Tree Physiology 36, 78–85
doi:10.1093/treephys/tpv087

Research paper

The influence of the soil on spring and autumn phenology in European beech

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Received March 30, 2015; accepted August 10, 2015; published online September 28, 2015; handling Editor Chunyang Li

Tree phenology is a key discipline in forest ecology linking seasonal fluctuations of photoperiod and temperature with the annual development of buds, leaves and flowers. Temperature and photoperiod are commonly considered as main determinants of tree phenology while little is known about interactions with soil chemical characteristics. Seedlings of 12 European beech (*Fagus sylvatica* L.) provenances were transplanted in 2011 to model ecosystems and grown for 4 years on acidic or calcareous forest soil. Spring bud burst and autumnal leaf senescence were assessed in the last 2 years, 2013 and 2014, which were characterized by contrasting annual temperatures with a very warm spring and autumn in 2014. In 2013, spring bud burst and autumnal leaf senescence were advanced on acidic soil with a greater effect on leaf senescence. Hence, the vegetation period 2013 was shorter on this soil type compared with that on calcareous soil. In 2014, a similar soil effect was observed for spring bud burst while autumnal leaf senescence and the length of the vegetation period were not affected, probably due to interferences with the overall extension of the vegetation period in this exceptionally warm year. A different soil responsiveness was observed among the provenances with early bursting or senescing provenances being more sensitive than late bursting or senescing provenances. The findings of this study highlight the soil as an ecologically relevant factor in tree phenology and might help explain existing uncertainties in current phenology models.

Keywords: bud burst, *Fagus sylvatica* L., leaf senescence, provenances, vegetation period.

Introduction

Spring bud burst and autumnal leaf senescence are key phenological events in winter-deciduous tree species shaping their seasonal lifestyle in cold and temperate areas. Winter chilling, rising spring temperature and photoperiod act in concert with genetic factors as the main determinants of bud burst. This external and internal regulation ensures an optimal timing of spring outgrowth when weather conditions become favorable and the risk of late frost damage is low. Late in the vegetation period, decreasing temperature and a shorter photoperiod are associated with a downregulation of leaf photosynthesis and growth activities (Arend et al. 2013, Kuster et al. 2014) accompanied by a gradual progression of autumnal leaf senescence until leaf abscission toward the end of the vegetation period. As spring bud burst and autumnal leaf senescence integrate temperature signals over a sustained period of time, records of these phenological events are used to detect past climate trends and related temporal shifts in the vegetation period (Menzel and Fabian 1999, Menzel et al. 2006). Based on this, several phenology models have been developed to predict future vegetation responses to global warming (e.g., Kramer 1994, Chuine et al. 2000, Cleland et al. 2007, Morin et al. 2009). Nevertheless, there is still a large uncertainty in these backward- and forward-directed modeling approaches; hence, a better understanding of tree phenology and its environmental control is needed (Parmesan 2007, Körner and Basler 2010, Pau et al. 2011, Way 2011, Jochner et al. 2013*a*, Mäkela 2013).

To date, the environmental control of tree phenology has been mainly attributed to temperature and photoperiod, although other environmental parameters may also play roles. In addition to elevated CO_2 and climatic drought, the soil might be an underestimated factor affecting tree phenology (Dickie et al. 2007, Nord and Lynch 2009). Indeed, soil fertilization has been shown to advance bud burst in Sitka and Norway spruce seedlings (Murray et al. 1994, Fløistad and Kohmann 2004, Luoranen and Rikala 2011) and delayed bud set in poplar trees (Sigurdsson 2001). Furthermore, several physical and chemical soil characteristics were found to correlate with the spring phenology of deciduous trees and shrubs growing along an oceanic–continental gradient (Wielgolaski 2001). Although these previous studies demonstrated first evidence for edaphic factors involved in controlling bud burst, the soil as a modulator of tree phenology has received little attention so far. This comes as a surprise as soil characteristics exert a significant, but often overlooked, influence on the plant's general responsiveness to other environmental variables (e.g., Maurer et al. 1999, Körner 2011). Hydraulic soil properties, pH, nutrient availability and soil biota may interact with climatic cues on phenological traits at different scales of plant organization and function. Root colonization by mycorrhiza, for instance, has been shown to correlate with earlier bud burst in transplanted oak seedlings, most likely through the improved mineral absorption capacity of mycorrhizal roots (Dickie et al. 2007). Such interactions must not be ignored in phenological studies with tree species growing over a wide range of differing soil conditions. This applies in particular to European beech (*Fagus sylvatica* L.), a dominant, late successional key species in European forests growing on mesic soils with contrasting pH and carbonate content (Peters 1997). Although these chemical characteristics are recognized as main criteria for soil classification in forest ecology (Osman 2013), no information exists regarding their relevance for phenological studies with beech and other tree species.

