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SHORT COMMUNICATION

Do variations in leaf phenology affect radial growth variations in *Fagus sylvatica*?

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Abstract We used a dendrochronological and leaf phenology network of European beech (*Fagus sylvatica*) in Slovenia, a transitional area between Mediterranean, Alpine and continental climatic regimes, for the period 1955–2007 to test whether year to year variations in leaf unfolding and canopy duration (i.e. time between leaf unfolding and colouring) influence radial growth (annual xylem production and tree ring widths) and if such influences are more pronounced at higher altitudes. We showed that variability in leaf phenology has no significant effect on variations in radial growth. The results are consistent in the entire region, irrespective of the climatic regime or altitude, although previous studies have shown that leaf phenology and tree ring variation depend on altitude. The lack of relationship between year to year variability in leaf phenology and radial growth may suggest that earlier leaf unfolding—as observed in a previous study—probably does not cause increased tree growth rates in beech in Slovenia.

Keywords Climate change · Leaf phenology · Tree rings · European beech

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Introduction

Observed responses of forests to climate change include changes in phenology, growth rates, species composition, increased fire and storm damage, as well as increased insect and pathogen damage. Many species have shifted their seasonal activities, and phenological change has been among the most obvious ecological effects of climate change. Numerous phenological studies of terrestrial ecosystems have reported earlier spring and later autumn phenophases as a consequence of the global increase in average temperatures (Peñuelas and Filella 2001; Menzel et al. 2006; Körner and Basler 2010). Among the most obvious signs of changed phenology in deciduous trees are earlier leaf unfolding in spring, later colouring of leaves in autumn and, consequently, a prolongation of canopy duration, when the leaves are able to carry out photosynthesis (Vitasse et al. 2009; Davi et al. 2011). Some studies have reported an increase in forest productivity associated with an increase in the canopy duration (e.g. Tegel et al. 2014). However, due to the divergent effects of climate on each phase of the plant life cycle, as well as the heterogeneous temporal trends of various climatic elements within the year, it is not clear whether a prolonged growth period increases the productivity of forests and trees (Richardson et al. 2010;

Fischer and Neuwirth 2013; Liu et al. 2013; Richardson et al. 2013).

European beech (*Fagus sylvatica*) has a wide natural range and is often used as a model forest tree species to study phenology and the effects of climate on its growth and survival. Beech has been investigated in numerous studies in which leaf phenology (Dittmar and Elling 2006; Caffarra and Donnelly 2011; Vitasse et al. 2011), dendrochronology (Dittmar et al. 2003; Jump et al. 2006; Di Filippo et al. 2007; Pluess and Weber 2012) and wood formation (Čufar et al. 2008b; Prislan et al. 2013) were investigated in order to understand the influence of environmental conditions on radial growth better.

In Slovenia, a transitional area between Mediterranean, Alpine and continental climatic regimes, recent climatic trends show pronounced warming in summer and spring, which is almost twice as high as in the neighbouring countries (De Luis et al. 2012). Studies on beech leaf phenology in Slovenia have shown significant trends of earlier leaf unfolding and delayed leaf colouring. The same data sets also showed that earlier leaf unfolding is more pronounced at higher elevations than at lower ones (Čufar et al. 2012). Dendroecological analyses in beech in the same area have shown that radial growth variation depends on climatic conditions during summer and also varies with altitude (Di Filippo et al. 2007; Čufar et al. 2008a). Moreover, the onset of cambial production of cells in the wood coincides with leaf unfolding and generally ceases nearly 2 months before leaf colouring (Čufar et al. 2008b; Prislan et al. 2013).

Although we use long-term series of both leaf phenology and tree ring widths across Slovenia, such datasets cannot be directly compared to determine a causal relationship among the observed changes in leaf phenology and their influence on radial growth of trees. Tree ring widths usually decrease as a tree becomes older and bigger, and dendrochronological series then need to be detrended to remove such biological effects before they are compared with climatic and/or phenological series (Holmes 1994). Furthermore, even detrended dendrochronological series cannot be compared with raw phenological series, which also show significant trends, since this may also provide spurious results.

