

Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps

LEA MOSER,^{1,2} PATRICK FONTI,^{2,3} ULF BÜNTGEN,² JAN ESPER,⁴ JÜRIG LUTERBACHER,⁵ JULIA FRANZEN² and DAVID FRANK²

¹ Institute of Geography, Climatology and Meteorology Research Group, University of Bern, Hallerstrasse 12, CH-3012 Bern, Switzerland

² Swiss Federal Research Institute WSL, Zürcherstrasse 111, CH-8903 Birmensdorf, Switzerland

³ Corresponding author (patrick.fonti@wsl.ch)

⁴ Department of Geography, Johannes Gutenberg University, Becherweg 21, D-55099 Mainz, Germany

⁵ Department of Geography, Climatology, Climate Dynamics and Climate Change, Justus-Liebig University of Giessen, Senckenbergstrasse 1, D-35390 Giessen, Germany

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Summary The 2007 European larch (*Larix decidua* Mill.) growing season was monitored along two elevational transects in the Lötschental valley in the Swiss Alps. Phenological observations and weekly microcore sampling of 28 larch trees were conducted between April and October 2007 at seven study sites regularly spaced from 1350 to 2150 m a.s.l. on northwest- and southeast-facing slopes. The developmental stages of nearly 75,000 individual cells assessed on 1200 thin sections were used to investigate the links between the trees' thermal regimes and growth phases including the beginning and ending of cell enlargement, wall thickening and maturation of the stem wood. Needles appeared ~3–4 weeks earlier than stem growth. The duration of ring formation lasted from mid-May to the end of October, with the length of the growing season decreasing along elevation from 137 to 101 days. The onset of the different growing seasons changed by 3–4 days per 100 m elevation; the ending of the growing season, however, appeared minimally related to altitude. If associated with the monitored altitudinal lapse rate of -0.5 °C per 100 m, these results translate into a lengthening of the growing season by ~7 days per degree Celsius. This study provides new data on the timing and duration of basic growth processes and contributes to quantification of the impacts of global warming on tree growth and productivity.

Keywords: elevational transect, forest growth, growing season length, phenology, temperature lapse rate, xylogenesis.

Introduction

Trees are known to respond sensitively to changing environmental conditions (Fritts 1976, Schweingruber 1996), which is demonstrated by the ability to crossdate trees over large

regions (e.g., Frank and Esper 2005a) and to reconstruct temperature (e.g., Büntgen et al. 2006) or drought variations (e.g., Esper et al. 2007). Observable effects of climate variation include both short- and long-term variations in radial growth and maximum latewood density (Frank and Esper 2005b) as well as inter-annual changes in the timing of phenophases (Cleland et al. 2007, Rutishauser et al. 2007). While tree-ring chronologies generally provide information on inter-annual to multi-centennial time scales (Esper et al. 2002), it remains less clear exactly when ring formation takes place and how specific environmental factors influence the cellular division, growth and maturation that collectively define ring characteristics.

Impacts of changing environmental conditions on the timing and duration of the growing season have been assessed by long-term plant phenological observations (Rutishauser et al. 2007), difference vegetation indices (Maignan et al. 2008) and by more theoretical analyses with surface air temperatures (see Linderholm 2006 for a review). All of these methods rely upon external clues at the beginning and end of the growing season and therefore provide few insights into the development of secondary growth throughout the entire growing season. Exceptions include a limited number of studies that showed the relevance of analysing the timing and the duration of the growing season by monitoring wood formation in cold (see, e.g., Deslauriers et al. 2003, 2008, Rossi et al. 2006a) or dry environments (see, e.g., De Luis et al. 2007). For trees growing in cold environments, temperature has primarily been identified as the key factor in determining cambial activity and cell production (Denne 1971, Antonova and Stasova 1993, 1997, Mäkinen et al. 2003, Deslauriers and Morin 2005). From analysis at different European and Canadian sites, Rossi et al. (2007, 2008) showed the relevance of threshold temperatures in controlling the onset and ending of xylogenesis in conifers, while other studies conducted at the

alpine treeline emphasized the importance of seasonal mean temperatures (Körner and Paulsen 2004, Körner and Hoch 2006). Yet, in these investigations, linkages between growth processes and changes in environmental conditions are challenged by a limited number of replicates and observed years. In addition, and aside from photoperiod differences and potential genetic variation and adaptation, the unique course of environmental variation for each and every year and location hinders direct comparisons among different years or along sub- to continental-scale latitudinal transects.