Improved knowledge on the interactions between the spatial variability of chemical soil characteristics and temperature-driven spring bud burst and autumnal leaf senescence could help explain existing uncertainties in phenology models describing past or estimating future responses of forest vegetation to climate change. Indeed, reducing uncertainty in phenology models is a crucial issue allowing more reliable predictions on how climate change may influence the length of the vegetation period and thus ecosystem productivity and its late frost susceptibility (e.g., Kramer 1994, Estrella and Menzel 2006, Cleland et al. 2007, Augspurger 2009). With respect to this, the present study aims to evaluate the effect of soils with contrasting pH and carbonate content on the spring and autumn phenology of European beech. Seedlings of different provenances were transplanted into large model ecosystems and grown on both acidic and calcareous forest soils. Spring bud burst and autumnal leaf senescence were assessed on both soil types in 2 years with cold or warm temperatures. The obtained phenological pattern was finally used to show whether and how the length of the vegetation period is affected on both soil types.

Materials and methods

Plants and growth conditions

Seedlings of 12 beech provenances were excavated in natural forest stands of two Swiss inner-alpine valleys (Table 1). From each provenance, 64 seedlings with a size of ~20 cm were transplanted in spring 2011 to the model ecosystem facility MODOEK of the Swiss Federal Institute for Forest, Snow and Landscape Research WSL (47°21′48″N, 8°27′23″E, 545 m a.s.l.). To avoid any interfering effects of transplantation in the subsequent phenological studies, the seedlings were acclimatized for two growing seasons to overcome the transplantation shock and regenerate their root system. At the end of the experiment in autumn 2014, the seedlings had a height between 50 and 200 cm. The MODOEK facility comprises 16 model ecosystems with a height of 3.5 m and movable side walls and sliding roofs that were kept open to avoid air warming. Belowground, each model ecosystem is split into two lysimeters with a depth of 150 cm, filled with acidic (haplic Alisol) or

Table 1. Environmental characteristics of the selected provenance sites. Climate data (annual mean temperature and annual sums of precipitation) are taken from nearby METEO SWISS stations (distances ≤10 km).

Provenance	Geographic location	Ann. temp. (°C)	Ann. precip. (mm)	Elevation (m above sea level)	Geology; soil pH
Ardon	46°13′N, 7°14′E	9.2	542	750–850	Limestone; 8.0–8.5
Chamoson	46°12′N, 7°12′E	9.2	542	750–850	Shale; 4.5–5.5
Saxon	46°8′N, 7°11′E	9.2	542	700–800	Shale/limestone; 5.0–8.0
Martigny	46°6′N, 7°6′E	9.2	843	500–700	Gneiss; 4.5–5.0
Collombey	46°16′N, 6°56′E	8.9	1055	550–650	Marlite; 4.5–5.0
Ollon	46°18′N, 6°59′E	8.9	1055	600–700	Limestone/gypsum; 8.0
Felsberg	46°51′N, 9°28′E	8.9	798	650–800	Limestone; 8.0
Chur	46°52′N, 9°32′E	8.9	798	700–800	Boulders; 4.5–7.5
Malans	46°59′N, 9°34′E	8.9	1102	600–700	Boulders; 4.5–5.5
Mastrils	46°58′N, 9°32′E	8.9	1102	550–650	Shale/limestone; 5.0–8.0
Sargans	47°3′N, 9°26′E	9.2	1325	650–750	Shale/limestone; 4.5–5.0
Mels	47°3′N, 9°24′E	9.2	1325	650–750	Sandstone; 4.5

