 trees), **B** tree-ring width of YS (raw ring-width data, means of, respectively, 40 trees), **C** DBH (= diameter at breast height) increment (normalized values), **D** basal area increment (normalized values), **E**  $\delta^{13}\text{C}_{\text{corr}}$  (corrected for the decline of  $\delta^{13}\text{C}$  in the atmospheric  $\text{CO}_2$ ), **F**  $\delta^{13}\text{C}_{\text{corr}}$  (corrected for the decline of  $\delta^{13}\text{C}$  in the atmospheric  $\text{CO}_2$ ; normalized values), **G** wood  $\text{N}_{\text{tot}}$  concentrations (normalized values), **H**  $\delta^{15}\text{N}$ , and **I**  $\delta^{15}\text{N}$  (normalized values) for the four forest types analyzed (that is,  $\text{MS}_{\text{Camb}}$ ,  $\text{MS}_{\text{Rego}}$ ,  $\text{YS}_{\text{Camb}}$ , and  $\text{YS}_{\text{Rego}}$ , with MS = mature stands, YS = young stands, Camb = Cambisols, Rego = Regosols). Values represent decadal means (of four plots per forest type, and error bars indicate +1 SE and -1 SE, respectively), with years referring to the last year of a respective decade (for **C–I**: assignment of forest types according to **C**). Curves for  $\text{YS}_{\text{Camb}}$  in **G–I** do not consider the decade 1948–1957 due to insufficient sample material.

$n = 4$  series (replicates), minima and maxima are not necessarily 0 and 1, respectively).

Repeated measures analysis of variance (RM ANOVA) was applied to compare shifts in growth and dendrochemical characteristics over time (using log-transformed data; Hart and Classen 2003). Relationships between dendrochemical and climatic variables were compared using Spearman's Rank Correlation Analysis (decadal averages; Bukata and Kyser 2007). RM ANOVA and correlation analyses were restricted to MS because of an assumed age effect in YS (Francey and Farquhar 1982; Peñuelas and others 2008).

All statistical analyses (with the exception of dendrochronological statistics) were performed using SPSS 18.0 package (SPSS Inc., Chicago, IL).

## RESULTS

### Descriptive Statistics, DBH Increment, and BAI

First-order autocorrelation of tree-ring series (raw TRW) were similar for all forest types (Table 1).  $\text{MS}_{\text{Rego}}$  showed the lowest standard deviation and  $\text{YS}_{\text{Rego}}$  the lowest mean sensitivity. DBH increment and BAI of MS were higher on Cambisols, but not for YS (Table 1; Figure 2A, B; raw tree-width). Stands of all forest types showed a peak in DBH increment in the decade 1978–1987, and decreasing values in the two subsequent decades (Figure 2C; with the exception of  $\text{YS}_{\text{Rego}}$  in the decade ending in 1997). This pattern also applied to BAI trends of MS, whereas the BAI of YS continuously increased (Figure 2D). Decreasing DBH increment

in recent decades was significant for 13 out of the 16 forest plots (Table 3).

Correlation analyses between decreasing DBH increment (since 1987) and competition indices as well as decreasing DBH increment and age of target trees showed that declining increment rates were neither related to crowding/increasing competition nor to the age of target trees ( $P = 0.37, 0.29, 0.91, 0.30$  and  $P = 0.19, 0.41, 0.15, 0.74$  for  $\text{MS}_{\text{Camb}}$ ,  $\text{MS}_{\text{Rego}}$ ,  $\text{YS}_{\text{Camb}}$ ,  $\text{YS}_{\text{Rego}}$ , respectively).

### Site Characteristics and Management History

All sites had acid soils ( $\text{pH}_{\text{H}_2\text{O}}$  3.7–4.4), with CN ratios ranging between 14.1 and 20.3 (A-horizon; Table 2).  $\text{YS}_{\text{Camb}}$  had the highest values for pH and S, and the lowest CN ratios. B-horizons of Cambisols exceeded 1 m in depth. Regosols, by contrast, were characterized by shallow A-horizons with C-horizons beginning at soil depths of 20 cm ( $\text{MS}_{\text{Rego}}$ ) and 14 cm ( $\text{YS}_{\text{Rego}}$ ). Hence, available water capacity was about four times higher in Cambisols compared to Regosols.

