Phyton (Horn, Austria)	**Vol. 51**	Fasc. 2	299–313	20. 12. 2011

Cambial Activity and Xylem Cell Development in *Pinus cembra* and *Pinus sylvestris* at their Climatic Limits in the Eastern Alps in 2007

By

Irene SWIDRAK*), Andreas GRUBER*) and Walter OBERHUBER*)

With 2 Figures

Received July 14, 2010

Accepted July 4, 2011

Key words: Alpine timberline, cambium, dry inner Alpine valley, intra-annual growth, Scots pine, Stone pine, wood anatomy, xylogenesis.

Summary

SWIDRAK I., GRUBER A. & OBERHUBER W. 2011. Cambial activity and xylem cell development in *Pinus cembra* and *Pinus sylvestris* at their climatic limits in the Eastern Alps in 2007. – Phyton (Horn, Austria) 51 (2): 299–313, with 2 figures.

It has been frequently stressed that at distributional boundaries, like at the Alpine timberline and within dry inner Alpine environments, tree growth will be affected first by changing climate conditions. Climate in 2007 was characterized by the occurrence of exceptionally mild temperatures in spring (3.4 and 2.7 °C above long-term mean (LTM) at timberline and the valley sites, respectively) with an almost continuous drought period recorded in April and slightly warmer than average temperatures throughout summer (1.3 °C above LTM at both sites).

We compared temporal dynamics of cambial activity and xylem cell development in *Pinus cembra* at the Alpine timberline (1950 m a.s.l.) and *Pinus sylvestris* at a xeric inner Alpine site (750 m a.s.l.) by repeated cellular analyses of micro-cores (n = 5 trees/site). While onset of wood formation in *P. sylvestris* and *P. cembra* differed by about two weeks (12 and 27 April, respectively), maximum daily growth rates peaked on 6 May at the valley site and on 23 June at timberline. At both sites maximum tracheid production was reached prior to occurrence of more favourable climatic conditions during summer, i.e. an increase in precipitation and temperature. Xylem

*) SWIDRAK I., GRUBER A., OBERHUBER W., Institut für Botanik, Leopold-Franzens-Universität Innsbruck, Sternwartestrasse 15, 6020 Innsbruck, Austria. Corresponding author: Walter Oberhuber, e- mail: Walter.Oberhuber@uibk.ac.at

formation ended on 31 August and 28 October at the xeric site and at timberline, respectively.

This study demonstrates the plasticity of tree-ring formation along an altitudinal transect in response to water availability and temperature. Whether early achievement of maximum growth rates is an adaptation to cope with extreme environmental conditions prevailing at limits of tree growth needs to be analysed more closely by taking belowground carbon allocation into account.

Zusammenfassung

SWIDRAK I., GRUBER A. & OBERHUBER W. 2011. Cambial activity and xylem cell development in *Pinus cembra* and *Pinus sylvestris* at their climatic limits in the Eastern Alps in 2007. [Kambiumaktivität und Xylementwicklung in *Pinus cembra* und *Pinus sylvestris* an ihren Verbreitungsgrenzen in den Ostalpen im Jahr 2007]. – Phyton (Horn, Austria) 51 (2): 299–313, mit 2 Abbildungen.

Es ist mehrfach darauf hingewiesen worden, dass an den Verbreitungsgrenzen wie an der alpinen Waldgrenze und in inneralpinen Trockentälern das Baumwachstum von Klimaänderungen zuerst betroffen wird. Da die Witterungsbedingungen im Jahr 2007 durch außerordentlich milde Temperaturen im Frühjahr (3,4 °C bzw. 2,7 °C über dem langjährigen Mittel (LMW) an der Waldgrenze bzw. im Talboden), einer nahezu durchgehenden Trockenperiode im April und leicht überdurchschnittlichen Sommertemperaturen (1,3 °C über LMW) charakterisiert waren, verglichen wir die zeitliche Dynamik der Kambiumaktivität und Xylementwicklung zwischen *Pinus cembra* an der alpinen Waldgrenze (1950 m MH) und *Pinus sylvestris* an einem inneralpinen Trockenstandort (750 m MH) an Hand zellulärer Analyse von Mikrobohrkernen (n = 5 Bäume/Standorte). Während der Beginn der Holzbildung in *P. sylvestris* und *P. cembra* sich um ca. 2 Wochen unterschied (12. bzw. 27 April), wurden die maximalen täglichen Wachstumsraten bereits am 6. Mai am Trockenstandort in montaner Lage bzw. am 23. Juni am Waldgrenzstandort erreicht. An beiden Standorten traten jedoch günstigere Wachstumsbedingungen, d.h. eine Zunahme der Niederschläge bzw. der Temperatur, nach dem Erreichen der Maximalraten auf. Die Xylembildung endete im Jahr 2007 am 31. August bzw. 28. Oktober am Trocken- bzw. Waldgrenzstandort.