calcareous (Fluvisol) forest soil. In each model ecosystem, four seedlings from each provenance were transplanted. The acidic and calcareous soils had a pH of 4.0 and 6.9, respectively, with different chemical composition but comparable soil texture and water conditions (see Kuster et al. 2013). The most differing mineral elements were calcium with a 10 times higher availability in calcareous soil and manganese with a 13 times higher availability in acidic soil.

Temperature regime and phenological observations in 2013 and 2014

The phenology of the seedlings was studied in 2 years with contrasting temperatures. Compared with the long-term average of the nearby METEO SWISS station 'Zürich Fluntern', the first year 2013 was characterized by a cold spring and warm autumn with temperatures decreased by −1.3 °C in March/April and increased by +1.0 °C in September/October. The annual temperature of 9.0 °C was close to the long-term average of 9.4 °C. In contrast, the second year 2014 was exceptionally warm with an annual temperature of 10.6 °C. Temperature in March/April and September/October was increased by +1.8 and +1.9 °C. Spring bud burst was assessed in all seedlings on a daily basis with a seedling considered to be bursting when the first bud broke out and the green leaf tissue became visible. For consistency, bud swelling and leaf unfolding were not considered as these gradually developing patterns are hard to precisely assess with a daily resolution. Moreover, strong correlations exist between the times of bud swelling and leaf unfolding on the one hand and bud burst on the other (Kuster et al. 2014). Autumnal leaf senescence was assessed in half of the seedlings per provenance from August to November by measurements of leaf chlorophyll loss using a SPAD chlorophyll meter (Konica Minolta Optics Inc., Osaka, Japan). In each seedling, 8–10 leaves were measured to account for variable senescence development within individuals. The date of 50% leaf chlorophyll loss (LCL_{50}) was derived from repeated measurements of chlorophyll content, carried out in intervals of 1–3 weeks from August to November. This approach, based on chlorophyll degradation as physiological indicator of leaf senescence (Buchanan-Wollaston 1997), allows a precise determination of gradually developing leaf senescence (Norby et al. 2000, Herrick and Thomas 2003, Fridley 2012).

Statistical analysis

To test for significance of the fixed factor 'soil' and the random factor 'provenance' in each of the 2 years, phenological data were subjected to analysis of variance (ANOVA). According to the experimental design of the MODOEK facility, the soil was considered as nesting factor for provenance. The significance of the factor 'year' was tested for each soil type separately by repeated-measures ANOVA. Relationships between the timing of the assessed phenological events and the effect size of the soil factor were analyzed by Pearson's correlation. The effect size was calculated as temporal difference ($\Delta t_{\text{calc./acidic soil}}$) between the average dates of spring bud burst and autumnal leaf senescence on calcareous and acidic soil. Treatment effects and correlations were considered to be significant at $P < 0.05$. All statistical analyses were performed with SPSS 17.0 (IBM Corporation, Armonk, NY, USA).