Alternatively, comparisons among detrended dendrochronological series and detrended phenological series may be used as an indirect protocol for testing how observed variations in leaf phenology may influence variations in radial tree growth. If significant correlations are observed when comparing detrended dendrochronological and phenological series, a link between the year to year variations of the two processes could be established.

The aim of the present study was to test two hypotheses: that (a) year to year variations in tree rings are related to year to year variations in canopy duration (expressed as the time between leaf unfolding and general leaf colouring) and (b) such relationships are more pronounced at higher elevations.

Materials and methods

We collected wood from old grown beech (*Fagus sylvatica*) trees at 15 forest sites distributed all over Slovenia (13.73–15.54° E, 45.55–46.45° N, altitudes 355–1330 m) to construct local tree ring chronologies. A total of 288 samples (1 to 2 per tree) from 153 trees (5 to 24 per site) were used. Sampled trees were on average 166 years old (range 81 to 270 years). All chronologies showed EPS (expressed population signal) (Wigley et al. 1984) values above the 0.85 threshold for the analysed period 1955–2007, which indicated reliable replication with tree ring data.

Leaf phenology data for the period 1955–2007 were obtained from the phenological archive of the Slovenian National Phenological Network of the Environmental Agency of the Republic of Slovenia (ARSO). From the available data at 47 localities, we selected those corresponding to 15 sites, for which we constructed tree ring chronologies. The day of the first leaf unfolding (LU) and general leaf colouring (LC), as well as the canopy duration (DL) (expressed as the time between LU and LC), were used for analysis. The period of analysis, 1955–2007, was selected based on the availability of reliable tree ring chronologies and phenological data.

We constructed raw and detrended tree ring chronologies for each of the sites. For the latter, the individual raw tree ring width series were detrended to remove age-related growth trends and potential disturbance or competition effects on mean tree ring widths using the ARSTAN program (Holmes 1994) by applying a two-step procedure (Cook and Peters 1997). First, the long-term trend was removed by fitting a negative exponential function or a regression line to each tree ring series. Second, more flexible detrending was performed by a cubic smoothing spline with a 50 % frequency response of 60 years to filter out the effect of localized potential disturbance events. Autoregressive modelling of the residuals and a bi-weight robust estimation of the mean were then applied to obtain detrended and non-autocorrelated residual local tree ring chronologies (Cook and Peters 1997). Raw non-detrended and detrended residual tree ring chronologies for the period 1955–2007 are shown in Fig. 1.

We also used raw and detrended series in the case of leaf phenological data. The long-term trend was removed by fitting a regression line to the series of leaf unfolding, leaf colouring and canopy duration for the period 1955–2007. Raw and detrended phenological series are shown in Fig. 2.

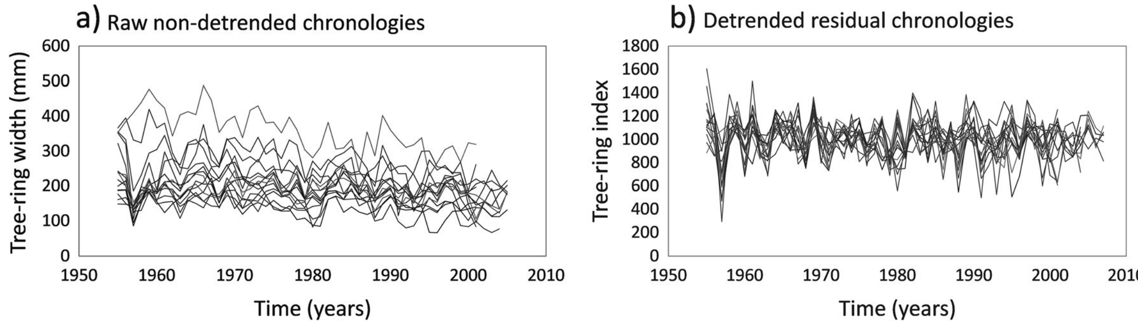

Fig. 1 Tree-ring chronologies of 15 study sites in Slovenia for the period 1955–2007: **a** non-detrended tree-ring width chronologies and **b** detrended ARSTAN residual chronologies