Stand volume of MS and YS was 603–798 and 155–580  $\text{m}^3 \text{ha}^{-1}$  (in 2007), respectively, and showed a slight increase in the last two decades (Table 3). Mean increment rates of the stand volume were low (about 6.3 and 5.3  $\text{m}^3 \text{ha}^{-1} \text{y}^{-1}$  for MS and YS, respectively). Wood harvest was low over the last five decades (in most cases  $< 3 \text{m}^3 \text{ha}^{-1} \text{y}^{-1}$  according to the information provided by local forest authorities; for mean wood harvest during the last two decades see Table 3). Competition indices calculated for all target trees only slightly increased, particularly as regards MS (Table 3).

### Regression Analyses of TRW–Climate Relationships

Regression models explained between 31 and 72% of the variance in ring-width ( $R_{\text{adj}}^2$  values in Table 4), in which values for Cambisols were higher compared to those for Regosols. MS (chronologies from 1850 to 2007) showed similar response patterns to climatic variables, despite differences in soil conditions. High values in TRW coincided with high precipitation during the growing season (previous year of tree-ring formation), and during spring and early summer (current year of tree-ring formation). Temperature effects were low. Only high July ( $\text{MS}_{\text{Rego}}$ ) and August temperatures ( $\text{MS}_{\text{Camb}}$ ; previous year) negatively affected TRW. However, the correlation coefficients of these predictors increased

(for MS), when chronologies from 1958 to 2007 were considered: Positive effects of precipitation (growing season of the previous year) and negative effects of high temperatures (August, previous year; annual means, current year) were more pronounced. In YS, high precipitation in June (current year; stands on Cambisols) and July (previous year; stands on Regosols) proved to be the most important predictor for increasing ring-width. In YS<sub>Camb</sub>, declining ring-width was also associated with high July temperatures (current year).

### Trends in $\delta^{13}\text{C}_{\text{corr}}$

$\delta^{13}\text{C}_{\text{corr}}$  showed significant long-term increase for MS<sub>Camb</sub>, whereas long-term trends for MS<sub>Rego</sub> were statistically not significant (Table 5; Figure 2E). Type related differences and type x time interactions were not significant (Table 5). Values for  $\delta^{13}\text{C}_{\text{corr}}$  (for MS) increased until 1977 (by about 1.4 and 0.8‰ for MS<sub>Camb</sub> and MS<sub>Rego</sub>, respectively), and then decreased in the subsequent decade (Figure 2E). YS showed a strong increase in  $\delta^{13}\text{C}_{\text{corr}}$  after the first decade, with a maximum for the decade 1988–1997. Stands on Cambisols tended to have higher  $\delta^{13}\text{C}_{\text{corr}}$  values than stands on Regosols, but long-term differences were statistically not significant (Table 5). A similar pattern was found for normalized  $\delta^{13}\text{C}_{\text{corr}}$  values (Figure 2F), but maximum peaks for the decades 1968–1977 and 1988–1997 (MS and YS, respectively) were more pronounced.

### Trends in Wood N Concentrations and $\delta^{15}\text{N}$

Wood N concentrations ranged between 0.08 and 0.18% (dry weight; all forest types; data not shown). Temporal trends were low within the time span 1848 to 1987, but values then increased, with maxima found for the outermost tree rings (that is, decade 1998–2007; Figure 2G). A slight increase in wood N concentration in the decade up to 1977 coincided with the heartwood-sapwood border. Between-type variations were statistically not significant (Table 5).

$\delta^{15}\text{N}$  values showed most pronounced shifts in recent decades, with an increase for YS<sub>Camb</sub> and a decrease for the other forest types (Figure 2H, I). MS<sub>Camb</sub> showed a continuous decrease until the 1950s, and then an increase in the following three decades. Moreover,  $\delta^{15}\text{N}$  values were less negative for stands on Cambisols compared to those on Regosols. Trends in recent decades were more pronounced when normalized data were considered (Figure 2I).