Results

Spring bud burst

The onset of spring bud burst was highly variable spanning a time period of 26 and 29 days over all seedlings in 2013 and 2014, respectively. Most of this variability was attributable to the very different dates of bud burst among individual trees within the same provenance and soil treatment. Despite this overall variability, the onset of bud burst differed among the provenances in both years (Figure 1a and b; $P < 0.001$) with Saxon being the earliest bursting provenance and Mastrils one of the latest bursting provenances. These differences, however, could not be explained by the environmental conditions at the sites of provenance origin as correlation analyses with spring or annual temperature and precipitation yielded low and nonsignificant correlation coefficients (data not shown). Comparing bud burst on acidic and calcareous soil, it became evident that the soil type is a significant factor affecting this phenological trait. Trees opened their buds earlier on acidic soil than those on calcareous soil with an overall difference of 1.3 days ($P = 0.003$) in 2013 and 1.6 days ($P = 0.001$) in the warm spring 2014. Early bursting provenances were more affected by the soil factor than late bursting provenances. In 2013, the onset of bud burst differed most in the earliest bursting provenance Saxon with an advancement of 2.7 days on acidic soil compared with the calcareous soil (Figure 3a). In the warm year 2014, this difference was even 3.4 days (Figure 3c). In contrast, the late bursting provenance Mastrils showed only a marginal response to the soil in 2014 or even an opposite response in the relatively colder year 2013. This provenance-specific soil responsiveness could also be demonstrated by correlation analyses showing in both years a close and significant relationship between the onset of bud burst and the effect size of the soil factor in the tested provenances (2013: $R = 0.82$, $P = 0.001$; 2014: $R = 0.65$, $P = 0.02$).

Autumnal leaf senescence

Autumnal leaf chlorophyll degradation measured as the date of LCL_{50} was used as a quantitative indicator of autumnal leaf senescence. The date of LCL_{50} was highly variable, spanning a time period of 38 and 43 days over all seedlings in 2013 and 2014, respectively. As for spring bud burst, most of this variability was attributable to the very different dates of LCL_{50} among individual trees within the same provenance and soil treatment. In both years, differences among provenances were not significant (Figure 2a and b; 2013: $P = 0.92$; 2014:

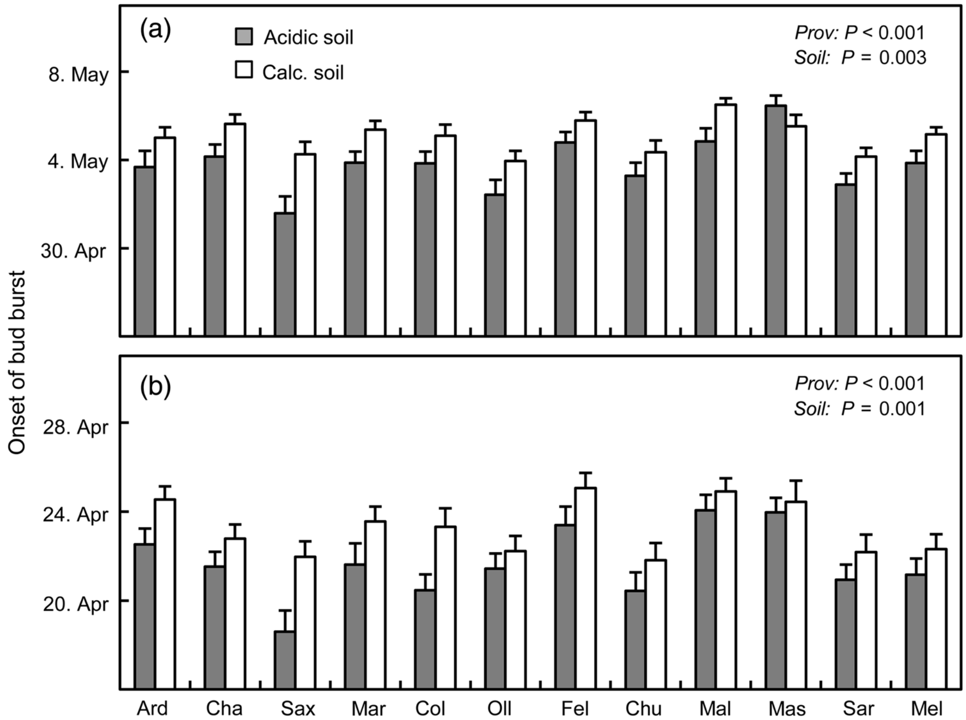

Figure 1. Onset of spring bud burst on acidic and calcareous soil in the transplanted beech provenances in (a) 2013 and (b) 2014 (means ± SE, $n \geq 16$). Ard, Ardon; Cha, Chamoson; Sax, Saxon; Mar, Martigny; Col, Colombey; Oll, Ollon; Fel, Felsberg; Chu, Chur; Mal, Malans; Mas, Mastrils; Sar, Sargans; Mel, Mels.

