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Spring tree phenology in the Alps: effects of air temperature, altitude and local topography

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Abstract A participatory network was set up to study tree phenology in the Western Alps. We used data collected in 2006 and 2007 on birch, ash, hazel, spruce and larch to assess how local air temperature, altitude and other topographic variables influenced dates of budburst and leaf unfolding. Altitude was, as expected, a main predictor variable of budburst and leafing dates with delays ranging from 2.4 to 3.4 days per 100 m. Ash was the only species with strong evidence of a year difference in the altitudinal gradient with the warm year (2007) characterized by a weaker altitudinal gradient. We found a latitudinal gradient in the appearance of budburst for one coniferous species (larch) and curvature affected leafing in ash. Thermal sum (sum of Degree-Days above 0 °C) was increasing with altitude for budburst (birch, ash and larch) and leafing (birch and ash). Understanding of altitude and topography effects in addition to temperature in phenological models should improve projections of future changes in mountain regions.

Keywords Budburst · Leaf unfolding · Participatory network · Thermal sum · Snow

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Introduction

The timing of phenological events is changing. For plants, spring events such as budburst and flowering are occurring earlier (Parmesan 2006; Miller-Rushing and Primack 2008). These changes reflect in part changes in weather conditions, and a large number of studies have now documented the effect of increasing temperature on the timing or the duration of phenological events (e.g., Cannel and Smith 1986; Kramer 1995; Chmielewski and Rötzer 2001; Scheifinger et al. 2002; Menzel 2003; Menzel et al. 2003; Chmielewski et al. 2004; Chen et al. 2005; Cleland et al. 2007; Menzel et al. 2008; Nordli et al. 2008).

However, species usually differ in how they respond to variation in environmental conditions and these differences have been investigated, for example in terms of functional traits and environment-specific responses (Castro-Diez et al. 2003; Campanella and Bertiller 2008; Inouye 2008). In particular, in high-altitude regions, phenology is strongly influenced by snowmelt in addition to air temperature (Bliss 1971; Inouye 2008; Hülber et al. 2010; Wipf 2010). Snow cover will influence soil temperatures and may delay spring phenology even in the tree vegetation layer which is characterized by having a substantial biomass above the snow layer. However, the snow layer also has a protective property; in that, it protects vegetation from subzero temperatures associated with high-altitude diurnal variation in temperature during early spring. Earlier snowmelt may therefore increase risk of frost damage for early flowering species (Inouye 2008). As such, species might be expected to show a delayed phenology at high altitude compared to low altitude in order to prevent risk of frost damage. However, species have to complete their reproduction cycle within the relatively short vegetation period at high altitudes, constraining them to early budburst and/or flowering (Defila and Clot

2005; Wipf 2010). This constraint may result in some high-altitude species lacking a response to higher temperature or earlier snowmelt (e.g., *Ranunculus glacialis*, Totland and Alatalo 2002), which may make them sensitive to invasion by more plastic species.

In mountain regions, phenology and growth of tree species are strongly related to altitude-dependent weather conditions (e.g., for beech (*Fagus sylvatica*), see Dittmar and Elling 1999, 2006). However, few studies have focused on the effect of altitude on phenological events besides the obvious delay due to decreasing temperature with increasing altitude (Defila and Clot 2001, 2005; Dittmar and Elling 2006; Rötzer et al. 2004; Vitasse et al. 2009a, b; Ziello et al. 2009). Climate projections show that the Alps are expected to see a large increase in temperature in the next decades, particularly so in the summer (e.g., Beniston (2006) gave changes of summer temperatures by 2100 of +5.5–6 °C for the A2 scenario, with associated large changes in snow duration). Studies which have analysed phenological data from alpine areas (Theurillat and Schlüssel 2000; Defila and Clot 2001, 2005; Inouye et al. 2003; Keller et al. 2005; Huelber et al. 2006; Vitasse et al. 2009a, b; Ziello et al. 2009) have mostly ignored topographic variables beside altitude, such as exposure and slope which may also influence the appearance of phenological events besides the direct effect of temperature changes (e.g., Jackson 1966).

In this study, we analysed how air temperatures, altitude and other topographic variables affected species-specific phenological responses. We focused on two spring events, budburst and leaf unfolding which are known to be strongly determined by temperature, in order to exemplify the spatial variation in the relationship between temperature and phenological events. We focused first on comparing altitudinal gradients in spring event dates among species and years. We then tested if the impact of air temperature, measured using thermal sum was independent of altitude. We used data from a volunteer-based research project, "Phénoclim" which aims on the long-term at determining the effect of the climatic changes on plant phenology in the Alps. This programme takes place in the entire French Alps and relies upon the public participation for the monitoring of the phenological events.