In assessing the impacts of past and future climate change, information gained along an elevational gradient may therefore be of particular value because such gradients allow so-called 'space-for-time/warming experiments' (Körner 2003a). In this approach, long-term changes in the timing and duration of tree growth per shift in degree Celsius (=time) are substituted by changes along altitudinal transects (=space). As temperature is likely the most important factor controlling intra-seasonal tree growth in temperate and cold climates and is the most important environmental variable along elevational gradients (Körner 2007), such 'experiments' are especially relevant in trying to assess the impact of the projected warming on tree growth.

Here, we examine the timing and duration of the 2007 growing season of European larch (*Larix decidua* Mill.) along two elevational transects from 1350 to 2150 m a.s.l. in the central Swiss Alps. We specifically quantify differences in growing season timing and duration in relation to temperature differences along the altitudinal gradient. With this study, we aim to estimate the influence of temperature on the period of growth and phases of cell differentiation.

Materials and methods

Study area

The two elevational transects are located in the Lötschental (46°23'40"N, 7°45'35"E), a southwest–northeast-oriented inner-alpine valley situated in the central Swiss Alps (Figure 1). The valley bottom is located between 1300 and 1500 m a.s.l. and surrounded by steep slopes (mainly >60%) covered by mixed European larch and Norway spruce (*Picea abies* Karst.) forests up to an elevation of about 2200 m a.s.l. The transects stretch from the valley bottom at 1350 m a.s.l. up to the upper timberline at 2150 m a.s.l. on both the southeast (S)- and northwest (N)-facing slopes. Seven study sites were situated about every 300 m elevation on both slopes: at the valley bottom (site code: N13), at 1600 (N16 and S16), 1900 (N19 and S19) and 2150 m a.s.l. (N22 and S22). All sites are located within a radius of 2 km. By taking place within a very confined spatial domain, such experiments broadly ensure that the sub-daily to seasonal changes in diverse environmental conditions (e.g., a cloudy day, photoperiod) are experienced by the trees of all sites in a similar fashion but at different mean temperature levels.

Temperature monitoring

Temperature was monitored at each site during the entire year of 2007 to evaluate differences along the transects. We used two temperature loggers (Onset StowAway TidbiT) for each site. One was fixed on a single tree stem at about 1.5 m above the ground and protected from direct solar radiation, and the other was buried in soil at 10 cm depth. Recording frequencies were every 15 min for the stem and hourly for the soil measurements. To compare the 2007 temperature and precipitation measurements with longer-term observations, temperature and precipitation data from the nearby MeteoSwiss weather station of Ulrichen (1345 m a.s.l., 46°29'59"N, 8°17'59"E) were used.

Growth monitoring

At each site, four mature larch trees (28 in total) were selected for continuous growth observation. The date of needle appearance was observed in order to assess the timing of shoot growth reactivation during spring. Needle appearance was determined when 50% of all buds were broken (Brügger and Vassella 2003). Weekly phenological observations allowed a daily date to be estimated via linear interpolation. The forming annual ring was monitored for each tree by analysing tracheid formation from microcores collected weekly between April and October. Microcores were collected from the stem at about 1.3 m height using a Trephor puncher (Rossi et al. 2006b). Punching was performed on the stem oriented perpendicular to the slope direction to avoid reaction wood. Sampling was conducted along an oblique line and 3–5 cm apart to minimize wound reactions caused by earlier samplings (Forster et al. 2000). Microcores were placed for 24 h in a dilution of acetic acid and ethanol to preserve forming cells from degradation and then stored in a 70% alcohol solution. Samples were then prepared for cellular analysis by cutting 20–30- μ m-thick transversal microsections with a sliding microtome. Microsections were stained with safranin and astrablue and fixed to microscope slides with Canada balsam.

Ring formation was analysed at a magnification of 400 \times –600 \times and the number of tracheids in the different phases of cell development, i.e., enlargement, wall thickening and the mature phases, was assessed by counting along three radial files on each microsection. Enlarging cells were characterized by thin primary cell walls with radial diameter roughly two or more times that of dividing cambial cells. Polarized light was used to discriminate between enlarging and wall thickening tracheids. Mature cells were recognized by completely lignified secondary walls and empty cell bodies (Rossi et al. 2006a, 2007). The first appearance of cells in the enlargement phase was determined as the onset of stem growth. When all tracheids of the developing ring reached maturity, i.e., cell wall thickening ceased, stem growth was considered finished. Average values of the three radial files were used for subsequent analyses.