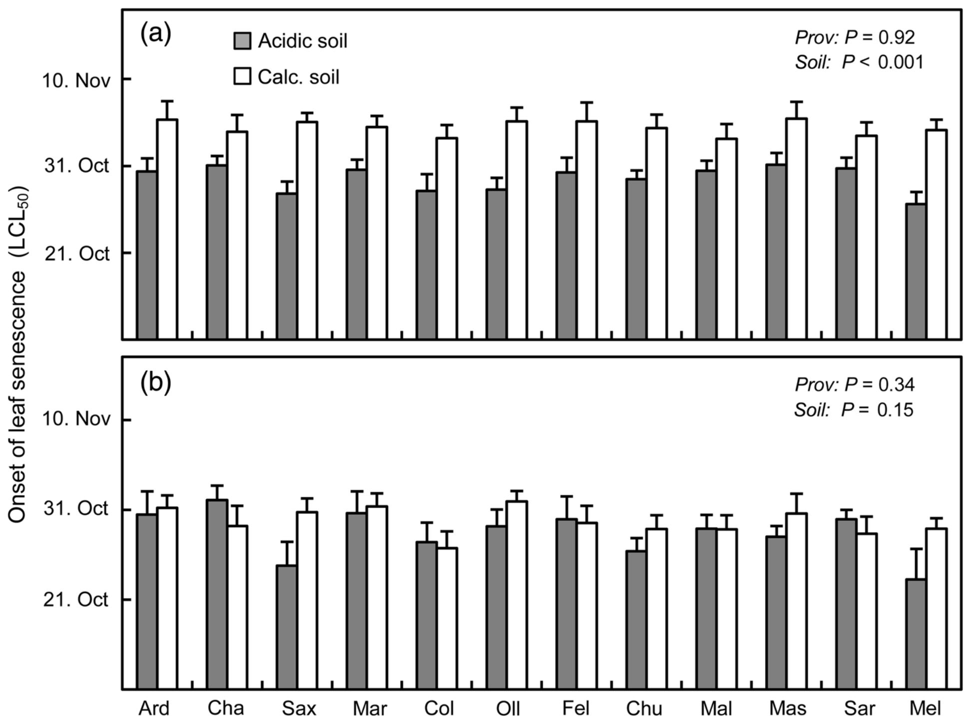

Figure 2. Onset of autumnal leaf senescence (LCL_{50}) on acidic and calcareous soil in the transplanted beech provenances in (a) 2013 and (b) 2014 (means ± SE, $n \geq 16$). Ard, Ardon; Cha, Chamoson; Sax, Saxon; Mar, Martigny; Col, Colombey; Oll, Ollon; Fel, Felsberg; Chu, Chur; Mal, Malans; Mas, Mastrils; Sar, Sargans; Mel, Mels.