Materials and methods

We used the initial 2-year period of the "Phénoclim" project, 2006 and 2007 based on phenological measurements made on tree/shrubs from 83 sites in the French Alps (Fig. 1). Thirty-six sites were equipped with meteorological stations, designed for the "Phénoclim" project. These stations measured air temperature at standard height (2 m) every 15 min with a DS18B20 Digital Thermometer (Dallas Semiconductor

MAXIM, www.maxim-ic.com), with an operating range of −55 to +125 °C and an accuracy of ±0.5 °C over the range of −10 to +85 °C. The stations are supplied with four batteries LR20 1.5 V. The temperatures recorded by these stations were highly correlated with standard temperatures obtained from national meteorological stations (e.g., at Chamonix: correlation coefficients = 0.97, 0.95 and 0.97, respectively, for minimum temperature, maximum temperature and mean temperature; data from Chamonix station obtained from Meteo France). We used the data from "Phénoclim" stations to calculate the daily mean temperatures as the national meteorological stations were too sparse in the study area.

For each phenological site, we used the following predictor variables in the statistical models: geographic coordinates (latitude and longitude in Lambert II extended projection), altitude, curvature (measured by the second derivative of altitude measured over neighbouring pixels (ArcGIS 2004); negative if concave and positive if convex), the slope (in degrees) and the exposure (measuring southness: N = 0; NE = NW = 0.75; E = W = 0.5, SW = SE = 0.75, S = 1) (Table 1). The altitude of the meteorological stations ranged from 245 to 1,921 m and that of the phenological sites was 240 to 2,136 m. Since all the phenological sites were not equipped with meteorological stations, we interpolated temperature on these sites from temperature data of sites with meteorological stations (see statistical modelling).

Phenology of budburst and leaf unfolding was studied in five shrub/tree species: two broad-leaved trees, birch (*Betula pendula*) and ash (*Fraxinus excelsior*); one shrub, hazel (*Corylus avellana*); and two coniferous trees, spruce (*Picea abies*) and larch (*Larix decidua*).

In the present study, budburst was defined as the first day the first leaf-stalk of the plant was visible. Leaf unfolding was defined as the first day a leaf was unfolded so the petiole could be seen. At each site, phenological events of three individuals per species were observed. Phenological observations were recorded weekly. The three individuals were chosen to be in the same topographic conditions and close to each other (between 5 and 500 m). Furthermore, as the age and height of a tree may influence its phenology, we used data from adult individuals with a minimum height of 7 m for trees and 3 m for shrubs. As species were not found at all sites, the design is unbalanced.

Many studies have shown that the timing of the spring phenological events is mainly induced by temperature (Defila 1991; Fitter et al. 1995; Sparks et al. 2000; Chmielewski and Rötzer 2002; Gormsen et al. 2005; Menzel et al. 2008). Most analyses so far have focused on temporal variations in timing of phenological events, but in this study, we focused on understanding the spatial variation, in particular, with respect to altitude and other topographic factors. If the effect of temperature was identical at
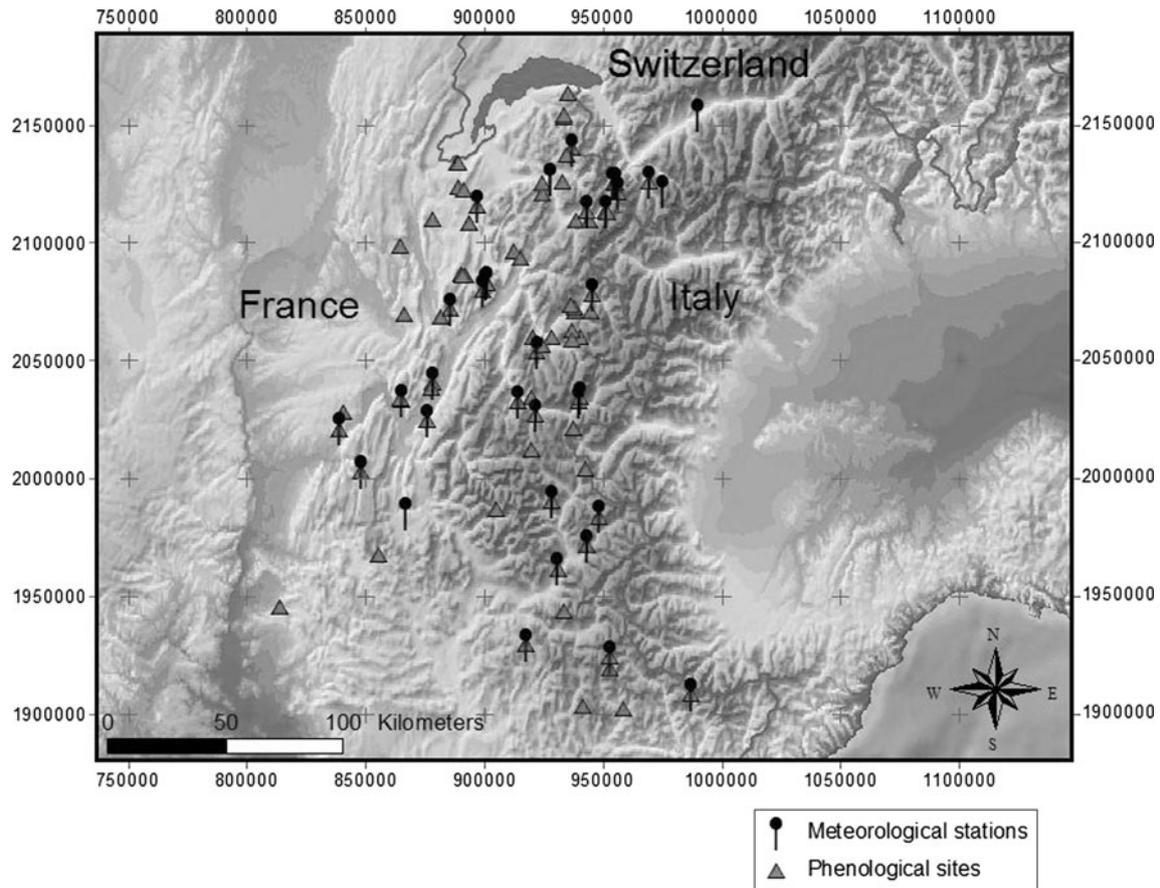
Fig. 1 Map of Western part of the Alps, showing the phenological sites (*triangle*) and the meteorological stations (*verticallinewithcircleabove*). Latitude and longitude in Lambert II extended projection