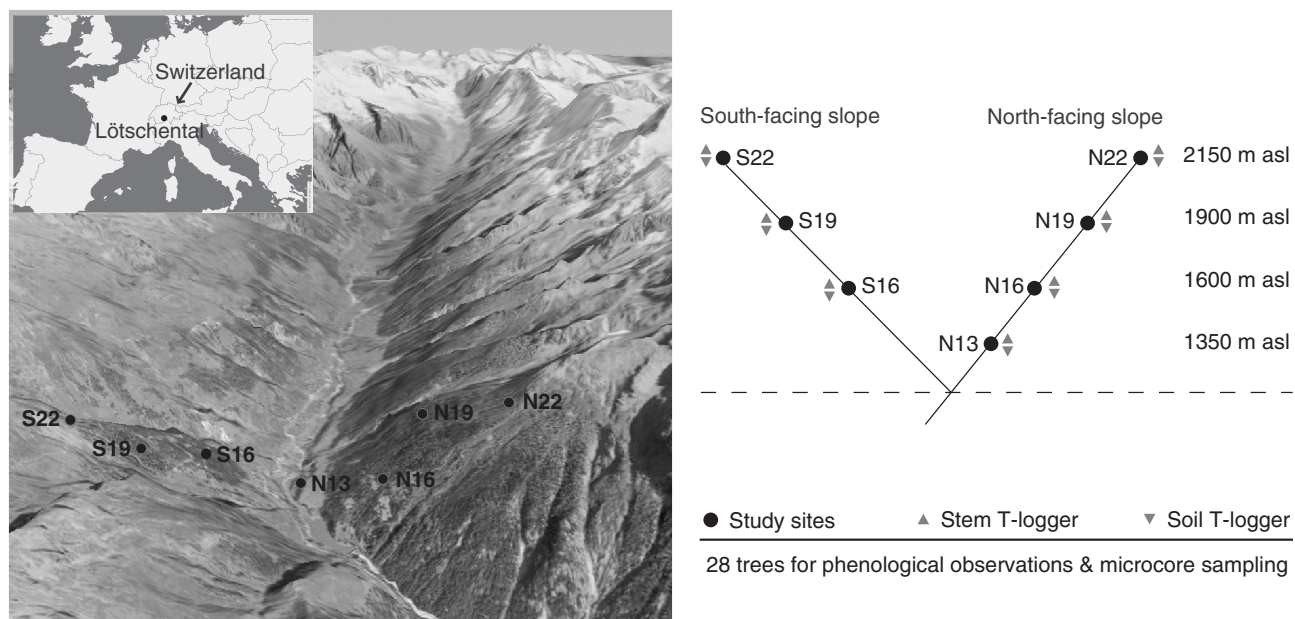


Figure 1. Location of the seven study sites along the two transects in Lötschental, Switzerland.

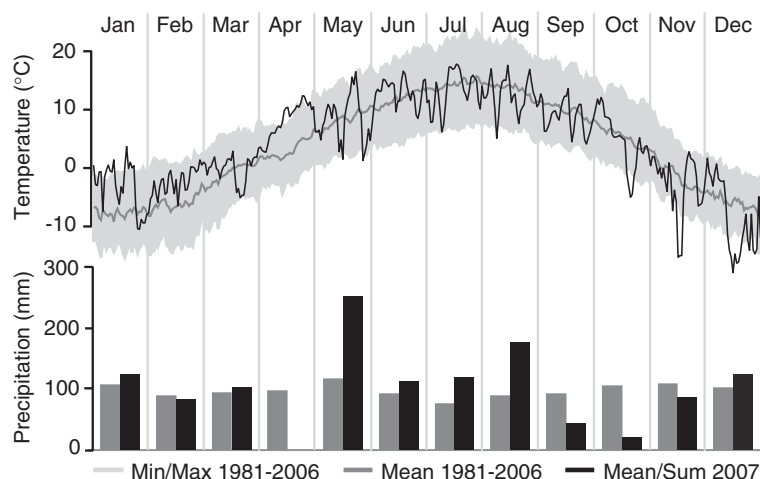


Figure 2. Daily and monthly climate data. Top panel shows a comparison of the 2007 daily average temperatures (black) and the 1981–2006 mean (grey) obtained from the MeteoSwiss weather station Ulrichen (1345 m a.s.l.). Shaded area indicates the mean minimum and maximum temperatures averaged over the 1981–2006 period. Bottom panel shows the 2007 monthly precipitation sums (black) related to the 1981–2006 mean (grey).

Data evaluation

The quantification of the length of 2007 growing season was defined in two different ways. The first defines the growing season as the period of secondary growth (stem level), i.e., from the onset of cell enlargement to the cessation of cell wall thickening of the forming ring. The second considers the growing season as the time from needle appearance (onset of primary growth) to the ending of ring formation (tree level). The differences in the timing of the growing phases—namely needle appearance, cell enlargement, wall thickening and maturation—between slopes were determined using the Wilcoxon–Mann–Whitney rank-sum test. Since no statistically significant ($P > 0.05$) difference was found, data from

both slopes were merged to quantify the delay in growing phases along altitude by using ordinary least-squares linear regression. Rate of temperature changes were derived from mean soil and stem temperatures for the period from April to October 2007. Results are only shown when regression coefficients were significant at $P < 0.05$.