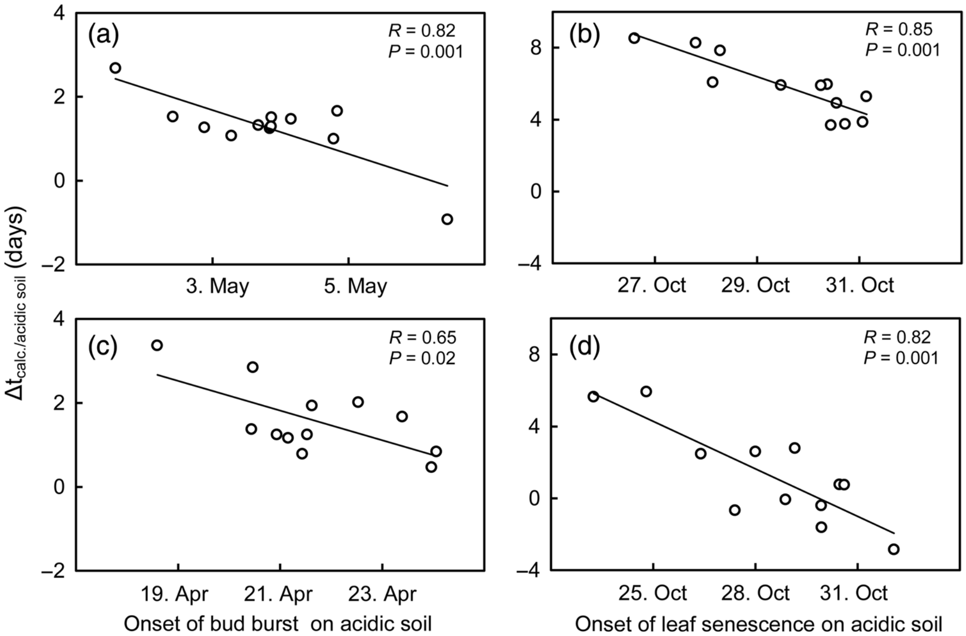

Figure 3. Relationships between the phenological development of the provenances on acidic soil and the effect size of the soil factor ($\Delta t_{calc./acidic\ soil}$). Onset of spring bud burst in (a) 2013 and (c) 2014 and autumnal leaf senescence (LCL_{50}) in (b) 2013 and (d) 2014. Early bursting/senescing provenances were more affected by the soil than late bursting/senescing provenances ($\Delta t_{calc./acidic\ soil}$: temporal difference between the dates of bud burst and leaf senescence on calcareous and acidic soil).

$P = 0.34$). In 2013, the date of leaf senescence was strongly influenced by the soil type on which the trees were grown. On average, the trees reached the LCL_{50} threshold 5.8 days earlier on acidic than on calcareous soil (Figure 2a; $P < 0.001$). This soil effect could, however, not be statistically confirmed in the following year 2014. In this exceptionally warm year, the overall threshold of LCL_{50} was reached only 1.2 days earlier on acidic than on calcareous soil (Figure 2b; $P = 0.15$). Nevertheless, it is worth noting that the first trees reaching the threshold of LCL_{50} were observed on acid soil (see Figure 4e, inset). As shown for spring bud burst, the soil effect on LCL_{50} was distinctly pronounced in early senescing provenances. For example, the advancement of LCL_{50} on acidic soil in 2013 was 8.3 and 8.5 days in the earliest senescing provenances Saxon and Mels compared with 3.9 days only in the latest senescing provenance Chamoson (Figure 3b). Also in the following year 2014, this trend was observed even though the overall soil effect was not significant (Figure 3d). Correlation analyses revealed in both years a close and highly significant relationship between the date of LCL_{50} and the effect size of the soil factor in the tested provenances (2013: $R = 0.85$, $P = 0.001$; 2014: $R = 0.82$, $P = 0.001$).

Length of the vegetation period in 2013 and 2014

In the exceptionally warm year 2014, seedlings started spring bud burst on average 12.1 and 11.8 days earlier on acidic and calcareous soil, respectively, than in the relatively colder year 2013 (Figure 4a and d; acidic and calcareous soil, $P < 0.001$). Autumnal leaf senescence showed less variability between the 2 years. In 2014, the average date of LCL_{50} was advanced by 1.1 and 5.6 days only on the acidic and calcareous soil, respectively, when compared with 2013 (Figure 4b and e; acidic soil, $P = 0.03$; calcareous soil, $P < 0.001$). Based on these data and the magnitude of the phenological responses to the soil, the length of the vegetation period was calculated for both years and soil types as time span between spring bud burst and autumnal leaf senescence (LCL_{50}). The cumulative curves showing the temporal progression of phenological development over all provenances provided a clear indication for a larger soil effect on autumnal leaf senescence than on spring bud burst in 2013 (Figure 4a and b) but not in 2014 (Figure 4d and e). As a consequence, the vegetation period 2013 was shorter on acidic soil compared with that on calcareous soil (−4.7 days over all provenances; $P < 0.001$; Figure 4c) covering a period of 178 days on acidic soil and 183 days on calcareous soil. In 2014, the length of the vegetation period did not differ on both soil types ($P = 0.072$; Figure 4f). The average length of the vegetation period was 190 days on acidic soil and 189 days on calcareous soil. Compared with 2013, it lasted 11.7 and 5.3 days longer on acidic and calcareous soil, respectively.

