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Dendroecological assessment of climate resilience of the rare and scattered forest tree species *Tilia cordata* Mill. in northwestern Europe

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To increase forest resilience to global change, forest managers are often directing forest stands towards a broader diversity of tree species. The small-leaved lime (*Tilia cordata* Mill.), a rare and scattered species in northwestern Europe, is a promising candidate for this purpose. Its life traits suggest a high resilience to climate change and a favourable impact on forest ecosystem services. This study used a dendroecological approach to assess how lime tree radial growth had responded to the past climatic change. First, 120 lime trees from nine sites were selected in southern Belgium based on criteria adapted to the rareness of the species. Chronology quality was assessed and resulting tree-ring series were validated at site and region levels. Second, a range of dendrochronological methods was used to analyze the changes over time in the variability and long-term trends of lime tree growth and their relation to climate during the period 1955–2016. Last, behaviour of lime trees was compared with that of beech from the same region and time period. For this purpose, the same methodology was applied to an additional beech tree-ring dataset (149 trees from 13 sites). Beech is the climax tree species of the region, but is known to be drought-sensitive and has shown weaknesses in the current climate. The quality of our tree-ring series attests that dendroecological investigation using rare and scattered species is possible, opening the way to further analysis on other such lesser-known forest tree species. The analysis showed that the small-leaved lime had been resilient to the past climatic change in multiple ways. Lime growth increased during the preceding decades despite an increased frequency and intensity of stressful climatic events. Lime growth quickly recovered in the years following the stresses. The growth–climate relationships were either stable over time or had a positive evolution. The behaviour of lime contrasted strongly with that of beech. Lime performed better than beech in every analysis. Small-leaved lime is thus a serious candidate for addressing climate change challenges in the region. It should be considered by forest managers planning to improve the sustainability and resilience of their forests, in particular in vulnerable beech stands.

Introduction

In northwestern Europe, climate models forecast increased frequency and intensity of heatwaves and droughts for this century (IPCC, 2014), which likely will probably result in increased stress for trees and forest ecosystems (Keenan, 2015). Forest managers are accordingly seeking new solutions to adapt forests to the uncertainties of the future climate. Directing forests towards a broader diversity of tree species is one of the recommendations most often proposed for the increasing resilience of forests and the sustainability of their services (Messier *et al*., 2013; Pretzsch *et al*., 2013). Most northwestern European forests are not optimal in this regard. Historic management practices have largely favoured a small set of tree species supplying a well-established demand for wood, such as spruce (*Picea abies* L.), beech (*Fagus sylvatica* L.) and oak (*Quercus* spp.), often in pure stands (Hemery *et al*., 2010). An important socio-economic sector has developed around these species. They are well-studied with regard to potential impacts of climate change, and their vulnerability has been noted (e.g. Lindner *et al*., 2010; Hanewinkel *et al*., 2013; Lindner *et al*., 2014). Other less dominant indigenous broadleaved tree species, such as *Sorbus, Acer, Alnus, Betula, Carpinus and Tilia* spp., are less sought after by the wood industry and have become rare in forests, even though some of them have value-added potential in the wood market.

Among the less common species, the small-leaved lime (*Tilia cordata* Mill.) may be valuable in a changing climate for its broad ecological amplitude, drought tolerance and the numerous ecosystemic services it brings to mixed stands (De Jaegere *et al*., 2016). Its high water efficiency due to economical water use (Aasamaa *et al*., 2004), and its strong, deep rooting (Pigott, 1991) make it one of the tree species best-suited to face the future climate trends in northwestern Europe (De Jaegere *et al*., 2016). Moreover, lime is robust and not affected by serious pests or pathogens. Its growth and productivity can be compared with those of valuable broadleaves such as ash (*Fraxinus excelsior* L.) or maple (*Acer pseudoplatanus* L.), though with less useful wood properties. Lime is also well-known for its tolerance to a wide variety of soils and has a positive effect on biodiversity (De Jaegere *et al*., 2016).

This study pursued three objectives. The first was to assess how lime has responded to past climatic events and how it is likely to behave in the future, using dendroecological methods (Fritts and Swetnam, 1989). Tree radial growth and its variation over time in relation to climate were analyzed in detail. The second objective was to compare the growth behaviour of lime trees with that of common beech (*F. sylvatica* L.). Beech is the climax tree species of a large part of northwestern Europe but is known to be drought-sensitive and has shown weaknesses in the current climate. During recent decades, beech climate sensitivity increased strongly in response to more frequent and more intense heat waves and warming-related droughts, even on sites with favourable growing conditions (Latte *et al*., 2015). It is thus of major interest to assess the capacity of lime trees to support diversification of beech stands at critical sites. The third objective was to assess whether the dendroecological methods, primarily developed for studying the historically dominant tree species (such as beech, oak or spruce), could be applied to rare and scattered tree species. To be statistically significant and representative of the tree population, dendrochronological field routines and resulting tree-ring datasets must obey certain rules (Mérian and Lebourgeois, 2011; Mérian *et al*., 2013), particularly concerning selection criteria for sites and trees and their total numbers. These rules can be challenging for rare and scattered tree species, which often occur in small groups of trees or even as single trees in mixed forests, and so offer limited study material.

Methods

Study area

The study was conducted in Wallonia (southern Belgium) (Figure 1), a territory of 16 844 km^2 located in the heart of northwestern Europe, consisting of low plateaus and hills with an altitude range of 100–700 m and some large plains. It has a temperate sub-oceanic climate with a mean annual temperature of 8–10°C and a total annual rainfall of 800–1400 mm, almost evenly distributed throughout the year. Past climate change produced wetter and warmer winters, and drier and hotter growing seasons, with more frequent and more intense drought events and heatwaves (Himpens *et al*., 2017). The forest cover is ~30 per cent, consisting mainly of spruce stands (*P. abies* L.) (34 per cent), oak stands (*Quercus* spp.) (18 per cent) and beech stands (*F. sylvatica* L.) (9 per cent), representing together 65 per cent of the total wood volume in the region (Alderweireld *et al*., 2015). Other indigenous broadleaved tree species (e.g. ash, hornbeam, birch, maple, alder and lime) make up ~15 per cent.