Results

Climate variability and gradients

A comparison of daily temperatures and monthly precipitation measured at the weather station of Ulrichen shows that

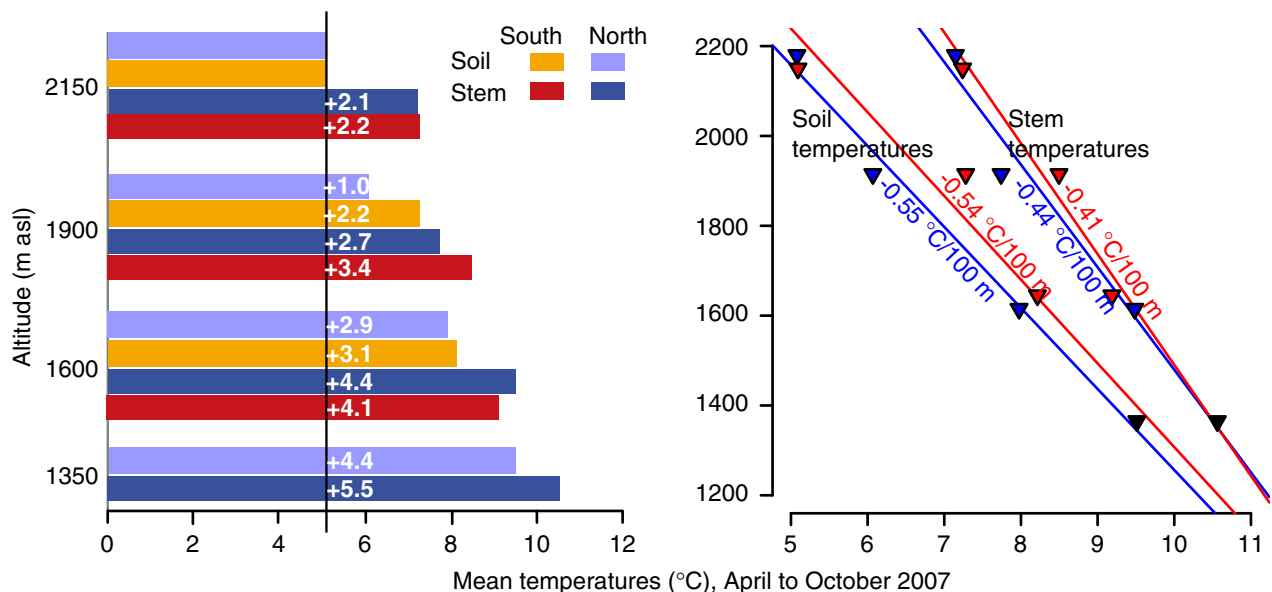


Figure 3. High-resolution soil and stem temperatures. The histogram shows the April–October 2007 soil and stem temperatures recorded at the seven study sites along the transects. White numbers denote the temperature differences of a site relative to the value recorded at the highest sites (N22 and S22: 5.1 °C). Right panel shows elevational gradients derived from April to October mean soil and stem temperatures for the sites on the north- (blue) and south-facing slopes (red).

2007 was both warmer (4.3 versus 3.7 °C) and slightly wetter (1240 versus 1170 mm) than the 1981–2006 reference period (Figure 2). Winter and spring conditions were exceptionally warm with temperatures in January, February and April up to 3–5 °C above the 1981–2006 average. In contrast, the late summer and fall months were slightly colder by 1–2 °C with respect to the 1981–2006 reference period. In terms of precipitation, the year 2007 was characterized by a dry April (no precipitation recorded) and a wet May to August period with 280 mm more rainfall than the reference period.

April to October mean temperatures recorded along the altitudinal transect indicate that stem temperatures are generally higher and more variable than soil temperatures (Figure 3). Using simple linear regression, stem temperatures were estimated to decline by 0.41 °C/100 m on the south- and 0.44 °C/100 m on the north-facing slope. Estimates for soil temperatures reveal steeper gradients: 0.54 °C/100 m on the south- and 0.55 °C/100 m on the north-facing slope. Even though between-slope differences were fairly small, temperatures on the south-facing slope were slightly higher than on the north-facing slope with differences ranging from 0.1 to 1.2 °C.