different altitudes, we would expect that a model including only altitude would result in good prediction of spatial variation in timing of phenological events. However, species may show different phenological responses to air temperatures at different altitudes (for example, because of an increasing impact of snowmelt and/or local adaptation to frost exposure). We therefore analysed spatial and temporal variation in thermal sum, defined as the sum of daily mean temperatures above a certain threshold temperature until the date of the phenological event (in Degree-Days (°d)). We chose 0 °C as base temperature because of the geographic location of the study area. Indeed, daily mean temperatures between 0 and 5 °C may contribute to budburst and leafing in mountain plants (Körner 1999; Hülber et al. 2010), and thus, in our case, 0 °C is a better threshold than the 5 °C value often used in the calculation of thermal sum (Myking 1997; Rötzer et al. 2004). Different starting dates, reflecting the phenology of the different species, were used to sum temperature values. The 1 March was used for birch, ash, spruce, larch (Hannerz 1999; Wielgolaski 1999; Rötzer et al. 2004), whereas 1 January was chosen for hazel (Wielgolaski 1999).

Statistical modelling

To interpolate temperatures, we applied additive generalized models (Wood 2006) to predict mean temperature with date and altitude as predictor variables. For each phenological site at a given altitude, we then added average values of residuals from the three nearest meteorological stations to the predicted values (to reconstruct the local daily variation). We thus obtained daily mean temperatures for all phenological sites.

To assess the effect of year, altitude, latitude, longitude, curvature, slope and exposure on the date and thermal sum of budburst and leafing, we fitted linear models (Gelman and Hill 2007) with date or thermal sum of budburst/leafing as the response variable, the year (2006 or 2007) as a two-modality fixed factor, and the exposure, altitude, latitude, longitude, curvature and slope as 6 quantitative covariates. We also assessed interaction between year and altitude to assess if the altitudinal gradients differed between years (e.g., Moser et al. 2010).

To assess which model(s) were the most appropriate, we used the Akaike's Information Criterion corrected for small

Table 1 ΔAIC values for the best model(s) fitted to budburst and leafing dates and thermal sums