Among these secondary species, the small-leaved lime is particularly rare and scattered. It is present on less than 1 per cent of the whole forest area in southern Belgium. Best growing conditions are mainly limited to low plateaus (<300 m) where forest cover is thinner. Lime trees are generally associated with oaks in mixed stands, individually or in small groups, and often as shoots in coppiced woodland. Owing to the lack of interest among foresters and unfavourable management, old tall trees are very rare, despite the long life of the species (>500 years). Plantations are rare in forests, so that populations of lime trees are most often of natural origin.

Site and tree selection

The main constraint of the study was the availability of trees. Owing to the small number of forest stands with lime trees, and the small number of lime trees in those mixed stands, it was not possible to apply an optimal dendrochronological routine (Mérian and Lebourgeois, 2011; Mérian *et al*., 2013) for all the targeted study stands. Ideally, the number of trees should be high enough to be representative of the population. This number depends on numerous factors (species, growing conditions, tree and stand characteristics, etc.). For climate impact analysis, selected trees should preferentially be dominant or co-dominant, as their growth is then less affected by competition and silviculture than dominated trees. When possible, trees were felled to collect disks instead of cores, improving ring-width measurement and cross-dating, and thus overall quality of tree-ring series (Latte *et al*., 2015). All resulting tree-ring series were statistically tested and validated at site and region levels.

First, 189 potential sites were identified: 139 from the regional forest inventory (Rondeux *et al*., 2010) and 50 through a survey of public forest managers and private forest owners. Second, these sites were visited to confirm the presence of *T. cordata* Mill. and avoid confusion with *Tilia platyphyllos* Scop. or any lime hybrids (80 sites). Many of the sites (71) were unacceptable for dendrochronological investigation (e.g. too few, too young, not dominant trees or too recent coppicing). Finally, only sites within a lime stand or including a group of at least 10 non-dominated lime trees were selected. In these sites, only (co-)dominant healthy trees, visually older than 50 years, were selected.

In all, 120 trees from nine sites were selected for dendrochronological investigation (Figure 1; Table 1). Owing to the low availability of trees, site selection was not based on soil, landform or silviculture criteria. The sites, thus, represent a wide range of lime stand ecological conditions, from acid to calcareous soils with contrasting but rather low water availability. Many stands were growing on dry soils that are not optimal for lime tree growth. More competitive species, such as beech, maple or ash, dominated better soils, or more readily commercialized species were favoured by foresters. Tree age (equation 1) ranged from 54 to 134 years (mean 71 years). Tree diameter at breast height ranged from 19 to 77 cm (mean 36 cm).

$$\mathrm{Age}_i = \mathrm{Max}\left(\boldsymbol{NrME}_{ij} + \boldsymbol{NrMR}_{ij} + 5\right), \tag{1}$$

where Age_i is the age of the tree $\boldsymbol{i}$, $\boldsymbol{NrME}_{ij}$ is the number of ring-widths measured on the sample $\boldsymbol{j}$ of the tree $\boldsymbol{i}$, $\boldsymbol{NrMR}_{ij}$ is the estimated number of missed tree-rings using the pith locator method (>0 when cores did not cross pith), and $\mathbf{5}$ is the estimated number of years for young trees to reach 1.3 m (height of wood sample extraction).

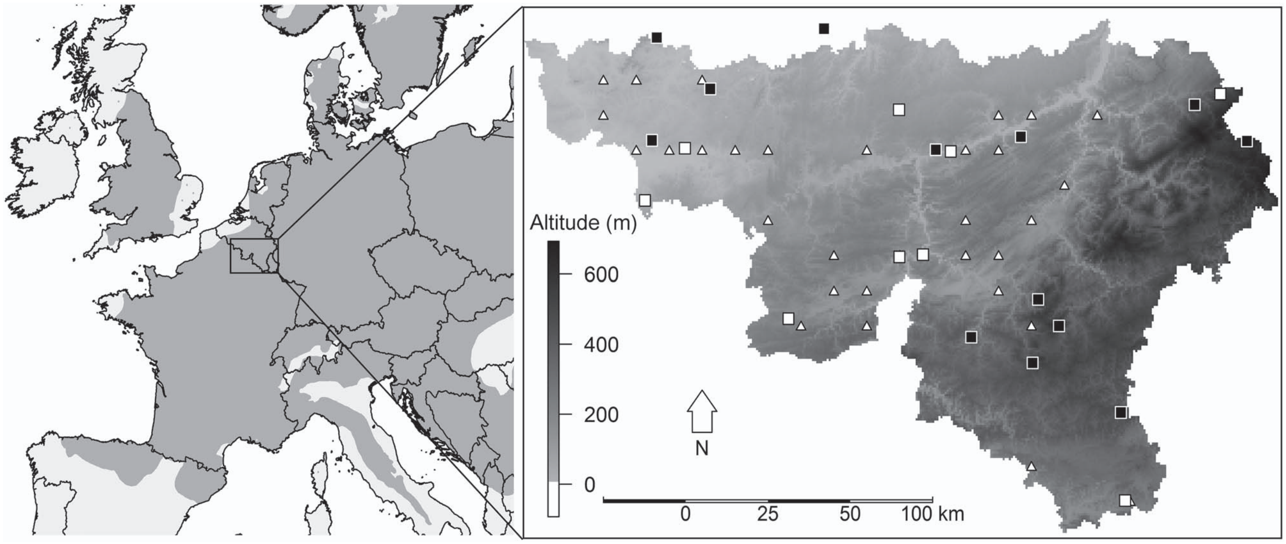

Figure 1 Distribution map of *T. cordata* in Europe (source: www.euforgen.org) and locations of the lime and beech sites in southern Belgium. The white triangles indicate the lime sites visited in the field with the presence of *T. cordata*. One triangle can represent several sites. The white squares indicate the nine lime sites selected for dendrochronological investigations. The black squares indicate the 13 beech sites selected for comparison with lime.