## Interrelations Between Isotope Signatures and Climatic Variables

Relationships between  $\delta^{13}\text{C}_{\text{corr}}$  and climatic variables were similar for MS<sub>Camb</sub> and MS<sub>Rego</sub>, but signatures for Regosols were not affected by precipitation (Table 4). Overall, increasing temperatures (annual means, winter and spring temperatures) corresponded with increasing  $\delta^{13}\text{C}_{\text{corr}}$  values at both sites. For MS<sub>Camb</sub>,  $\delta^{13}\text{C}_{\text{corr}}$  values increased with decreasing (February) precipitation. A comparison of long-term trends in annual mean temperatures and  $\delta^{13}\text{C}_{\text{corr}}$  signatures (Figures 1A, 2E) also reflected interrelations between these two variables: High  $\delta^{13}\text{C}_{\text{corr}}$  values, for example, were found for the decades ending in 1877, 1937, 1977, and 1997, all of which corresponded with high annual mean temperatures (8.8°C for the first three decades, and 9.3°C for the last decade). By contrast, low values for  $\delta^{13}\text{C}_{\text{corr}}$  (for example, decades up to 1897 and 1987) corresponded with low mean temperatures (7.9 and 8.3°C, respectively).

Only  $\delta^{15}\text{N}$  signatures of MS<sub>Camb</sub> responded to climatic variables. Negative correlations were found for annual mean, spring, and winter temperatures, whereas relationships were positive with (spring) precipitation. No significant correlations were found between  $\delta^{13}\text{C}$  signatures and growth variables (DBH, BAI; results not shown in Tables).

## DISCUSSION

### Effects of Temperature and Precipitation on TRW

Beech trees sensitively responded to shifts in climate variables. This is indicated by the high percentage of variance in ring-width explained by the regression analyses (up to 72%; Table 4). Precipitation proved to be the most important predictor for high radial increment, when chronologies from 1850 to 2007 were considered. This is in agreement with findings of other studies with a focus on beech stands of central and western Europe (Dittmar and others 2003; Lebourgeois and others 2005). However, results of the regression analyses suggest an increasing susceptibility of MS to elevated temperatures in recent decades, indicated by an increase of the relative importance of annual mean (current year) and August (previous year) temperatures as predictors for narrow tree-rings (chronologies from 1850 to 2007 vs. chronologies from 1958 to 2007 in Table 4). Because this response was accompanied by an increasing sensitivity of ring-width to precipitation (Table 4), it is

**Table 4.** Climate-Tree Ring and Climate-Isotope Signature Relationships

|                        |               | Type of analyses:   |                    |                    |                    |                    |                    | Correlation analyses                |                    |                    |                    |                    |                    |  |
|------------------------|---------------|---------------------|--------------------|--------------------|--------------------|--------------------|--------------------|-------------------------------------|--------------------|--------------------|--------------------|--------------------|--------------------|--|
|                        |               | Regression analyses |                    |                    |                    |                    |                    | $\delta^{13}\text{C}_{\text{corr}}$ |                    |                    |                    |                    |                    |  |
|                        |               | Tree-ring width     |                    |                    |                    |                    |                    | $\delta^{15}\text{N}$               |                    |                    |                    |                    |                    |  |
| Chronology:            |               | 1850–2007           |                    |                    | 1958–2007          |                    |                    | 1850–2007                           |                    |                    | 1850–2007          |                    |                    |  |
| Forest type            |               | MS <sub>Camb</sub>  | MS <sub>Rego</sub> | MS <sub>Camb</sub> | MS <sub>Rego</sub> | MS <sub>Camb</sub> | MS <sub>Rego</sub> | YS <sub>Camb</sub>                  | YS <sub>Rego</sub> | MS <sub>Camb</sub> | MS <sub>Rego</sub> | MS <sub>Camb</sub> | MS <sub>Rego</sub> |  |
| Increment              | Previous year | Grow seas           | 0.21**             | 0.26***            |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Jul                 | 0.31***            | 0.19*              | 0.58***            | 0.43**             |                    |                                     | 0.45***            |                    |                    |                    |                    |  |
|                        |               | Oct                 |                    | 0.17*              |                    |                    | 0.35**             |                                     |                    |                    |                    |                    |                    |  |
|                        | Current year  | Dec                 |                    |                    |                    |                    | 0.25*              |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Grow seas           |                    |                    |                    |                    | 0.27*              |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Feb                 |                    |                    |                    |                    |                    | 0.27*                               |                    |                    |                    |                    | 0.60*              |  |
|                        | Previous year | Mar                 | 0.14*              | 0.14*              |                    |                    |                    |                                     |                    |                    |                    |                    | 0.52*              |  |
|                        |               | Apr                 | 0.14*              |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | May                 | 0.21**             | 0.23**             | 0.21*              |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Jun                 | 0.36***            | 0.18*              | 0.32**             |                    | 0.40***            |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Aug                 |                    |                    |                    |                    |                    |                                     |                    | 0.28*              |                    |                    |                    |  |
|                        |               | Jul                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
| Temp                   | Previous year | Jul                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Aug                 | -0.20**            |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        | Current year  | mean                |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Jan                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Mar                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Apr                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | May                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Jul                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Sep                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Nov                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Dec                 |                    |                    |                    |                    |                    |                                     |                    |                    |                    |                    |                    |  |
|                        |               | Dec                 | 0.66               | 0.60               | 0.84               | 0.69               | 0.87               | 0.59                                |                    |                    |                    |                    |                    |  |
| $R^2_{\text{adj}}$     |               | 0.41                | 0.33               | 0.66               | 0.44               | 0.72               | 0.31               |                                     |                    |                    |                    |                    |                    |  |
| df <sub>residual</sub> |               | 92                  | 90                 | 34                 | 39                 | 32                 | 35                 |                                     |                    |                    |                    |                    |                    |  |
| P                      |               | <0.001              | <0.001             | <0.001             | <0.001             | 0.005              | <0.001             |                                     |                    |                    |                    |                    |                    |  |