		Best model	Best parsimonious model	Model: altitude + Year	Model: altitude	Model: constant
Budburst dates						
Birch		Alt + Year	Alt + Year, 0	0	17.36	43.05
Hazel		Alt + Year + Exp	Alt + Year + Exp, 0	2.42	14.34	33.51
Ash		Alt + Year + Alt:Year	Alt + Year + Alt:Year, 0	4.58	14.58	67.15
Spruce		Alt + Year	Alt, 1.84	0	1.84	15.47
Larch		Alt + Year + Lat + Alt:Year	Alt + Year + Lat, 0.27	8.96	23.57	44.25
Leafing dates						
Birch		Alt + Year	Alt + Year, 0	0	18.10	49.73
Hazel		Alt + Year	Alt + Year, 0	0	12.01	48.29
Ash		Alt + Year + Curv + Alt:Year	Alt + Year + Curv, 0.99	8.34	34.10	84.86
Spruce		Alt + Year + Long	Alt + Year, 0.01	0.01	7.04	32.69
Larch		Alt + Year	Alt + Year, 0	0	22.26	38.74
Budburst thermal sum						
Birch		Alt	Alt, 0	1.73	0	2.21
Hazel		Year + Exp + Curv	Year + Exp + Curv, 0	6.52	25.44	23.33
Ash		Alt + Year	Alt, 1.18	0	1.18	9.81
Spruce		Constant	Constant, 0	2.59	2.02	0
Larch		Alt	Alt, 0	1.18	0	2.78
Leafing thermal sum						
Birch		Alt + Lat	Alt, 1.12	3.39	1.12	9.68
Hazel		Alt + Year + Curv	Year, 0.88	1.57	18.43	17.02
Ash		Alt + Curv	Alt + Curv, 0	7.17	5.14	16.05
Spruce		Lat	Constant, 1.50	3.81	1.40	1.50
Larch		Constant	Constant, 0	3.78	2.33	0

The best model in terms of AIC is given first (and is defined by ΔAIC = 0), then the best parsimonious model (simpler than the best model and within 2 AIC units of the best model), and finally some simple models given for comparison and assessment of statistical evidence. Alt = Altitude, Lat = Latitude, Long = Longitude, Curv = Curvature, Exp = Exposure. The interaction Altitude-Year is denoted by Alt:Year

Table 2 Altitudinal gradients (days/100 m for Date and Degree-Days/100 m) for budburst and leafing (A), and differences between 2006 and 2007 (B), estimated using the same model with the predictor variables altitude and year

	Birch	Hazel	Ash	Spruce	Larch
(a) Altitudinal gradients					
Budburst					
Date	**2.7 [0.3]**	**2.9 [0.5]**	**2.7 [0.3]**	**2.4 [0.5]**	**2.7 [0.4]**
Degree-Days	**7.5 [3.5]**	−2.0 [4.6]	**11.7 [3.4]**	49.9 [37.4]	**7.7 [3.6]**
Leafing					
Date	**3.1 [0.3]**	**3.4 [0.4]**	**3.2 [0.3]**	**3.0 [0.4]**	**2.4 [0.4]**
Degree-Days	**12.1 [3.6]**	6.6 [5.2]	**13.7 [3.7]**	11.6 [36.2]	0.6 [4.5]
(b) Year differences					
Budburst					
Date	**−10.4 [2.2]**	**−12.0 [3.1]**	**−7.3 [2.0]**	**−7.0 [3.4]**	**−12.4 [2.8]**
Degree-Days	−16.9 [21.6]	**136.2 [27.4]**	46.2 [25.1]	49.9 [37.4]	−26.1 [− 23.2]
Leafing					
Date	**−10.6 [2.2]**	**−9.5 [2.4]**	**−12.1 [2.1]**	**−9.6 [3.0]**	**−13.0 [2.3]**
Degree-Days	−8.1 [22.6]	**149.2 [31.6]**	−14.0 [27.6]	7.5 [4.9]	−27.0 [26.8]
(c) Interaction altitude × year					
Budburst					
Date	0.07 [0.71]	−0.11 [1.05]	**−1.39 [0.53]**	0.15 [1.02]	−1.11 [0.85]
Leafing					
Date	−0.01 [0.69]	−0.49 [0.80]	−0.99 [0.56]	0.49 [0.88]	−0.76 [0.77]

The interaction altitude × year is given in C. Standard errors in parenthesis, and significant effects at the 0.05 level indicated in bold

sample size (AIC$_c$) (Burnham and Anderson 2002) and we retained the model(s) with the lowest AIC$_c$ value(s). When the difference between two models was less than 2, we have presented the simplest, most parsimonious model (Burnham and Anderson 2002). We also present results based on a common model including only the additive effect of year and altitude, to provide comparable values among species. We assessed the goodness-of-fit of linear models by using diagnostics based on residuals and influence plots. Constant variance of residuals (Gelman and Hill 2007) was fulfilled for all species. We used the average value of trees measured at a given station to avoid pseudo replication at the station level, and models including altitude and other environmental covariates resulted in residuals with no spatial autocorrelation.

All statistical analyses were performed using the software R (version 2.11; R Development Core Team 2010), distributed under the GNU General Public License.