Seasonal growth development

Needles appeared ~3–4 weeks earlier than stem growth. When averaging between slopes, needle appearance started on 20 April (day of the year, DOY: 110), 26 April (DOY 116), 7 May (DOY 127) and 17 May (DOY 137) at 1350, 1600, 1900 and 2150 m a.s.l., respectively. Stem growth, characterized as the number of cells in each growing phase averaged per site, shows two different growing patterns

(Figure 4). The developmental phases occurred earlier at the lower elevations and the overall growth tended to decrease with increasing elevation. The data tend to be noisier towards the end of the growing season when local variations around the stem are more variable due to the greater absolute number of cells. The mean onset of stem growth—that is the first appearance of cells in the enlargement phase—was observed on 15 May (DOY 135) at the lowest site but on 9 June (DOY 160) at the highest sites. Cell wall thickening and cell maturation started on 9 June (DOY 160) and 26 June (DOY 177) at N13 and on 5 July (DOY 186) and 1 August (DOY 213) at 2150 m a.s.l., respectively.

Between the valley bottom and the timberline sites, differences in the timing of needle appearance and the onset of cell growing phases (enlargement, wall thickening and maturation) are statistically significant (Wilcoxon–Mann–Whitney rank-sum test, $P < 0.05$). Growth was completed on 16 September (DOY 259) at the highest sites but on 25 September (DOY 268) at the valley bottom. Differences in the timing of the end of growth between these lowest and highest sites were, however, not statistically significant at $P < 0.05$.

If the beginning of needle appearance and the different growing phases are expressed as a function of elevation, onset delays ranging from 2.9 to 3.7 days/100 m are derived (Figure 5). Associated with the recorded altitudinal temperature differences of about 0.5 °C/100 m, the monitored growth differences translate into shifts of 7.2, 5.8, 7.2 and 7.4 days/°C for needle appearance, the onset of cell enlargement, wall thickening and maturation, respectively. On average, changes of ~7 days/°C are observed. Importantly, linear fits explained a higher percentage of the elevational dependence during ear-

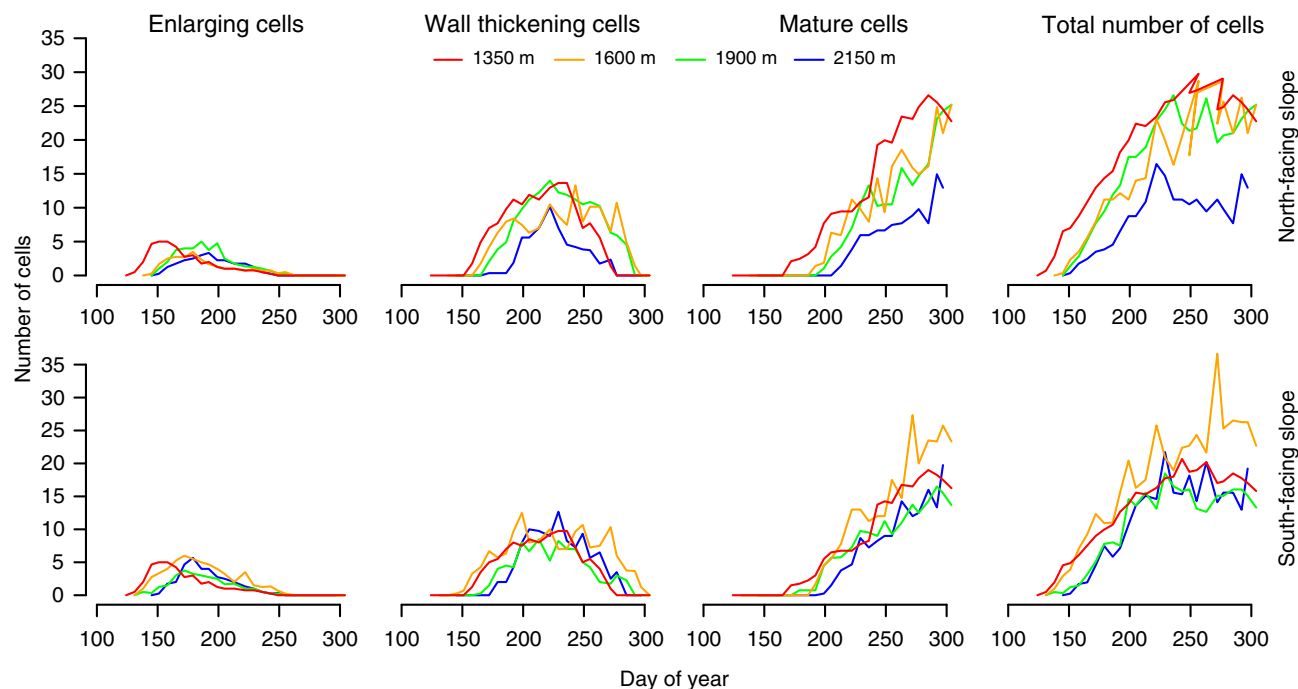


Figure 4. The timing and development of ring formation during the May–October 2007 period. Shown is the weekly number of cells in the enlarging, wall thickening and mature phases as well as the weekly total number of xylem cells. Upper and lower rows show results for the north- and south-facing slopes, respectively. The colours denote the different elevations, i.e., 1350 (red), 1600 (yellow), 1900 (green) and 2150 m a.s.l. (blue).