Tree sampling and ring-width measurement

Wood samples were collected in early 2017. Two types of wood sample were used: cores for standing trees and disks when felling was allowed (Table 1). For 97 trees, two perpendicular cores were taken at breast height (1.3 m). For the 23 remaining trees, one disk per tree was collected at breast height. From each disk, two bars (12-cm wide) were extracted along a diameter through the tree core. Bars are a good compromise between disks and cores and increase the precision of ring measurement (Latte *et al.*, 2015).

Air-dried cores and bars were progressively sanded with finer grits of sandpaper (up to 240) and scanned at high resolution (≥1200 dpi). Tree-ring widths were measured from pith to bark with an accuracy of 1/100 mm using WinDENDRO (Regent Instruments Canada Inc, 2009). Ring-width series of wood samples were carefully cross-dated from the tree level to the site and region levels.

Dendrochronological investigations

Tree-ring series pre-processing and dendrochronological analysis were done using R (R Core Team, 2019). The package 'dplR' (Bunn, 2008) was used for chronology building, detrending and statistics computation. The package 'PointRes' (van der Maaten-Theunissen *et al.*, 2015) was used for pointer year identification and resilience computation.

Tree-ring series detrending and quality statistics

Sample ring-width series were detrended using a cubic smoothing spline with a 50 per cent frequency cut-off at 10 years to maximize the climate signal and minimize the effect of age, competition and silviculture in the chronologies (Cook and Kairiukstis, 1990; Latte *et al.*, 2015). Detrended series of wood samples were averaged by tree, tree series by site and site series were averaged at the region level (Figure 2).

Series statistics were computed at site and region levels for the period 1955–2016. For this period, we ensured that the number of trees (≥60) and the resulting tree-ring series met the requirements for being representative of the lime growth at the scale of the study region (Latte *et al.*, 2015). The quality of ring-width series was assessed with the expressed population signal (EPS) and signal-to-noise ratio (SNR). EPS estimates how well a finite sample of tree-ring data represents an infinite population chronology. SNR estimates the strength of the observed common signal among the trees (Wigley *et al.*, 1984).

High-frequency variability in growth

Change over time in growth variability, caused primarily by annual climatic variation, was estimated using Generalized Autoregressive Conditional Heteroscedasticity (GARCH) models ('fGarch' R package) (Wuertz *et al.*, 2013). A GARCH (1, 1) model was fitted to each site-level detrended series and the conditional standard deviation was extracted (Latte *et al.*, 2016b). This method was strongly recommended in preference to mean sensitivity and Gini coefficient (Bunn *et al.*, 2013).

Focus on exceptional growth years

Pointer years are years with unusually narrow or wide ring-widths found in most of the trees in a particular site or region. They often indicate extreme climatic events occurring at a large scale (Matisons *et al.*, 2013). Their analysis, thus, highlights positive and negative effects of weather anomalies on tree growth. Pointer years were detected from ring-width series at site level using Neuwirth's method (Neuwirth *et al.*, 2007).