Discussion

The present study provides evidence for a distinct but interannually variable soil effect on spring and autumn phenology of European beech. Seedlings showed an advanced onset of bud burst on acidic soil in both years. This soil effect was pronounced

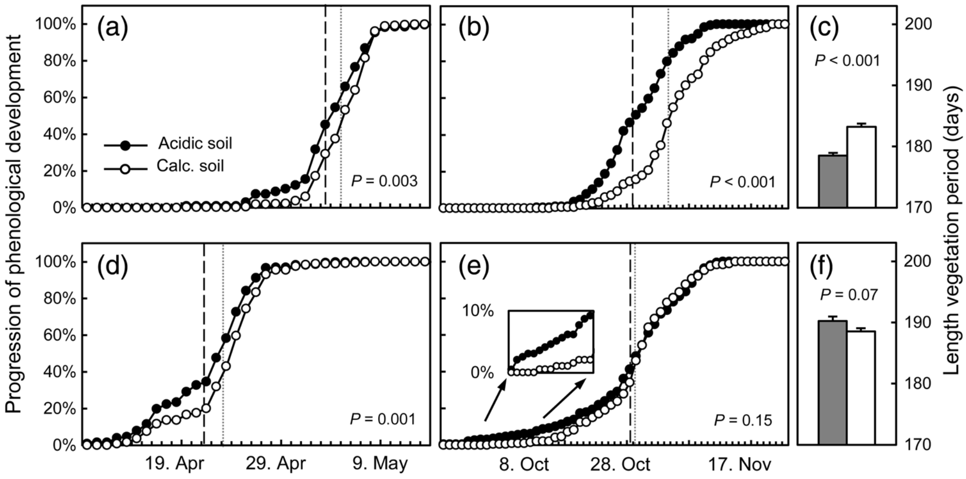

Figure 4. Overall soil effect on spring and autumn phenology. Cumulative number of seedlings starting bud burst in (a) spring 2013 and (d) spring 2014 and cumulative number of trees reaching the stage of LCL_{50} in (b) autumn 2013 and (e) autumn 2014. Average length of the vegetation period on acid and calcareous soil in (c) 2013 and (f) 2014 (means ± SE, $n \geq 180$). Dashed and punctuated lines indicate average onset dates of bud burst and LCL_{50} on acidic and calcareous soil, respectively.

in the exceptionally warm year 2014 as particularly shown in the early bursting provenance Saxon. Together with the overall advancement of spring bud burst in this warm year, it complements the finding of phenological development in early bursting seedlings being more affected by the soil than in late bursting seedlings. Autumn phenology did not show a consistent response pattern as leaf senescence was advanced on acidic soil in the first year 2013 only. The missing soil effect on leaf senescence in 2014 may be attributable to the exceptionally high spring temperatures that not only caused an earlier bud burst but also a distinct prolongation of the vegetation period. In fact, leaf senescence is an age-dependent process, being influenced by the length of the vegetation period with a maximum leaf age being assumed (Lim et al. 2007). Hence, the prolongation of the vegetation period in 2014 might have triggered the earlier leaf senescence on calcareous soil (when compared with 2013) and thus overridden the soil effect on autumn phenology.