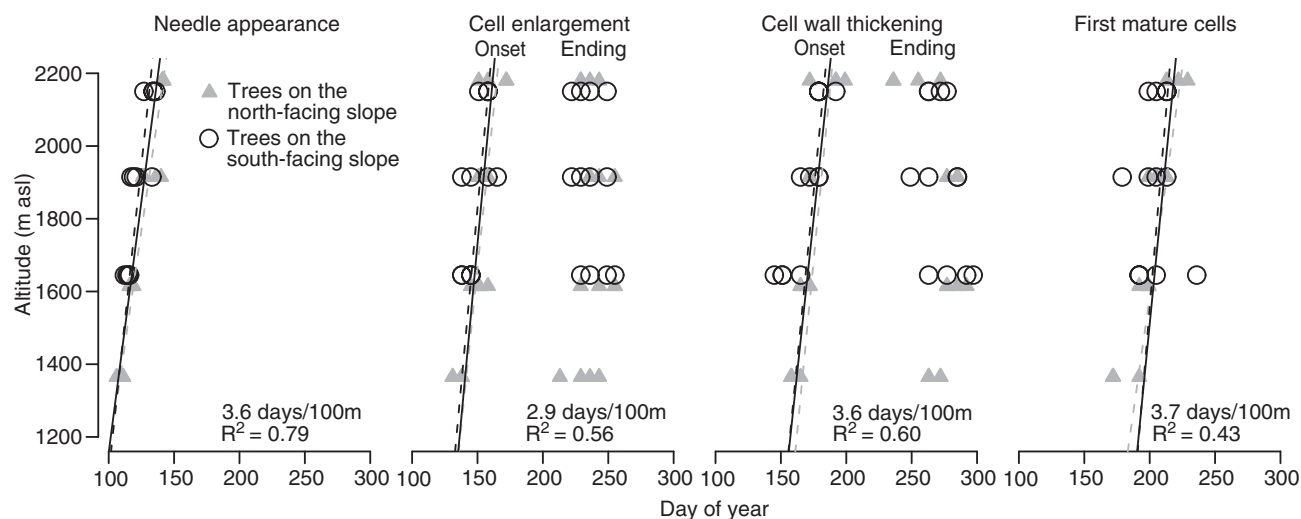


Figure 5. Altitudinal changes in the timing of growing phases. Shown are the elevational gradients (from left to right) for needle appearance, and the onset and ending of cell enlargement, wall thickening and cell maturity. Triangles and circles (some points are superimposed) indicate all 28 larch trees from the north- and south-facing slopes, respectively. Black lines are least-squares regression fits (DOY as independent variable) to growth phases for both slopes merged, whereas the dashed lines refer to trends calculated for north-facing (light grey) and south-facing (black) slopes only. Trends and coefficients of determination are indicated at the bottom.

lier growing phases. The endings of both cell enlargement and wall thickening phases were found to be less affected by elevation.

Results on the length of the 2007 growing season indicate that longest growth activity occurred at the medium-elevation sites N16 and S16 (stem level: 137, tree level: 168 days) and

shortened with increasing elevation to 126 (stem) and 150 (tree) days at 1900 m a.s.l. and to 101 (stem) and 123 (tree) days at the highest sites (Figure 6). While needle appearance and stem growth at the valley bottom began earliest, the growing season at N13 (stem: 134, tree: 159 days) was shorter than that at 1600 m a.s.l. due to its early ending.