The comparison of tree ring and leaf phenological data was done in two steps. In the first step, raw tree ring width chronologies were compared with raw phenological series using Pearson correlation coefficients. Since using non-detrended series can lead to false interpretation of the obtained results, due to biological trends in tree ring and phenological series, a second analysis was done using the detrended series. In this case, the residual tree ring chronologies were compared with detrended phenological series using Pearson correlation. Significant correlations obtained from these analyses would indicate that year to year variations in the timing of leaf phenology are significantly reflected in tree ring variation patterns. The existence of such relations would suggest that long-term trends, as observed in the timing of leaf phenology, are likely to have long-term consequences for radial growth.

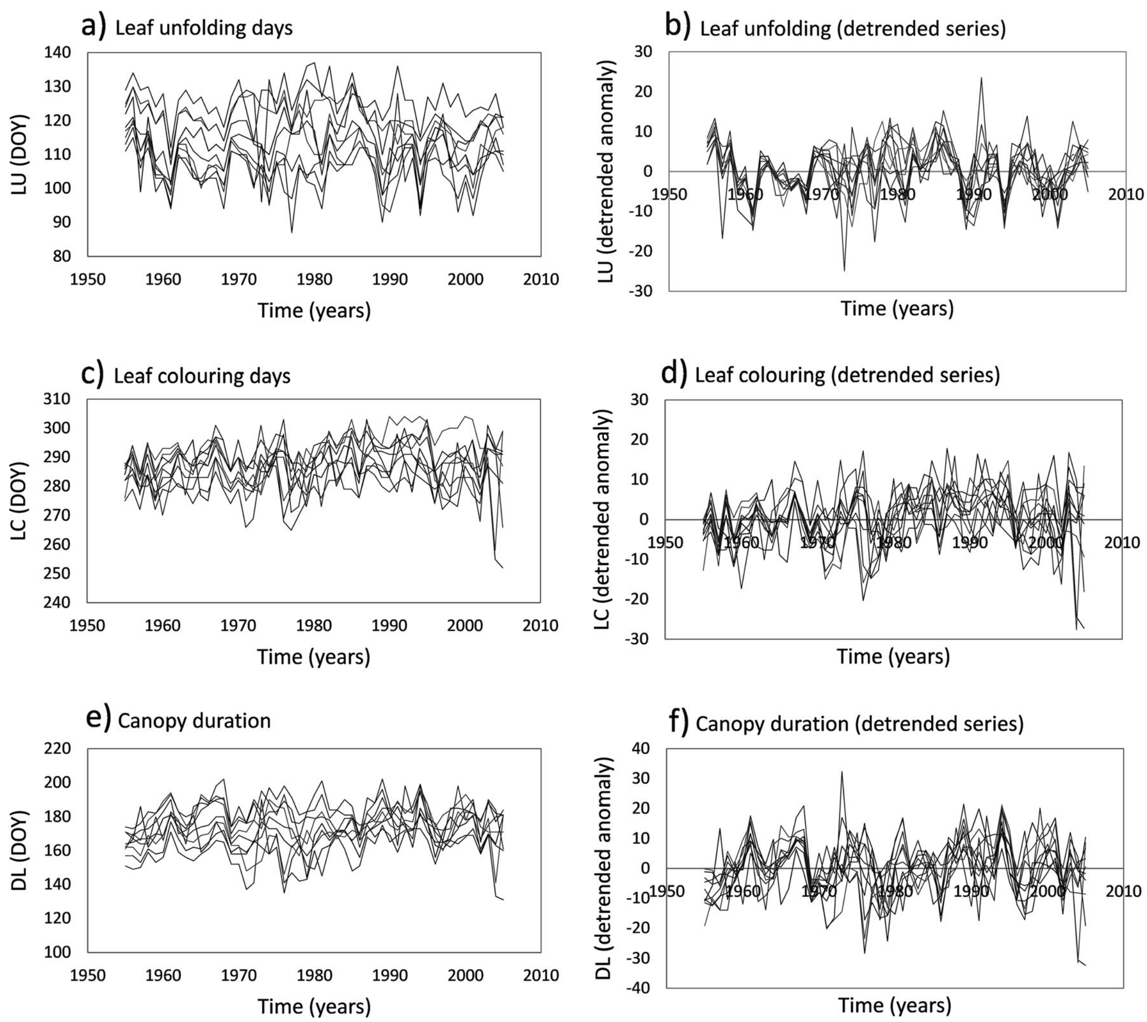

Fig. 2 Leaf unfolding (LU), general leaf colouring (LC) and canopy duration (DL), expressed as the time between LU and LC, for the period 1955–2007 at the 15 study sites in Slovenia: **a**, **c**, **e** raw and **b**, **d**, **f** detrended time series. *DOY* day of the year

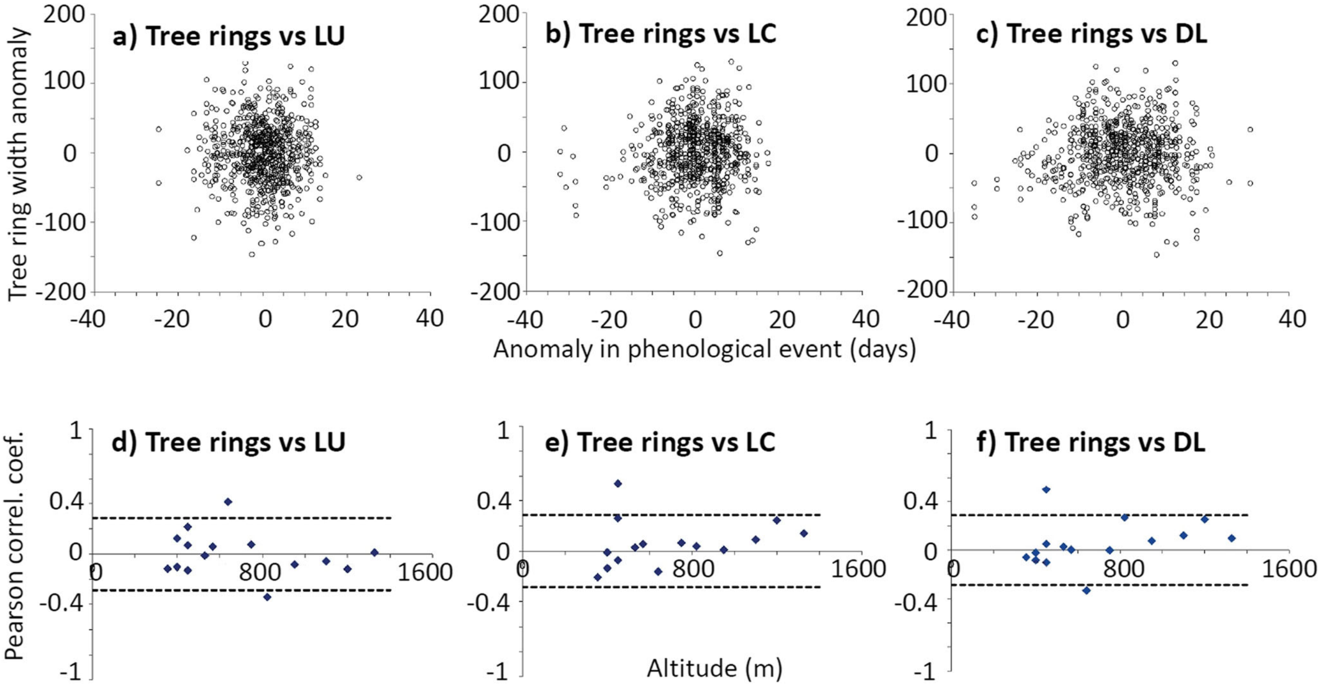

Fig. 3 Tree-ring width deviations in relation to non-detrended series of leaf unfolding (LU), general leaf colouring (LC) and canopy duration (DL), for a network of 15 sites from Slovenia (**a**, **b**, **c**). Pearson correlation coefficients between deviations in tree-ring widths and leaf phenology (LU, LC, DL) in relation to altitude (**d**, **e**, **f**). *Dashed horizontal lines* in **d**, **e** and **f** indicate thresholds of significance levels