Results

Daily mean temperatures were much warmer in 2007 than 2006, particularly so at the beginning of the vegetative season (March–April). Differences of monthly mean temperature (estimated from data of all meteorological stations) were +4.5 °C in January (monthly mean temperature = −1.4 °C in 2006/3.1 °C in 2007), +4.7 °C in February (−0.3 °C/4.4 °C), +9.5 °C in March (2.8 °C/12.3 °C), +4.3 °C in April (8.2 °C/12.5 °C) and +3.5 °C in May (12.1 °C/15.6 °C). In comparison, monthly mean temperatures obtained from national meteorological station of Chamonix, estimated between 1987 and 2007, were as follows: −1.9 °C (±4.1) in January, −0.2 °C (±4.1) in February, 3.4 °C (±3.9) in March, 6.6 °C (±3.6) in April and 11.4 °C (±3.4) in May.

The ranges of the timing of budburst (including the 2 years and all altitudes) were 26 February–2 May for

Fig. 2 Budburst and leafing dates, budburst and leafing thermal sums for ash (**a**), birch (**b**) and larch (**c**). Altitudinal gradients are shown for the 2 years: 2006 (*grey triangle*) and 2007 (*black circle*). *Lines* superimposed are *regression lines* for the 2 years: 2006 (*solid line*) and 2007 (*dotted line*)