Diese Studie hat die Plastizität der Jahrringbildung in Abhängigkeit von der Wasserverfügbarkeit und Temperatur entlang eines Höhentransektes gezeigt. Inwieweit die frühen maximalen Wachstumsraten eine Anpassung an die extremen Umweltbedingungen an den Grenzen des Baumwachstums darstellen, muss in zukünftigen Untersuchungen unter Berücksichtigung der Kohlenstoffverteilung zu ober- und unterirdischen Organen nachgegangen werden.

Introduction

Several dendroecological and ecophysiological studies conducted in dry inner Alpine valleys have shown that precipitation in spring limits radial growth of trees and severe drought during the growing season results in abrupt growth reductions (e.g., OBERHUBER & al. 1998, RIGLING & al. 2002, ZWEIFEL & al. 2006). On the other hand, there is extensive evidence that at timberline, i.e. the upper limit of trees forming a closed ca-

nopy, temperature throughout the growing season has a direct effect on tree growth and xylem development (e.g., Körner 1998, Grace & al. 2002, Oberhuber 2004, Rossi & al. 2007). Dendroecological and -climatological studies, which analyse long-term data sets comprising several decades to centuries, provide information on climate-growth relationships and about the year-to-year variability of radial growth, but not about variability of crucial phenological stages, i.e. onset, maximum rate, and ending of annual tree ring formation. Several studies on cellular phenology of annual ring formation in cold-environments and at drought-exposed sites have been published recently (e.g., Deslauriers & al. 2003, Rossi & al. 2006b, 2007, De Luis & al. 2007, Camarero & al. 2010, Gruber & al. 2009, 2010), to better understand the effect of climate variables on xylem development and to determine the period of cambial activity and wood formation.

A comparison of intra-annual xylem cell development at contrasting climatic limits of tree growth in the Alps, i.e. at timberline and at xeric inner Alpine sites, where tree growth is considerably limited by summer temperature and spring precipitation, respectively, has not yet been published. Furthermore, at these distributional boundaries climate change is expected to have a pronounced impact on tree growth (e.g. Oberhuber 2001, Saxe & al. 2001, Wieser & al. 2009), whereby lengthening of the growing season in spring is one major aspect of climate warming (Menzel & Fabian 1999).

The present study therefore focuses on the comparison of timing, dynamic and duration of cambial activity and wood formation in Scots pine (*Pinus sylvestris* L.) exposed to soil dryness in the lower montane region and in stone pine (*Pinus* cembra L.) at timberline of the Eastern Central Alps (Austria) during 2007, when exceptionally warm and dry conditions prevailed at the beginning of the growing season in April. Cambial activity and xylem cell development were monitored at both sites by repeatedly taking small punched cores of the outermost tree rings (micro-cores) during short time intervals (e.g., Deslauriers & al. 2003, Rossi & al. 2006b, Mäkinen & al. 2008). We hypothesized that (i) cambial resumption in spring is triggered by temperature at both study sites, whereas (ii) the temporal dynamic of wood formation differs among sites due to varying environmental constraints limiting tree growth at the xeric montane site and at timberline.

Material and Methods

Study Sites

Xeric Inner Alpine Site

This study site (for the geographical location see Oberhuber & al. 1998) is part of a postglacial rock-slide area situated in the montane belt (c. 750 m asl) within the inner Alpine dry valley of the Inn River (Tyrol, Austria, 47° 14′ 00″ N, 10° 50′ 20″ E) and has a relatively continental climate with mean annual precipitation and tem-

perature of 715 mm and 7.3 °C, respectively (long-term mean during 1911–2007 at Ötz, 812 m a.s.l., 5 km from the study area). The open south-facing stand (c. 33 % canopy coverage) is growing on shallow stony soil, where pioneer vegetation prevails in the ground flora. Soils are of the protorendzina type, i.e. rendzic and lithic leptosols according to the World Base for Soil Resources (FAO 1998), and consist of unconsolidated, coarse-textured materials with low water holding capacity.

Alpine Timberline Site

The timberline site (1950 m a.s.l., c. 80 % canopy coverage) is located at Mt. Patscherkofel (2246 m a.s.l., 47°12′N, 11°27′E), c. 50 km in linear distance of the xeric inner Alpine site. Mt. Patscherkofel is situated in the Central Austrian Alps within an inner-alpine dry zone, where the local climate is strongly influenced by warm and dry southerly winds (Föhn), which most frequently occur in spring (March-May). During the period 1967–2004 mean annual precipitation at the top of Mt. Patscherkofel was 890 mm with a maximum during summer (June-August: 358 mm) and minimum in winter (December-February: 147 mm). Mean annual temperature at timberline during the same period was 2.5 °C and the coldest and warmest months were February (–4.3 °C) and July (10.0 °C), respectively. The geology of the Mt. Patscherkofel region is dominated by gneisses and schist. The soil at the study site is classified as a haplic podzol (FAO 1998), a soil type typical for the Central Austrian Alps (Neuwinger 1970).