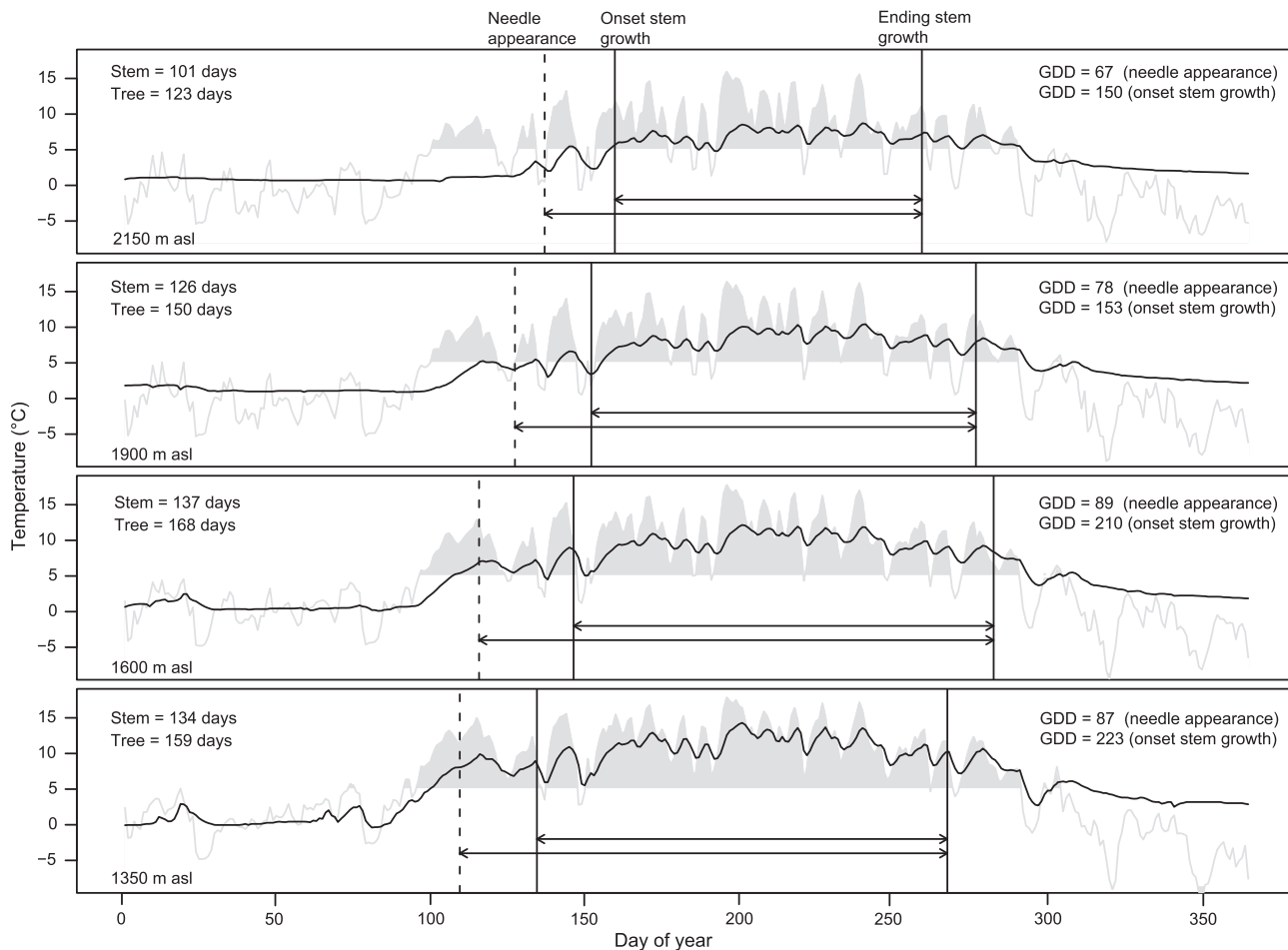


Figure 6. Timing and duration of the 2007 growing season derived from observations of stem (continuous line) and tree growth (dashed line). The data from opposing north- and south-facing sites were averaged. Black and grey curves indicate daily soil and stem temperatures throughout the year. Grey surfaces indicate stem temperature above 5 °C. Growing degree days (GDD) until needle appearance and onset of stem growth are indicated for each elevation as well.

Discussion

Altitudinal gradients provide a useful basis to perform space-for-time/warming experiments of mature trees in natural environments. In this study, we quantified the differences in timing and duration of the 2007 growing season of the sub-alpine *L. decidua* along two opposite-facing elevational transects of ~800 m.

The temperature measurements performed along the two transects revealed an altitudinal lapse rate of about $-0.5\text{ }^{\circ}\text{C}/100\text{ m}$ with non-significant exposure effects. Slight differences in the observed lapse rate from those described in other studies (e.g., Tang and Fang 2006) are likely due to differences in latitude and distance from sea or related to local characteristics such as topography, atmospheric circulation and vegetation cover, for example. The non-significant exposure effect between the opposing slopes is in agreement with previous observations (Innerebner 1933, Körner and Paulsen 2004, Rossi et al. 2007).