Tree-ring width (regression analyses); predictors: mean monthly and growing season precipitation, and mean monthly and annual mean temperatures of the previous and current year of tree-ring formation; df corrected for lag-1 autocorrelation). Isotope signatures (Spearman's Rank Correlation; climatic variables were calculated on a decadal basis; df = 15). MS<sub>Camb</sub> and MS<sub>Rego</sub> = mature stands on Cambisols and Regosols, respectively. YS<sub>Camb</sub> and YS<sub>Rego</sub> = young stands on Cambisols and Regosols, respectively. Precip = precipitation, Temp = temperature, grow seas = growing season, first three letters were used for the naming of months.  
 \* P < 0.05, \*\* P < 0.01, \*\*\* P < 0.001.

**Table 5.** Time and Forest Type Related Effects on Tree Growth Responses (DBH Increment, BAI,  $\delta^{13}\text{C}$ ) in Mature Stands

| Variable                            | Comparisons        | df | F     | P      |
|-------------------------------------|--------------------|----|-------|--------|
| DBH incr                            | MS <sub>Camb</sub> | 15 | 1.14  | n.s.   |
|                                     | MS <sub>Rego</sub> | 15 | 1.59  | n.s.   |
|                                     | Type × time        | 15 | 0.83  | n.s.   |
|                                     | Type               | 1  | 21.99 | 0.03   |
| BAI                                 | MS <sub>Camb</sub> | 15 | 29.01 | <0.001 |
|                                     | MS <sub>Rego</sub> | 15 | 13.63 | <0.001 |
|                                     | Type × time        | 15 | 3.71  | <0.001 |
|                                     | Type               | 1  | 32.40 | 0.001  |
| $\delta^{13}\text{C}_{\text{corr}}$ | MS <sub>Camb</sub> | 15 | 9.87  | <0.001 |
|                                     | MS <sub>Rego</sub> | 15 | 1.80  | n.s.   |
|                                     | Type × time        | 15 | 1.11  | n.s.   |
|                                     | Type               | 1  | 2.81  | n.s.   |
| N                                   | MS <sub>Camb</sub> | 15 | 10.13 | <0.001 |
|                                     | MS <sub>Rego</sub> | 15 | 10.09 | <0.001 |
|                                     | Type × time        | 15 | 0.54  | n.s.   |
|                                     | Type               | 1  | 0.05  | n.s.   |
| $\delta^{15}\text{N}$               | MS <sub>Camb</sub> | 15 | 1.82  | n.s.   |
|                                     | MS <sub>Rego</sub> | 15 | 0.58  | n.s.   |
|                                     | Type × time        | 15 | 0.41  | n.s.   |
|                                     | Type               | 1  | 5.31  | n.s.   |

RM ANOVA; n of plots = 4; n of decades = 16.

DBH incr = diameter at breast height increment, BAI = basal area increment, MS<sub>Camb</sub> = mature stands on Cambisols, MS<sub>Rego</sub> = mature stands on Regosols, n.s. = not significant.

likely that the beech stands analyzed have become more drought-limited in recent decades.