As beech phenology is under genetic control (Falusi and Calamassi 1996), the soil responsiveness of the seedlings was tested across a range of provenances. Differential responses were observed, with early bursting/senescing provenances being more affected than late bursting/senescing provenances. This response pattern suggests a genetic component that contributes to provenance-specific soil responsiveness. However, direct genetic control in the sense of a monocausal soil–gene–phenology function is unlikely. Indeed, climatic determinants of tree phenology, i.e., temperature and photoperiod, become increasingly influential with the progression of the spring or autumn season, thereby triggering a faster phenological development (Kuster et al. 2014), and this in turn might have overridden the soil effect in late bursting/senescing provenances. Thus, the provenance-specific soil effect on beech phenology most likely reflects the superior ability of early bursting/senescing seedlings to respond to additional environmental variables other than temperature and photoperiod. Also, other signs of adaptation were not evident among the provenances as differences in bud burst and leaf senescence could not be statistically explained by any environmental variable of the provenance sites of origin. This is not surprising with respect to the small size of the study areas and their strong ecological fragmentation interfering with adaptational forces.

As spring bud burst and autumnal leaf senescence determine the sum of seasonal activities of winter-deciduous trees in terms of transpiration and photosynthesis, the number of days between these phenological events was calculated to test for the influence of soil type on the length of seasonal activities. This time period, here referred to as the vegetation period, is of particular interest in phenological research as it is crucial for estimating climate change effects on annual carbon balances of deciduous ecosystems (Goulden et al. 1996, Menzel and Fabian 1999, Richardson et al. 2010). In our study, the length of the vegetation period 2013 was extended on average by 5 days on acidic soil. A seemingly contradictory result was obtained for 2014, where the previously detected soil effect seemed to be missing. In 2014, however, the seedlings experienced very warm spring temperatures leading to early spring bud burst and, as a consequence, a distinct extension of the vegetation period compared with the previous year. As mentioned above, it might, therefore, be assumed that in 2014, the leaves from seedlings growing on both soils approached the maximum age for beech foliage. In fact, leaf senescence is an integrated response to endogenous and external environmental signals (Lim et al. 2007). Thus, it is reasonable to assume that endogenous cues become dominant in aging leaves after a particular life span. Such leaf age-related factors may have overridden the soil effect on autumnal leaf senescence and the length of the vegetation period in 2014.

The observed soil effect on the length of the vegetation period is almost consistent with the magnitude of 10.8 and 12 days as previously observed by Menzel and Fabian (1999) and Zhou et al. (2001), respectively, for past global-warming effects on the length of the growing season in temperate regions. Hence, the soil factor may constitute a considerable bias to phenology models predicting the length of the vegetation period based on temperature and photoperiod only. The need for more comprehensive modeling approaches integrating soil variables was recently emphasized in a study of birch phenology where the onset of flowering and early leaf phenophases varied with the mineral nutrient status of the trees (Jochner et al. 2013*b*). These results, from a descriptive study, are reinforced by the experimental results from the present study with beech, a late successional key species in European forests growing on soils with contrasting pH and carbonate content (Peters 1997). Even though the observed effects cannot yet be generalized and need further functional analysis, they provide a clear example of how the soil may influence temperature-driven tree phenology.

Conclusion

Tree phenology has received an increasing interest in recent years as an indicator of climate change impacts on terrestrial ecosystems. Several ecological and biogeochemical processes are directly linked to forest phenology determining the cycle of energy, water and carbon at the plant–atmosphere interface (Hanes et al. 2013, Richardson et al. 2013). Hence, changes in the timing of spring and autumn phenology in response to climate change will affect the seasonal course of these fundamental ecosystem processes. As shown in this observational study with European beech, chemical soil characteristics may influence temperature-driven spring bud burst and autumnal leaf senescence and consequently change the length of the vegetation period. This soil factor should be considered when assessing the effects of climate variability on tree phenology and the feedbacks on ecosystem processes.

Acknowledgments

We thank P. Bleuler for his valuable technical assistance and the maintenance of the research facility MODOEK. We also thank the internship students F. Schreyer, P. Buri, D. Hanimann and J. Schuler for helping us with the phenological assessments.

Conflict of interest

None declared.

Funding

This study was financially supported by the Swiss Federal Office for the Environment FOEN and the Swiss Federal Institute for Forest, Snow and Landscape Research WSL.

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