Fig. 2 continued

b

Budburst date Birch

R² = 0.61   p < 0.001
Slope = 0.027

Budburst thermal sum Birch

R² = 0.06   p = 0.090
Slope = 0.075

Leafing date Birch

R² = 0.68   p < 0.001
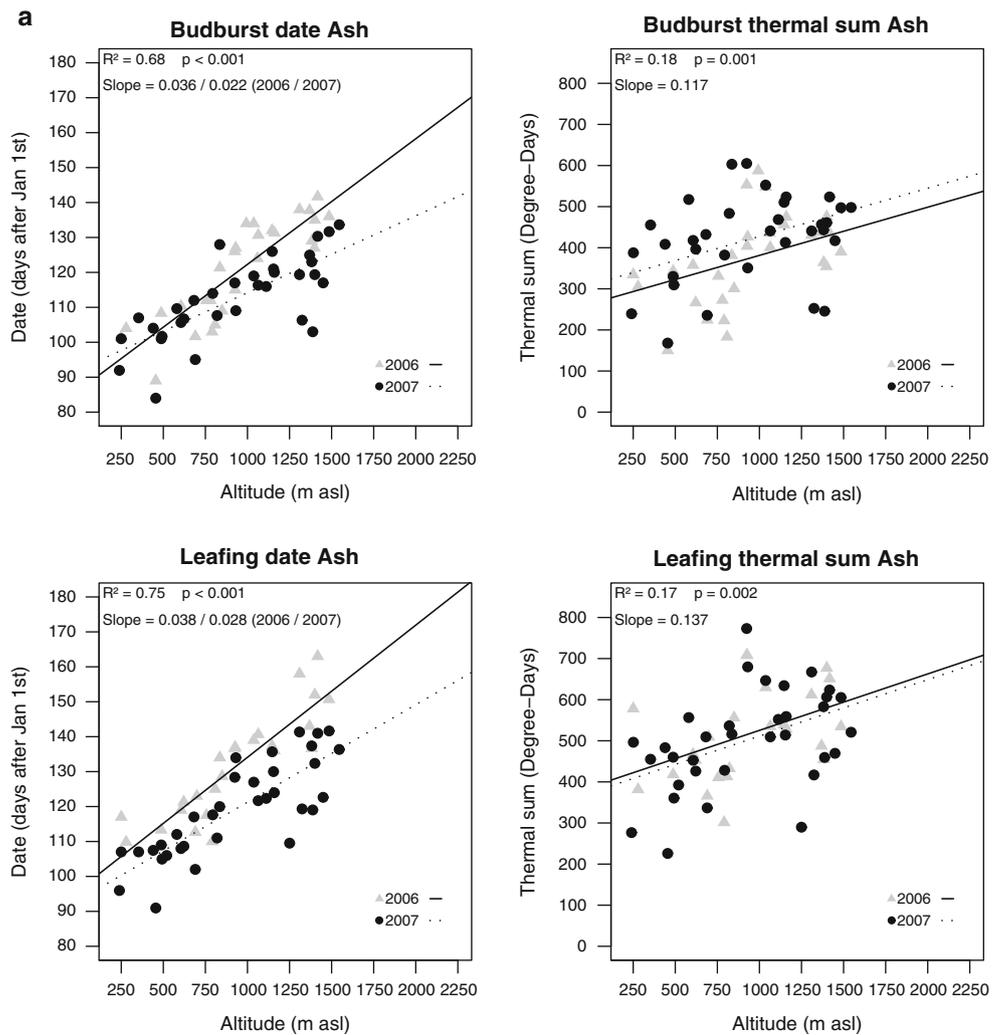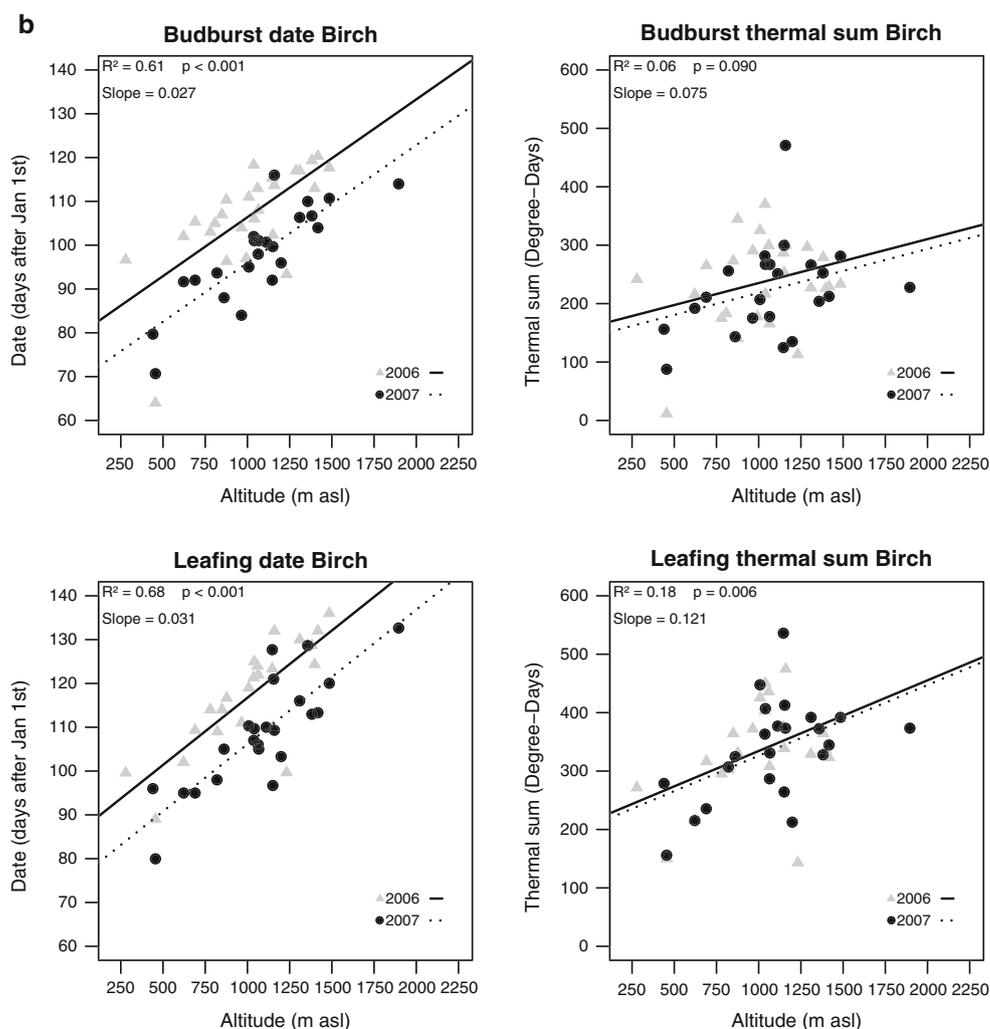Slope = 0.031