Results and discussion

Correlation coefficients obtained when comparing raw tree ring chronologies and raw phenological series show that, in general, variations in leaf phenological dates are not significantly correlated with tree ring widths (Fig. 3a–c). Such a lack of correlation is observed at all altitudes across Slovenia (Fig. 3d–f).

Moreover, correlation coefficients between residual tree ring chronologies and detrended series of leaf phenology

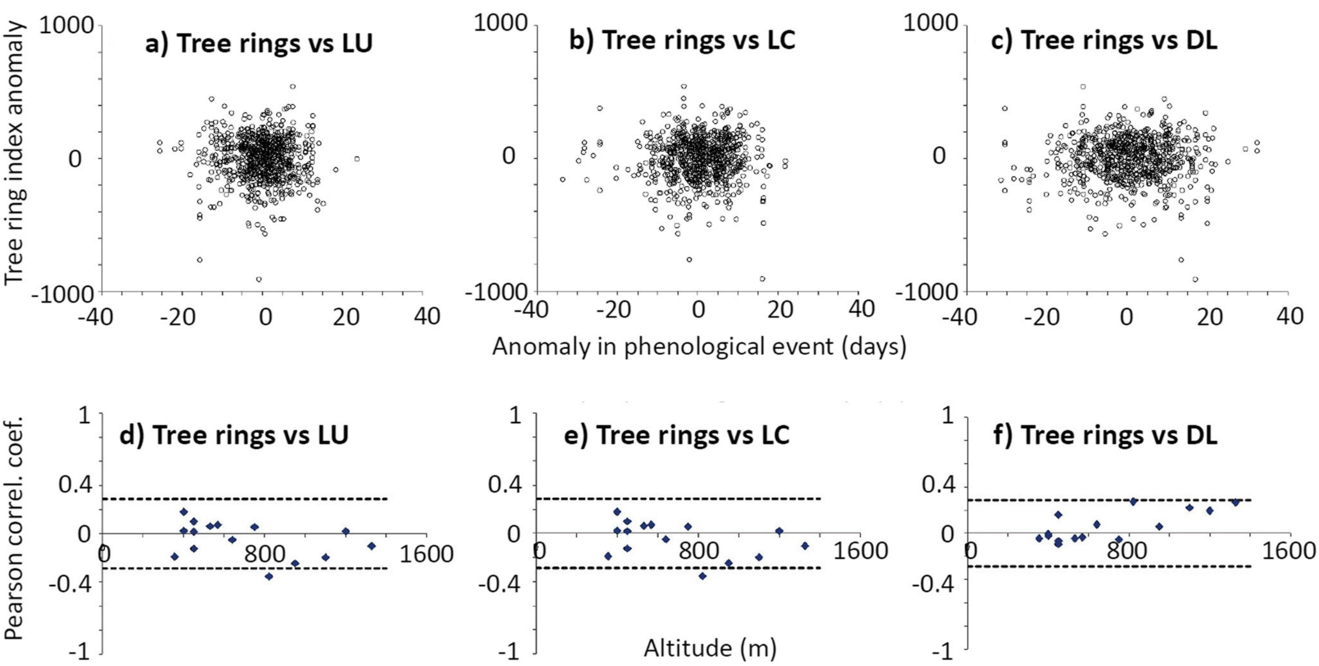

Fig. 4 Deviations of tree-ring indexes (detrended residual values) in relation to detrended series of leaf unfolding (LU), general leaf colouring (LC) and canopy duration (DL), for a network of 15 sites from Slovenia (**a**, **b**, **c**). Pearson correlation coefficients between deviations in tree-ring indexes and detrended series of leaf phenology (LU, LC, DL) in relation to altitude (**d**, **e**, **f**). *Dashed horizontal lines* in **d**, **e** and **f** indicate thresholds of significance levels