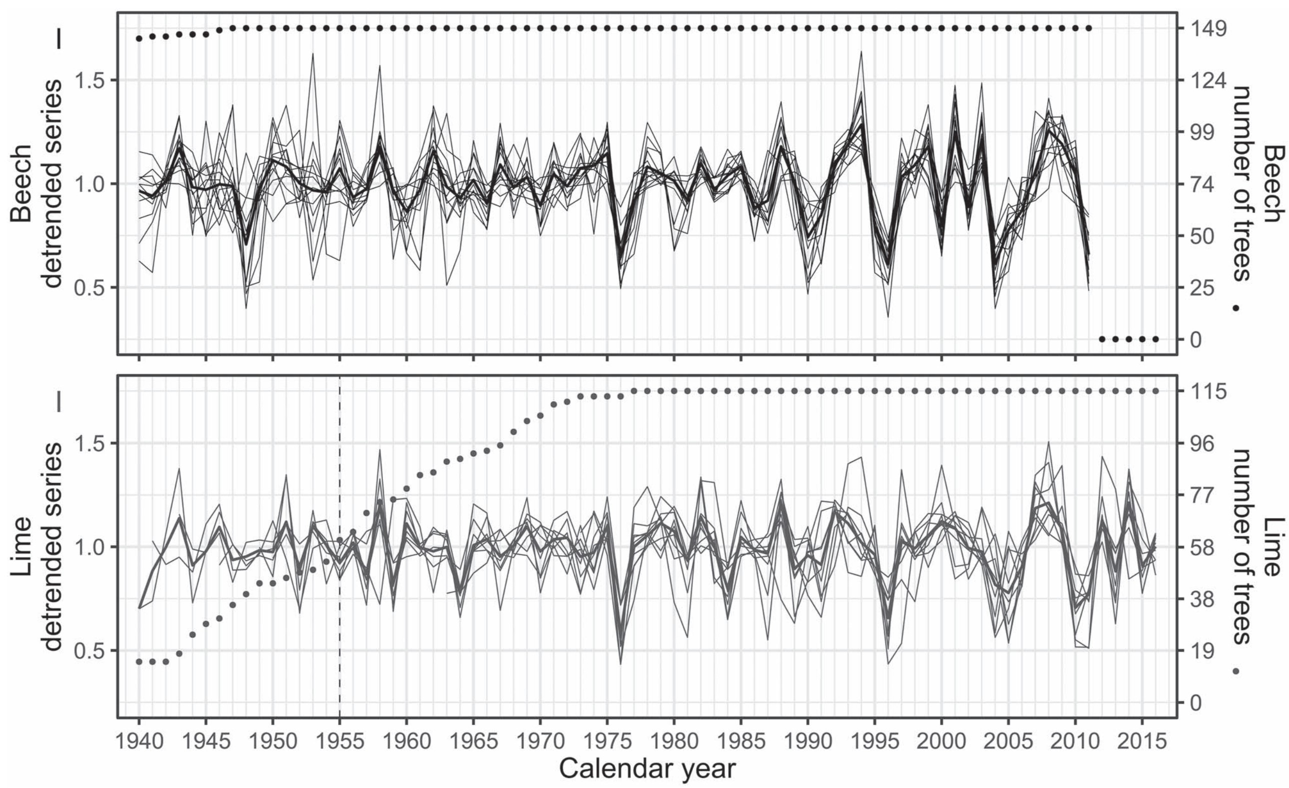

Figure 2 Detrended tree-ring series (at least two trees) for beech (black) and lime (grey) at region level (thick lines) and site levels (thin lines) from 1940 to 2016 (left *y*-axis). The vertical dashed line indicates the year 1955, the first year of the period 1955–2016 for which the number of sites and trees sufficed for dendrochronological analysis. Right *y*-axis: dots indicate the number of trees available (sample depth).

Meteorological data

Daily mean, minimum and maximum temperatures (T_{mean}, T_{min} and T_{max}, respectively, in °C), and precipitation (*P*, in mm) were extracted for each site from the gridded ensemble version (0.1°) of the European Climate Assessment Dataset (Cornes *et al.*, 2018). This dataset, represented by the climatic diagram of the study area in Figure 3, was used to generate 504 climatic variables for the climate–growth analysis. Single and multi-month climatic variables were obtained by averaging the daily values of T_{mean}, T_{min}, T_{max} and *P* for periods of 1–7 months. The final month of these periods ranged from April of the previous year to October of the current year. These meteorological data were also used to describe the climatic conditions of highlighted pointer years.

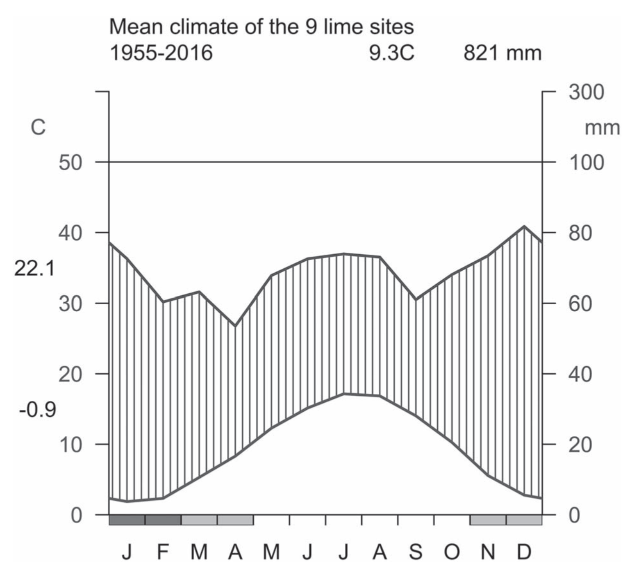

Figure 3 Climatic diagram (Walter and Lieth) of the study area. Mean values of the nine lime sites for the period 1955–2016.

Climate–growth analysis

The climate–growth relationship was analyzed for the period 1955–2016 using R (R Core Team, 2019). The best explanatory variables common to all sites (site-level detrended series) were identified using the sparse partial least squares (sPLS) method ('mixOmics' package; Rohart *et al.*, 2017). This method can be used when the number of variables exceeds the number of observations and in cases of multi-collinearity. sPLS (single component) was computed between the detrended series and standardized climatic variables (i.e. mean 0 and SD 1) of each site. The most explanatory climatic variables were identified based on variable importance in projection (highest VIP). Significance of the correlation coefficients was tested by the bootstrap method

Table 1 Characteristics of the small-leaved lime sites and trees. Mean (Minimum–Maximum)

Site	Tree number	Tree age	DBH (cm)	Number of cores	Number of bars	Mean ring-width (mm)	Altitude (m)	Group or Stand	Soil type	Water availability	Mean annual temperature (°C)	Mean annual precipitation
CHIM	31	72 (55–87)	32 (21–45)	52	10	2.14	240	Stand	Very shallow calcareous brown soil	Low	9.1	812
DOLO	11	69 (59–77)	32 (23–47)	22	0	2.13	120	Group	Mesic brown soil	Medium	9.2	867
ENFR	8	77 (75–79)	32 (28–35)	0	16	1.87	194	Group	Very shallow mesic brown soil on heavy slope	Low	9.3	839
EUPE	14	54 (54–55)	31 (19–40)	28	0	2.89	480	Plantation	Humid acid soil	Medium	8.6	1010
FALM	7	84 (74–86)	43 (34–55)	0	14	2.57	157	Group	Very shallow calcareous brown soil	Low	9.3	839
GHLI	11	79 (66–87)	47 (31–64)	22	0	2.91	60	Group	Sandy acid soil	High	9.4	744
GRLZ	11	62 (55–68)	33 (22–49)	22	0	2.54	165	Group	Humid loamy soil	High	10.0	756
HONN	18	68 (60–78)	35 (27–48)	30	6	2.58	70	Stand	Very shallow acid brown soil	Low	9.6	717
MUSS	9	91 (70–134)	60 (39–77)	18	0	3.42	330	Group	Calcareous brown soil	High	9.0	939
All sites	120	71 (54–134)	36 (19–77)	194	46	2.47	202 (60–480)				9.3 (8.6–10)	836 (717–1010)

with a 95 per cent confidence interval ('bootres' package; Zang and Biondi, 2013).