The present study, although based on data collected after an extraordinary warm winter and spring (Auer et al. 2007,

Luterbacher et al. 2007, Rutishauser et al. 2008), reveals a clear shortening of both tree level and stem level growing season with increasing elevation. At the upper timberline growing season—i.e., from the onset of cell enlargement to the cessation of cell wall thickening—lasted for 101 days, supporting previous evidence that the minimum period of growth is around 100 days (Schmitt et al. 2004, Rossi et al. 2008). The lengthening towards the valley bottom has been quantified with $\sim 3\text{--}4\text{ days}/100\text{ m}$, which corresponds to a change of $\sim 7\text{ days}/^{\circ}\text{C}$, and is attributed to an earlier beginning rather than a later cessation. This pattern, characterized by a temperature-induced change in the onset but a parallel ending of growing phases, is consistent with the pioneering investigations along an altitudinal transect of Tranquillini and Unterholzer (1968) as well as results from studies based on long-term phenological observations (e.g., Menzel and Fabian 1999, Walther et al. 2002). This effect of temperature on externally visible shoot growth is widely known (Defila 1991, Menzel et al. 2006), and the later needle appearance towards higher elevations of 3.6 days/100 m agrees well with the gradient of 4.1 days/100 m reported from

the Swiss Engadin region (Defila 2002). Translating the delay of 7 days/°C to the projected temperature increase for northern Switzerland of 0.8–3.3 °C in spring and 1.4–4.7 °C in summer (OcCC 2007), we estimate shoot and stem growth in the Lötschental to start between 5 and 33 days earlier in 2050 in comparison to 1990.

A caveat to such projections is that observed growth timing is primarily forced by temperature changes along the transects (Ohsawa and Ide 2008). Site-specific characteristics (unable to be fully controlled in natural field settings) and genetic adaptation of trees selected in this study may contribute to differences in observed timing in natural setting experiments. Although these possibilities cannot be excluded, the close proximity of the two transects (~2 km radius) guarantees that differences in factors such as photoperiods and climatic variations are minimal. Furthermore, the similar gradients and timing observed between north- and south-exposed transects indicate that site-specific influence is small.

To our knowledge, this is the first investigation relating direct observations of intra-seasonal wood formation to temperature changes along an altitudinal gradient. Direct observations of temperature-related cambial activity and differentiation performed so far have demonstrated a high cambial responsiveness to spring temperatures under both artificially manipulated and natural conditions. Heating experiments carried out in early spring (Oribe and Kubo 1997, Gričar et al. 2006, 2007) induced earlier reactivation of the cambium. Similarly, significant differences of the onset and ending of cell enlargement as well as the beginning of cell wall thickening were observed when comparing growth of Italian *Pinus leucodermis* during two climatologically differing years. However, the cessation of wall thickening, i.e., the ending of the growing season, did not change between 2003 and 2004 (Deslauriers et al. 2008). Temperature seems to be an important factor especially for determining the beginning and thus the duration of the phases of xylem differentiation, but has reduced influence in controlling the ending of phases.

These new data support the hypothesis that temperature determines the onset of growth whereas other wood formation processes like maximum growth rate (Rossi et al. 2006c) and growth cessation (Jackson 2008) are rather controlled by photoperiod. This developmental control should not only optimize the time available for earlywood tracheid formation but also guarantee sufficient time before winter for the latewood tracheids to complete cell wall formation and lignification. Notably, in this investigation, we see indications that temperature affects the onset phases whereby the timing of cell enlargement, wall thickening and maturing tend to delay in a somewhat cumulative manner and cause increasing lags with elevation (see Figure 5). This cumulative behaviour is not observed for phase endings. Accordingly, cellular processes occurring at the ending of the growing season (e.g., cell wall thickening) have disproportionately less time at higher elevations than processes occurring at the beginning of the growing season (e.g., cell enlargement). Xylem cell

differentiation is a considerable energy sink and is particularly demanding of sucrose (Oribe et al. 2003). Changes in the length of the growing season and in the time available for the different phases of xylem differentiation likely require different strategies in the use, storage and allocation of the carbon. Specifically, due to the relatively long time needed (up to 50 days) for latewood tracheid lignification, under unfavourable thermal conditions this last differentiation stage might become particularly time and resource limited. This result might help explain why latewood maximum density of high elevation trees is a better temperature proxy than tree-ring width (Frank and Esper 2005a).

Based upon measurements from 28 larch trees, we have showed that intra-seasonal growth data collected along an elevational transect can contribute to the understanding of impacts of climate change on tree growth. More specifically, an increased understanding of the response season and growth processes along environmental gradients may lead to better interpretation of growth-limiting mechanisms (carbon assimilation versus allocation; Körner 2003b) and the calibration of dendroclimatic reconstructions (Frank et al. 2007) including the new possibilities to use wood anatomical features such as cell size and wall thickness as additional novel climatic proxies (Fonti et al. 2009).

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