### Long-Term Trends in DBH and BAI

All stands showed a more or less continuous increase in BAI (in MS about 140 years). This finding was unexpected, because it contradicts the sigmoid tree growth model according to which growth should plateau (and decline) with progressing tree aging (Weiner and Thomas 2001). However, several recent studies have demonstrated continuously increasing BAI for several tree species during the last century, likely due to shifting environmental conditions (Johnson and Abrams 2009; Kint and others 2012). In a meta-analysis of Peñuelas and others (2011) half of the sites analyzed showed a positive trend in growth (in terms of standardized TRW) attributable to enhanced CO<sub>2</sub> levels. Although we do not know the reason for the generally increasing trend in BAI, it is possible that trees responded to increasing atmospheric CO<sub>2</sub>, either directly through CO<sub>2</sub> fertilization or indirectly through CO<sub>2</sub> effects on intrinsic water use efficiency (Hari and Arovaara 1988).

However, the most conspicuous congruence in radial/DBH increment in all stands (and BAI in MS)

was a peak in the decade ending in 1987, followed by a (mostly significant) decline of values in subsequent decades (normalized values in Figure 2C, D; Table 3). Several reasons may account for declining DBH increment and BAI (in MS): (i) increasing drought limitation caused by increasing summer temperatures during the last two decades (Drogué and others 2005; Figure 1A), (ii) the development of denser canopies (that is, crowding and thus increased competition; Skomarkova and others 2006; Table 3), and (iii) decreasing vitality due to increasing tree age (Pretzsch 1999). We hypothesize that declining DBH increment and BAI were mainly attributable to the significant increase of (annual means and August) temperatures that took place in the last two decades (Drogué and others 2005; Figure 1A), suggesting an increasing drought limitation of stands. This interpretation is supported by several findings. The onset of declining DBH increment (and of BAI in MS) occurred in parallel with peak values for temperatures, and the last two decades were the hottest on record (1.1 and 1.5°C, respectively, above the mean value of the decade ending in 1987; Figure 1A). In addition, declining DBH increment was observed simultaneously across forest types, and also occurred, for example, in stands dominated by other tree species (Friedrichs and others 2009). Our interpretation is corroborated by findings of the regression analyses and the fact that tree-rings  $\delta^{13}\text{C}_{\text{corr}}$  values showed a peak for the decade ending in 1997 (see interpretation of  $\delta^{13}\text{C}_{\text{corr}}$  signatures). In conclusion our findings suggest that the negative effects of climate change (that is, increasing temperatures) outweighed the positive effects (such as increasing atmospheric CO<sub>2</sub>, prolonged growing seasons) for older trees in recent decades.

We consider the effects of increasing competition between tree individuals on DBH increment to be of minor importance (despite increases in the stand volume), because relationships between shifts in the competition index of target individuals (Table 3) and declining increment rates were statistically not significant. Two reasons may account for this finding and the low increases in competition indices during the last 20 years: (i) Increasing stand volume may have increased competition at the stand level, but hardly affected target trees (that is, the individual level) due to their dominant position in the upper canopy; (ii) overall increment rates of the stands were very low, and stands still have not achieved their potential biomass carrying capacity (as reflected by very low quantities of dead wood). However, it is conceivable that management effects (in combination with climate) may be responsible



for stronger oscillations in the DBH increment found in the 19th and at the beginning of the 20th century (Figure 2C). As demonstrated by Skomarkova and others (2006), effects of forest management may even mask growth responses to shifts in temperature and precipitation. Due to the lack of intensive management measures in the past five decades, however, we exclude a strong management impact on more recent DBH increment rates.

We rule out that declining DBH increment was related to the age of the target trees, because we found no significant relationship between decreasing increment rates and the age of tree individuals of a respective forest type. Thus, the most plausible explanation for decreasing increment rates in recent decades is an increasing drought limitation of all forest types, likely induced by increasing temperatures. However, only MS showed decreasing BAI values in recent decades. Diameter increment of young trees typically increases during the first decades of growth as the tree establishes itself. The positive trend is then typically followed by a transition toward a negative trend due to the emergence of the geometric effect of increasing stem area on radial increment growth. It is possible, therefore, that the flattening and slight negative trends in YS ring-widths was also mediated by this typical growth pattern of young trees.