Long-term growth changes and resilience

Although detrended series allow a focus on high-frequency variability in growth and annual effects of climate, whereas another method is required to assess long-term growth changes. Tree ring-width series were converted into ring-area (also called basal area increment) to enable a more accurate quantification of wood production (Weber *et al*., 2013). The regional curve standardization (RCS) method was then applied on the tree ring-area series to remove the overall age effect at the regional level (Bontemps and Esper, 2011). Resilience (Lloret *et al*., 2011) was computed from the resulting regional series to assess the long-term impact of exceptional climate events (highlighted pointer years). Resilience (equation 2) is an estimation of a tree's capacity to reach pre-disturbance growth level.

$$\text{Resilience} = {\text{Growth}_{y+4}}\Big/{\text{Growth}_{y-4}}, \qquad (2)$$

where y is the year of disturbance, $\textbf{Growth}_{y+4}$ is the average growth for the 4 years following year y, and $\textbf{Growth}_{y-4}$ is the average growth for the 4 years preceding year y.

Comparison with beech

The same dendrochronological investigation was conducted on an additional beech (*F. sylvatica* L.) tree-ring dataset allowing detailed comparisons between lime and beech for the same region and time period. This validated published dataset (Latte *et al*., 2015, 2016a) comprised 149 beech trees from 13 sites (Figure 1).

There are two main differences from the lime tree dataset: (1) only sites with optimal growing conditions (no noticeable topographic or soil constraints) were selected, and (2) the beech trees were older than the lime trees. Mean, minimum and maximum ages of beech trees were 145, 70 and 215 years, respectively (71, 54 and 134 years for lime trees). The effects of these two differences are discussed.

Results

Lime tree-ring series quality

At a region level, EPS values (0.98) and SNR values (48.6) indicate that the chronologies adequately represented the population of lime trees in southern Belgium (Table 2). Site EPS values were >0.85 for most sites (7/9), except for FALM and GRLZ (0.80).

High-frequency variability in growth and long-term changes

During the period 1955–2016, the high-frequency variability in growth (i.e. the conditional standard deviation of GARCH models) increased for both species (Figure 4, top). However, the increase was much more pronounced for beech (about +90 per cent) than for lime (about +10 per cent).

Table 2 Statistics of the ring-width and detrended series at site and region levels for the period 1955–2016

	Ring-width series		Chronology quality	
Site	Mean (mm)	Standard deviation (mm)	Expressed population signal	Signal-to-noise ratio
CHIM	2.14	0.53	0.95	19.1
DOLO	2.13	0.76	0.93	13.8
ENFR	1.87	0.50	0.93	12.6
EUPE	2.89	1.14	0.95	20.0
FALM	2.57	0.51	0.80	4.0
GHLI	2.91	1.11	0.88	7.2
GRLZ	2.54	0.82	0.80	4.0
HONN	2.58	0.55	0.91	10.2
MUSS	3.42	0.83	0.86	5.9
Region	2.47	0.46	0.98	48.6

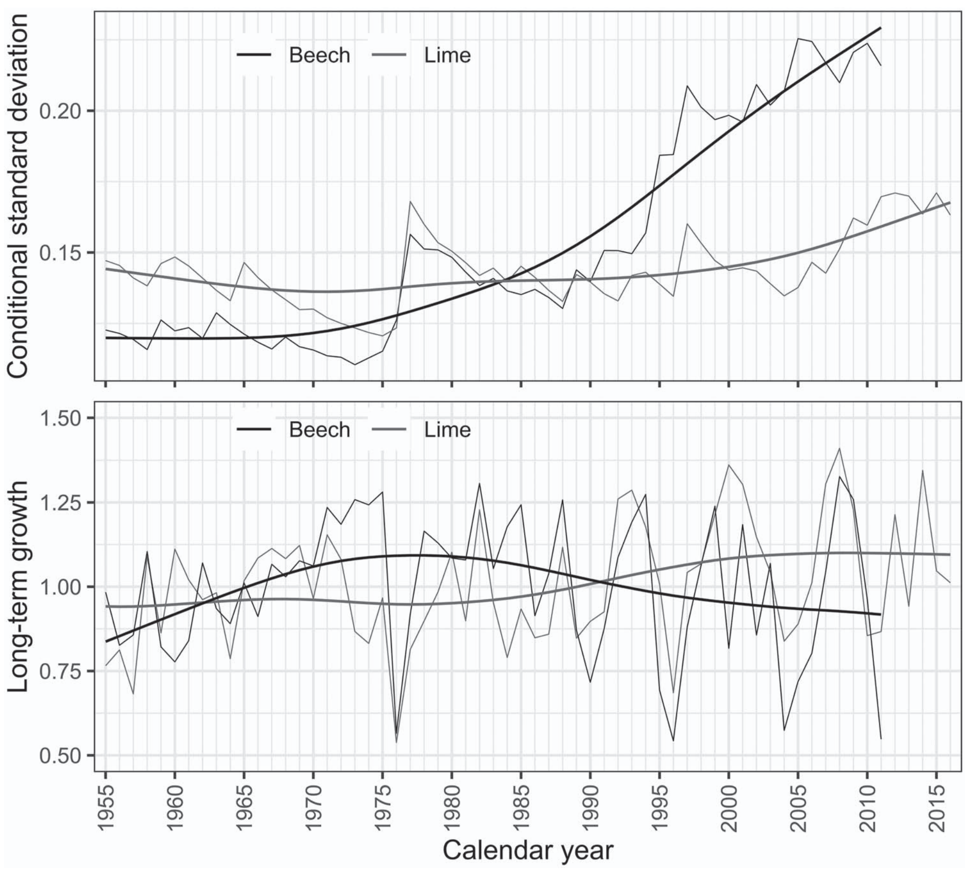

Figure 4 Growth changes over time for beech (black) and lime (grey) during the period 1955–2016. Top: changes in high-frequency variability (i.e. conditional standard deviation of GARCH models). Bottom: changes in long-term growth (i.e. standardized ring-area series at region level without tree age effect). The thicker lines correspond to 40-year splines.