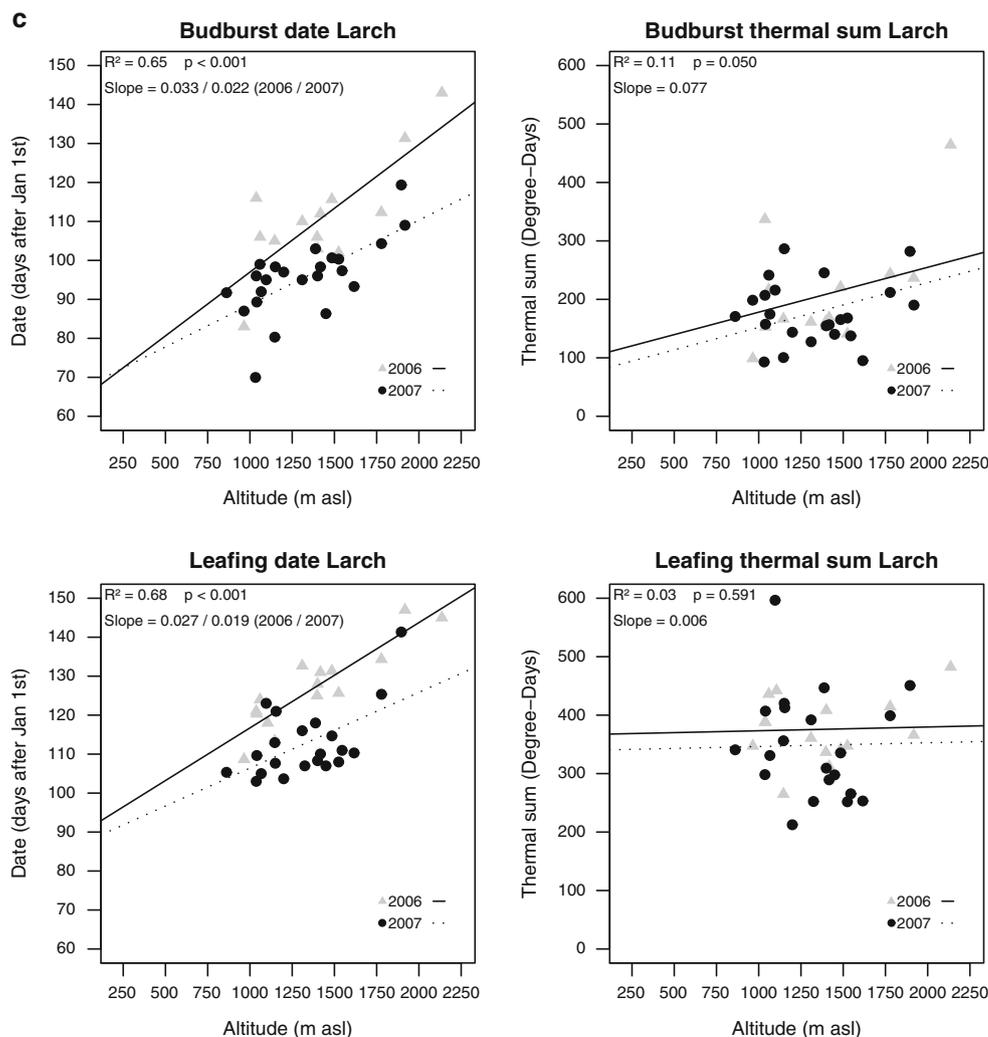Leafing thermal sum Birch

R² = 0.18   p = 0.006
Slope = 0.121

hazel (number of observations $n = 52$), 12 March–24 May for larch ($n = 37$), 6 March–1 May for birch ($n = 49$), 26 March–23 May for ash ($n = 62$) and 7 April–3 June for spruce ($n = 43$). Leaf unfolding occurred between 15 March–14 May for hazel ($n = 46$), 22 March–17 May for birch ($n = 46$), 14 April–28 May for larch ($n = 36$), 2 April–13 June for ash ($n = 59$) and 17 April–11 June for spruce ($n = 37$).

The best linear models as well as some simple models for each species for the time of budburst and leafing are presented in Table 1. All models included altitude and year. There was strong evidence for different altitudinal gradients in 2006 and 2007 (i.e. interaction year:altitude) only for ash (Table 2; Fig. 2), whereas for larch, the evidence was weak even if the difference was of the same magnitude (Table 2). Altitudinal gradients were rather similar among species and events (budburst: 2.4–2.9 days/100 m; leafing: 2.4–3.4 days/100 m). Differences between 2006 and 2007 were also consistent between events and species, being consistently larger for larch than for spruce

but more variable among deciduous trees (Table 2). We found evidence for an effect of geographic and topographic variables only on some species and not for the same variables (b[] = regression coefficient; hazel, budburst date, b[exposure] = 10.5 (se = 4.9); ash, leafing date: b[curvature] = −0.2 (0.1); larch, budburst date, b[latitude] = 0.1 (0.02) days/km).

The best linear models as well as some simple models for each species for thermal sum of budburst and leafing are presented in Table 1. We had evidence that altitude influenced budburst thermal sum positively for three species (ash, birch and larch, Tables 1, 2; Fig. 2), whereas altitude positively influenced leafing thermal sum only for birch and ash. As for timing of events, we found evidence for an effect of geographic and topographic variables only on some species and not for the same variables (b[] = regression coefficient; hazel, budburst thermal sum, b[exposure] = 88.6 (41.1), b[curvature] = 1.6 (0.8); ash, leafing thermal sum, b[curvature] = −2.6 (0.9)).