### Long-Term Trends in $\delta^{13}\text{C}_{\text{corr}}$ Signatures

Tree-ring  $\delta^{13}\text{C}_{\text{corr}}$  signatures showed a temporal coherence with climatic signals, particularly with temperature. High  $\delta^{13}\text{C}_{\text{corr}/\text{norm}}$  values, for example, found for the decade 1988–1997 coincided with a first maximum in mean temperatures (Figure 2E, F). Positive temperature– $\delta^{13}\text{C}$  and negative precipitation– $\delta^{13}\text{C}$  relationships are in agreement with other studies (Peñuelas and others 2008; Saurer and others 2008), and may be interpreted as a consequence of an increasing iWUE following increasing temperatures or droughts, finally resulting in higher tree-ring  $\delta^{13}\text{C}$ . However, ring-width was more strongly related to precipitation, and the months with significant temperature effects were only partly the same for ring-width and  $\delta^{13}\text{C}_{\text{corr}}$  signatures (Table 4). Thus, both response variables were at least partly mediated by different climatic factors (Mölder and others 2011). This discrepancy may explain the weak and statistically not significant correlation between  $\delta^{13}\text{C}$  signatures and ring-width in our study. Skomarkova and others (2006) found that wood growth was disconnected from carbon assimilation due to carbon

storage in the early growing season. Moreover, other carbon sinks (for example, masting events) may compete with wood growth and thus decouple  $\delta^{13}\text{C}$  signatures and TRW to a certain degree (Mölder and others 2011). Our findings on long-term trends in  $\delta^{13}\text{C}$  signatures are in accordance with those of other authors (Hemming and others 1998; Mölder and others 2011), who also found increasing values until 1976 (corresponding with an extremely dry and hot summer in that year; Hemming and others 1998). Other factors that might influence long-term trends in  $\delta^{13}\text{C}$  signatures are such as environmental pollution (for example,  $\text{SO}_2$  emission; Mölder and others 2011) and “age effects” (see discussion below).

### Long-Term Trends in $\delta^{15}\text{N}$ Signatures

$\delta^{15}\text{N}$  values showed a strong decreasing trend in recent decades (with the exception of  $\text{YS}_{\text{Camb}}$ ). We hypothesize that shifts in N deposition and soil N cycling were the most important factors accounting for this trend (Poulson and others 1995). In Luxembourg, (wet) N deposition showed a peak in 1980, corresponding with increasing values for  $\delta^{15}\text{N}$  in MS after 1950 (Figures 1B, 2H). In subsequent decades N deposition declined in the study area, possibly associated with shifts in the isotope composition of allochthonous N inputs (for example, atmospheric deposition of isotopically lighter ammonium; Poulson and others 1995). This in turn causes decreasing  $\delta^{15}\text{N}$  values (Bukata and Kyser 2007). Increasing temperatures might have contributed to decreasing  $\delta^{15}\text{N}$  values, because temperature and  $\delta^{15}\text{N}$  were negatively correlated (Table 4). In  $\text{YS}_{\text{Camb}}$  differences in soil chemistry (see Table 2; higher nitrification rates and thus production of  $^{15}\text{N}$  depleted nitrate; Högberg 1997) as well as deposition of isotopically heavy  $\text{NO}_x$  from car exhausts (two out of the four  $\text{YS}_{\text{Camb}}$  plots were situated close to motorways) might have contributed to increasing  $\delta^{15}\text{N}$  values (Saurer and others 2004b). We rule out that fractionation against  $^{15}\text{N}$  accompanying nitrogen translocation between tree rings is responsible for the divergent trends in tree-ring  $\delta^{15}\text{N}$ . This process would have affected all forest types. Moreover, fractionation against  $^{15}\text{N}$  during radial translocation of N is comparatively low (Elhani and others 2005). Wood N concentrations could not support the interpretation of  $\delta^{15}\text{N}$  signatures in our study due to the high radial mobility of N. A slight increase in wood N concentrations in the decade 1968–1977 coincided with the heartwood-sapwood border. However, the strong gradient in N concentrations within the sapwood was attributable

to the radial transport of N (Poulson and others 1995).