The long-term growth (i.e. the standardized ring-area series at region level without tree age effect) changed over time for both species, but differently (Figure 4, bottom). Before 1976, beech growth increased, and lime growth was stable. After 1976, beech growth decreased (about −15 per cent), and lime growth increased (about +15 per cent).

Pointer year analysis and resilience

The pointer year analysis focused on years with pronounced growth responses to exceptional climatic events. To be able to compare the pointer years of both species with different numbers of sites (beech 13 and lime 9), the number of sites with positive or negative pointer years was expressed as a percentage (Figure 5).

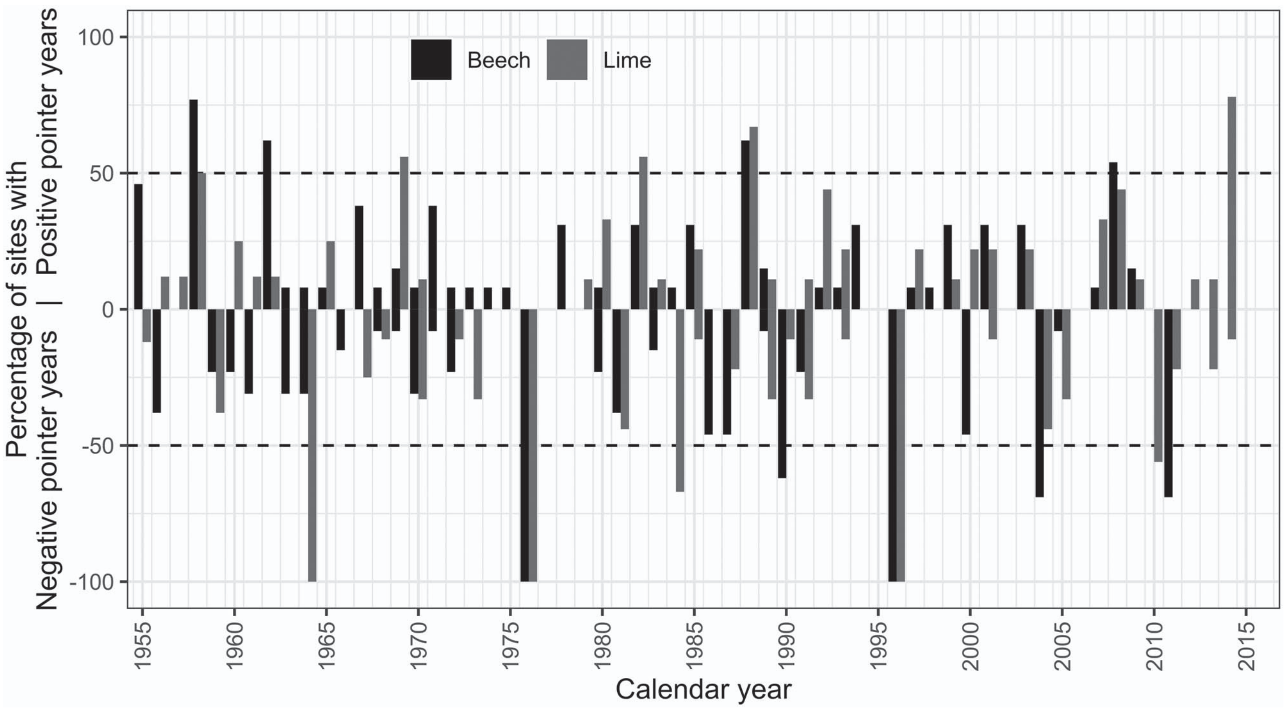

Figure 5 Proportion (in percentage) of beech sites (black) and lime sites (grey) with positive (up) or negative (down) pointer years. The two dashed lines indicate the threshold of 50 per cent used to highlight preponderant pointer years at region level (i.e. common to most sites).

Pointer years that included at least 50 per cent of sites were described based on the meteorological data. Negative pointer years were 1976, 1990, 1996, 2004 and 2011 for beech, and 1964, 1976, 1984, 1996 and 2010 for lime. Positive pointer years were 1958, 1962, 1988 and 2008 for beech, and 1958, 1969, 1982, 1988 and 2014 for lime. Some of these years were common to both species: 1976 and 1996 (negative), and 1958 and 1988 (positive).

The lime negative pointer years 1964, 1976 and 2010 coincided with a combination of very low rainfall and high temperature with heatwaves during the growing season. The negative pointer year 1996 corresponded to a long period of low precipitation from August 1995 to September 1996. The negative pointer year 1984 corresponded to an exceptionally and continually cold growing season with low rainfall. For the lime positive pointer years, the percentages of sites were smaller. 1958, 1969, 1982, 1988 and 2014 coincided with higher rainfall than the mean values of the period 1955–2016 and temperature at least equal to the mean.