show that year to year variations in leaf unfolding, leaf colouring and canopy duration do not have a significant effect on year to year tree ring variations at any of the 15 study sites (Fig. 4a–c). This result suggests that the previously observed earlier dates of leaf unfolding and delayed dates of leaf colouring as a consequence of climate warming probably do not cause a significant change in the radial growth of *Fagus sylvatica*. A lack of relationship was observed at all altitudes (Fig. 4d–f), suggesting that such results may be consistent across the whole of Slovenia.

The presented results do not therefore support the assumption that trends towards earlier leaf unfolding, later leaf colouring and longer canopy duration trigger increased radial growth.

Although several studies have shown clear trends towards earlier leaf unfolding, later leaf colouring and, consequently, longer canopy duration in beech (Hájková et al. 2010; Vitasse et al. 2010; Čufar et al. 2012), our results suggest that these changes are possibly not reflected in increased radial growth. One of the reasons for a lack of clear linkage between the two processes might be that different climatic variables drive leaf phenology and radial growth. Previous studies in the same area (Slovenia) have shown that leaf unfolding is positively affected by March/April temperatures and leaf colouring by July/August temperatures (Čufar et al. 2012). Furthermore, leaf colouring occurs ca. 2 months after the cessation of wood production by the cambium (Čufar et al. 2008b; Prislan et al. 2013). The products of photosynthesis accumulated after the cessation of wood production are therefore probably deposited as reserves, although it is not clear whether and how they affect wood production in the following year.

On the other hand, radial growth of *F. sylvatica* mainly depends on June precipitation and temperatures, with a positive response if June is wet and cool (Di Filippo et al. 2007; Čufar et al. 2008a, b). Wood formation studies have shown that tree ring width depends on the rate and duration of xylem production during the growth season. A longer growth season proved to be associated with less intense maximum growth rate during May and June (Prislan et al. 2013). This suggests that some compensatory processes may cause trees to adjust wood formation rates to variable climatic conditions and could at least partly explain the lack of a significant relation between leaf phenology and radial growth at the breast height of the stems of mature trees. With a longer growing season, increases in carbon losses through respiration can also outpace gains made through photosynthesis, thereby reducing the strength of the carbon sink in forest ecosystems. There is currently no consensus about which process will end up dominating, so the direction and extent to which changes in climate and subsequent changes in growth season length will affect rates of carbon sequestration in temperate forests remain uncertain (Polgar and Primack 2011).

The presented high frequency (year to year) variation in tree rings and leaf phenology shows no clear relation to altitude, although previous studies for the same area (Slovenia) have shown that the influence of climate on both radial growth (Čufar et al. 2008a) and leaf phenology greatly varies along altitudinal gradients (Čufar et al. 2012). Although it was shown that different climatic elements drive leaf phenology and tree ring variation at low and high elevation sites, the expectation that radial growth might increase at higher elevations (due to changes in leaf phenology) cannot be confirmed. A great dependency of leaf phenology on elevation has also been shown in other European countries, such as Switzerland, Germany and France (Davi et al. 2006, 2011; Vitasse and Basler 2013) but whether such changes affect tree growth is still not sufficiently explored.

In addition to the general role of climate, which shows pronounced seasonal and altitudinal changes in the sampling area in Slovenia (De Luis et al. 2012), the increasing frequency of extreme weather events, such as extreme minimum temperatures in spring, increased risk of late frosts, heat waves in summer, droughts, wind-storms, fires, pest outbreaks and ice storms may additionally affect relations between leaf phenology and tree growth (Jentsch and Beierkuhnlein 2008; Menzel et al. 2011; Limousin et al. 2012; Reyer et al. 2013).

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