### Effects of Soil Conditions

MS on Cambisols showed higher growth rates than those on Regosols (Tables 1, 5). However, contrary to our hypothesis, trees on Cambisols showed a similar decrease in DBH increment and BAI (MS) and thus increasing drought limitation in recent decades as trees on Regosols (Figure 2A–D). This finding is in line with both  $\delta^{13}\text{C}$ –climate relationships and long-term trends for  $\delta^{13}\text{C}_{\text{corr}}$ , which did not differ between stands on Cambisols and Regosols (Tables 4, 5; Figure 2E). As a consequence, growth of beech forests on soils with higher available water capacity may be affected by climate change to a similar extent as stands on shallow soils, even under sub-oceanic climate. Beech trees on shallow soils, in turn, may exhibit a high resilience to increasing drought events (Dittmar and others 2003). This interpretation is supported by the finding that climatic predictors in the regression analyses explained a higher proportion of ring-width variance for stands on Cambisols than for stands on Regosols (Table 4). In addition, stands on Regosols tended to have a lower mean sensitivity (Table 1). We hypothesize that stands on Regosols are characterized by beech tree ecotypes that are well adapted to the prevailing soil conditions (Schraml and Rennenberg 2002). This interpretation is supported by studies that confirmed a strong “provenance effect” of beech trees originating from dry sites (Peuke and Rennenberg 2004). Ecotypes from wet habitats, in contrast, were found to be more sensitive to drought events (Peuke and Rennenberg 2004; Friedrichs and others 2009).

Stands on Cambisols always had higher  $\delta^{15}\text{N}$  values than stands on Regosols (Figure 2H). This finding is related to the general pattern that soil  $\delta^{15}\text{N}$  increases with depth by about 5–10‰ as a result of fractionation against  $^{15}\text{N}$  during the mineralization-plant uptake pathway (resulting in a  $^{15}\text{N}$  depleted surface layer and  $^{15}\text{N}$  enriched deeper soil layers; Högberg 1997). Deep-rooting trees thus have better access to N sources enriched in  $^{15}\text{N}$ , while at shallow sites, plants are forced to satisfy their N demands in the upper soil layers that are generally  $^{15}\text{N}$  depleted (Emmett and others 1998). Fractionation against  $^{15}\text{N}$  in the upper soil layer also explains why forest soils and thus plant tissue show a continuous  $\delta^{15}\text{N}$  decline over time as long as allochthonous N loads are low (Högberg 1997). This is illustrated by decreasing  $\delta^{15}\text{N}$  values until the end of the 1940s (in  $\text{MS}_{\text{Camb}}$ ; Figure 2H, I),

when natural N cycles were, at the most, minimally affected by human activities (Figure 1C).

### Effects of Stand Age

Both tree-ring formation and  $\delta^{13}\text{C}$  signatures were related to stand age (i.e., MS vs. YS). YS showed the highest DBH increment (Table 1), which is generally attributable to the high vigor of young trees (Pretzsch and Dursky 2002). Our results also suggest that an “age effect” has contributed to a strong increase in  $\delta^{13}\text{C}$  values (about 1‰) within the first decade analyzed (Figure 2E; Duquesnay and others 1998). This age effect is attributable to both physiological changes linked to tree (structural) development and shifts in environmental factors associated with stand maturation (for example, canopy closure, competition of tree individuals, vertical within-stand  $\text{CO}_2$  gradients; Francey and Farquhar 1982; Peñuelas and others 2008).

### CONCLUSIONS

Our study demonstrated that beech forests in Luxembourg have become increasingly drought limited in recent decades, likely attributable to the increase of mean annual temperatures by 1.5°C. Contrary to our expectations, stands on Cambisols showed a similar susceptibility to shifts in temperature and precipitation as stands on Regosols (in terms of both decreasing increment rates and tree-ring  $\delta^{13}\text{C}$  signatures). This indicates that growth of European beech may be affected by climate change even at sites that are characterized by a high available water capacity (such as Cambisols). Ecotypes grown at drier sites, in turn, may become particularly important within the context of adaptive forest management strategies in the future, for example for the selection of appropriate ecotypes for tree plantations.  $\delta^{13}\text{C}$  signatures showed long-term trends that were generally similar with findings of other studies across central Europe and thus may be appropriate to record large-scale climatic signals.  $\delta^{15}\text{N}$  signatures responded to spring precipitation and temperatures only at Cambisol sites. Our results suggest that values are strongly shaped by local site conditions, such as prevailing soil chemistry and local patterns of allochthonous N inputs.

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