The resilience of both species was computed for the highlighted pointer years, in particular the four pointer years common to both species (Figure 6). The difference between the two species was pronounced. Lime growth recovered after stressful climatic events, while beech growth did not. Lime growth also benefited more than beech from favourable climatic years. Average resilience for all positive pointer years was 1.30 for beech and 1.13 for lime. Average resilience for all negative pointer years was −1.05 for beech and 4.34 for lime.

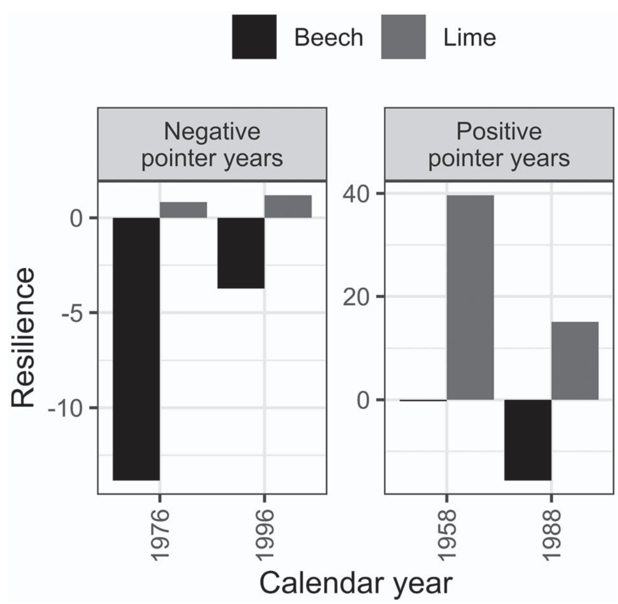

Figure 6 Resilience (i.e. tree's capacity to reach pre-disturbance growth level) for the four pointer years (two negative and two positive) common to both species (black for beech and grey for lime).

Lime climate–growth relationship

The R^2 value of the sPLS model was 14.7 per cent. The main driving climatic variables for the period 1955–2016, in order of

Table 3 BCCs between the best explanatory climatic variables and the detrended series at region and site levels for the period 1955–2016

Climatic variable	Region level	Site level Minimum	Maximum
Mean of daily precipitations from March to July (P–MJ)	0.46	0.3	0.61
Mean of daily minimum temperatures in May (T_{min}–M)	0.30	0.30	0.44
Mean of daily maximum temperatures in June and July (T_{max}–JJ)	-0.23	-0.23	0.02

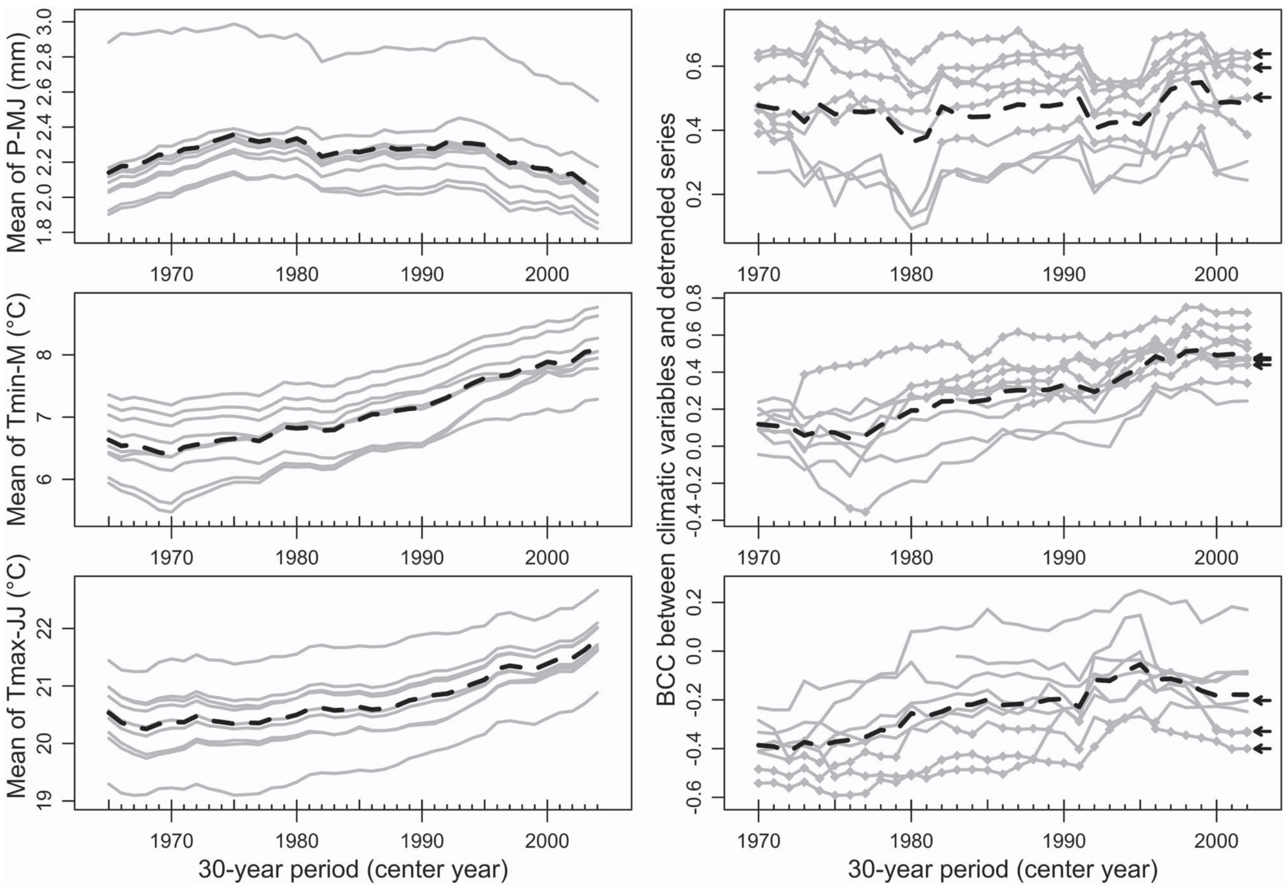

Figure 7 Lime growth–climate relationship. (Left) Moving mean of the best explanatory climatic variables in a 30-year moving window for the period 1955–2016 (one solid grey line per site; dashed lines indicate means of the site values). P–MJ: mean of daily precipitations from March to July. T_{min}–M: mean of daily minimum temperatures in May. T_{max}–JJ: mean of daily maximum temperatures in June and July. (Right) Moving bootstrapped correlation coefficient (BBC) between the same climatic variables and the site-level detrended series. Grey squares indicate significant BCCs. Black arrows indicate the three driest sites (CHIM, ENFR and FALM).