Fig. 2 continued

c

Budburst date Larch

$R^2 = 0.65$ $p < 0.001$
Slope = 0.033 / 0.022 (2006 / 2007)

▲ 2006 —
● 2007 ⋯

Budburst thermal sum Larch

$R^2 = 0.11$ $p = 0.050$
Slope = 0.077

▲ 2006 —
● 2007 ⋯

Leafing date Larch

$R^2 = 0.68$ $p < 0.001$
Slope = 0.027 / 0.019 (2006 / 2007)

▲ 2006 —
● 2007 ⋯

Leafing thermal sum Larch

$R^2 = 0.03$ $p = 0.591$
Slope = 0.006

▲ 2006 —
● 2007 ⋯

Discussion

The range of budburst and leafing dates in this study was roughly 2 months. This is equivalent to a 2,000 km distance at these latitude and longitude (Menzel et al. 2005). In mid-European regions, temperature is the main determinant of spring phenology (Chmielewski and Rötzer 2001, 2002; Menzel et al. 2008) and the addition of other climatic parameters such as air humidity, precipitation, radiation or depth of snow pack, or non-climatic parameters such as soil moisture or nutrient level may not significantly improve the models (Menzel 1997; Studer et al. 2005). As expected, we found that altitude was a main predictor variable of spatial variation of phenological phases and that budburst thermal sum was also significantly positively influenced by altitude for 3 out of 5 species (2 out of 5 for leafing). Altitudinal gradients were similar in both years, even if the 2 years studied were extremely contrasted in terms of mean temperatures. Several topographic parameters contributed to the timing of these

phenophases, but the effects were relatively small and inconsistent among species. Therefore, our results emphasize similar altitudinal gradients for dates of events for the 5 species studied but different altitudinal gradients for thermal sums.

The altitudinal gradients of budburst and leafing dates were similar to recent studies of mountainous areas: 2.4–3.4 days/100 m (our study) compared to Richardson et al. (2006) 2.7 days/100 m, Vitasse et al. (2009a) 1.1–3.4 days/100 m, Ziello et al. (2009) 0.9–4.5 days/100 m, Migliavacca et al. (2008) 3.7 days/100 m (larch), Moser et al. (2010) 3.6–4.3 days/100 m (larch and spruce). Ziello et al. (2009) compared these values to what is expected from a temperature gradient of 0.6 °C/100 m and a temperature response of 1–5 days/°C (Menzel et al. 2006), resulting in an altitudinal gradient of 0.6–3 days/100 m, whereas the Hopkin's law states that a value of 3.3 days/100 m is expected (e.g., Vitasse et al. 2009a). Our values are clearly in the high range, which is most likely due to a higher response of phenology to temperature since

temperature gradients are rather homogeneous. One species (ash) showed a change in the altitudinal gradient between years, the warmer year in 2007 being characterized by a weaker gradient (2006: 3.6 days/100 m vs. 2007: 2.2 days/100 m), whereas for larch, the change was similar but more uncertain. For both species, the difference between years resulted in a more advanced phenology in the warm year at high altitude. It is clearly difficult to conclude from a 2-year study whether altitude can influence phenological responses to temperature. The studies by Ziello et al. (2009) and Studer et al. (2005) did not find consistent responses, and our study showed evidence of a different response in one species, whereas others did not response clearly.

Thermal sums increased with altitude for birch, ash and larch (budburst) and birch and ash (leafing). This is the inverse of what would be expected from chilling effects (Hunter and Lechowicz 1992), since chilling should be larger at high altitudes. Both snow and frost can explain such a delay. Snow accumulation is larger at high altitude, resulting in a delay in soil temperature at high altitudes. This delay could explain the increase in thermal sum if phenological phases, especially the early ones (budburst) are influenced more by soil than air temperatures. The phenomenon is known for alpine plants which can start their development only when the snow has melted away (e.g., Totland and Alatalo 2002; Wipf 2010) but to our knowledge has not been thoroughly studied for trees. Another possible explanation is an increase in frost damage with altitude (Inouye 2008), but we are not aware of any direct measurements of frost damage on trees in alpine areas. Birch and larch are pioneer species and are expected to be more sensitive to temperature and chilling effects than late successional species such as spruce (Körner and Basler 2010). The position of ash on the pioneer-late successional gradient is less clear as it is both a colonizing species of mountain landscapes following agriculture abandonment (Gibon et al. 2010) but is also shade tolerant and is found in old forests (Diekmann et al. 1999). Assuming ash is also a pioneer species in alpine landscapes, it seems that pioneer species differ in their response of thermal sums to altitude.

Our results have implications for the further development of phenological models and field measurements. If the increase in thermal sum with altitude is due to the delaying effects of snow cover and snowmelt, expected climatic changes will result in larger phenological changes at high altitude than at low altitude because we expect both higher temperatures and reduced snow cover at high altitudes (at low altitudes, snow does not affect phenology). Further, monitoring of phenological phases in alpine areas should include detailed measurements of snow cover and soil temperatures in order to disentangle these effects and

models tailored to high altitude (or latitude) areas need to be developed.

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