decreasing explanation (Table 3), were: (1) the mean of daily precipitations from March to July (P–MJ), (2) the mean of daily minimum temperatures in May (T_{min}–M) and (3) the mean of daily maximum temperatures in June and July (T_{max}–JJ). The remaining variables, including those of the previous year, did not explain a significant part of the common inter-site growth variation. The bootstrapped correlation coefficients (BCCs) between P–MJ, T_{min}–M and T_{max}–JJ and the detrended series were significant for nine, seven and five sites, respectively. Though significant, BCCs were low for most combinations of sites and variables (Table 3).

Changes over time of the climate variables and their correlation with lime tree growth are shown in Figure 7. For rainfall (P–MJ), the climatic variable with the most explanatory power, no major change was observed. As expected, growths at the driest sites CHIM, ENFR and FALM (Table 1) were the most dependent on precipitations during the growing season.

T_{min}–M and T_{max}–JJ increased at similar rates (about +1°C) during the period 1955–2016. T_{min}–M had a positive, increasing effect on growth. As water is still available at the beginning of the growing season, warm weather is known to be favourable for most forest tree species (Latte *et al.*, 2015). In the case of lime

Table 4 Synthesis of the dendroecological results and comparison between lime and beech species

Results	Small-leaved lime	Common beech
High-frequency variability in growth (Figure 4, top)	Slightly increasing (about +10%)	Strongly increasing (about +90%)
Long-term growth (Figure 4, bottom)	Increasing (about +15%)	Decreasing (about −15%)
Pointer years (PY) analysis (Figure 5)	Stable frequency of negative PY	Increasing frequency of negative PY
Growth resilience (Figure 6)	Complete recovery after negative PY	Partial recovery after negative PY
	Pronounced gain after positive PY	No gain after positive PY
Growth–climate relationship over time	Rather stable or positive evolution (Figure 7)	Negative evolutions (Latte *et al*., 2015)

trees, this positive influence increased over time. T_{max}–JJ had a low and negative but decreasing effect on growth. The driest sites were the most affected (significant BCCs).

Discussion

As expected from its biology (e.g. ecophysiology, natural distribution area, deep rooting), the dendroecological analysis showed that small-leaved lime has been resilient to the past climatic events. Long-term growth increased slightly during the preceding decades (Figure 4) despite the increase in the frequency and intensity of stressful climatic events, highlighted by the pointer year analysis (Figure 5). Lime growth had quickly recovered in the years following the stresses (Figure 6) resulting in stable or positive growth–climate relationships over time (Figure 7).

This behaviour is consistent with some life traits of the species (De Jaegere *et al*., 2016): (1) a high water use efficiency (Pigott and Pigott, 1993), partly due to the sensitivity of its stomata (Aasamaa et al., 2004) and the resistance of its fine roots to embolism (Köcher et al., 2012), and (2) very strong rooting that allows the trees to access deep water reserves, even in rocky soils (Pigott, 1991).

The behaviour of lime trees contrasted strongly with that of beech, especially after 1976, the first and most stressful year, with extreme drought and heatwaves that strongly impacted the growth of both species. The results of the dendrochronological analyses differed systematically in favour of lime (Table 4). While beech growth progressively declined in the long term as a result of repeated stressful years, lime growth recovered fully after each climatic stress, and benefited from favourable climate events. This difference is still more evident given that selection of beech sites was restricted to optimal growing conditions with no noticeable topographic or soil constraints (Latte *et al*., 2015), whereas four out of nine lime sites had a high level of soil dryness (Table 1). Even on the most stressful sites, lime seemed little affected by stressful climate events.

Although the beech trees were older (145 years on average) than the lime trees (71 years on average), the effect of age on changes over time was negligible (Latte *et al*., 2016b). Furthermore, a specific dendrochronological method (RCS) was used to remove the effect of age, allowing a more straightforward comparison between the two species.

Because the lime tree is a rare and scattered species (small tree groups or single trees in mixed forests), it was uncertain whether the dendrochronological routine could provide appropriate tree-ring series. Despite the limited study material and a less strict selection of sites and trees than usual (Mérian and Lebourgeois, 2011; Mérian *et al*., 2013), the good quality of the tree-ring series (Table 2) attests that dendroecological investigation on such species is possible. This opens the way to further dendroecological analysis using other lesser-known forest tree species, and by extension could facilitate the development of forest management alternatives that favour forest diversification in the context of global change (Messier *et al*., 2013; Pretzsch *et al*., 2013).

Conclusion

As expected from its life traits, the small-leaved lime is a favourable candidate for addressing future climate change challenges. Considering the numerous other ecosystem services it provides (De Jaegere *et al*., 2016), this species should be considered by forest managers planning to improve the sustainability and resilience of their forests. More specifically, lime could potentially replace beech on less favourable sites. Our work also suggests that dendroecological investigation on tree resilience to climate change needs to be extended to other such lesser-known forest tree species.

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Conflict of interest statement

None declared.

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