Xylem Sampling and Determination of Wood Formation

The dominant conifer at timberline in the central part of the Eastern Alps and on xeric sites within dry inner Alpine valleys is *P. cembra* and *P. sylvestris*, respectively. Therefore, we concentrated on the analysis of growth dynamics of these tree species, whereby all measurements were carried out at dominant trees to reduce the influence of competition on radial growth.

Seasonal wood formation dynamics was monitored during the growing season 2007 by taking small punched cores from 5 trees/site of the outermost tree rings (micro-cores) with a diameter and length of 2.5 mm and c. 2 cm, respectively (Rossi & al. 2006a). To determine the variability in intra-annual wood formation between trees at each plot (inner Alpine and timberline site), individual mature trees were randomly selected. However, selected trees showed no more than modest damage due to extreme environmental conditions, i.e. wind and/or snow breakage and lightning at timberline and mistletoe infection at the valley site. Micro-cores were taken starting in early March and late April at the xeric inner Alpine site and at timberline, respectively, to the end of October in weekly to 10-day intervals to include the whole dynamics of xylem formation at both study plots. Samples were taken on the slope-parallel side of the stem following a spiral trajectory up the stem starting at c. 1 m stem height. A distance of c. 2 cm in tangential and longitudinal direction was kept to avoid lateral influence of wound reactions on adjacent sampling positions.

Immediately after extraction, cores were placed in a solution of 70 % ethanol, propionic acid, and 40 % formaldehyde (mixing ratio: 90/5/5), subsequently embedded in glycolmethacrylate (Technovit 7100) and polymerized after adding an accelerator. Transverse sections of c. 12 μm were cut with a rotary microtome, stained with a water solution of 0.05 % cresyl fast violet and observed under a light micro-

scope with polarized light to differentiate the development of xylem cells, i.e. the discrimination between tracheids in enlarging and cell-wall thickening phase (Deslauriers & al. 2003, Rossi & al. 2006b). Onset and end of cambial activity was defined when the standard deviation of the number of cambial cells did not cross the number of dormant cells in the cambial zone, whereas xylem cell differentiation was considered to have begun and to be complete when one horizontal row of cells was detected in the enlarging phase and cell wall thickening and lignification were completed, respectively. Total xylem cell number was determined by adding the number of cells in radial enlargement, cell wall thickening, and the number of mature xylem cells (Deslauriers & al. 2003, Rossi & al. 2006c). Values, i.e. the number of cells in different zones of 5 cores (trees) per date and for each site, were averaged. Because cell number varies within the tree circumference and hence among different samples standardization is required (Rossi & al. 2003). The total cell numbers of the previous three tree rings were recorded in every sample and used for a cell number correction for each tree (cf. Gruber & al. 2010). Short-term variation in total number of tracheids (sum of enlarging, wall-thickening and mature cells) were modelled with a Gompertz function using the nonlinear regression procedure included in the Origin software package (OriginLab Corporation, Northampton, MA, USA).

The time of bud break in the south-facing crown was recorded at the same trees. Bud break was defined as readily identifiable swelling of buds. At this time, bud scales were still covering the new needles. At the end of the growing season 2007 increment cores from each tree were extracted with an increment borer at c. 1 m. Each core was mounted on a holder and the surface prepared with a sharp razor blade. Ring widths were measured to the nearest 0.01 mm using an incremental measuring table. To permit a direct comparison of tree ring series standardized indices were calculated by z-transformation according to the formula:

$$z_i = (v - m)/\text{std},$$

where v is the ring width value, m is the mean and std is the standard deviation of the entire series length.

Microclimate Records

During the study period daily precipitation and air temperature were collected automatically at 2 m height (ONSET, Pocasset, MA, USA) at both study plots. Long-term records (LTM) of total monthly precipitation and mean monthly temperatures were available from the meteorological station in Ötz (812 m a.s.l.) for the inner Alpine site (5 km from the study site) and top of Mt. Patscherkofel (2246 m a.s.l.) for the timberline site. Soil temperature in the upper 5–10 cm of the soil layer was continuously monitored at each plot, whereby at timberline the sensor was placed in a manner that complete shading by the forest canopy was ensured. On the other hand, at the xeric montane site only transient shading of the root zone throughout the day was intended, which was justified by largely open canopy. Measuring intervals for all sensors were 30 min. Mean daily air and soil temperature were calculated by averaging all measurements (48 values/day).

Climate During Growing Season 2007

Climate in 2007 was characterized by exceptionally mild temperatures in spring (Table 1). An almost continuous drought period was recorded from 20 March to 6 May

2007 and mean monthly air temperature in spring was 2.7 and 3.4 °C above LTM at the inner Alpine site and at timberline, respectively. Difference in deviation from LTM between study sites is caused by frequent occurrence of temperature inversion during spring. Air temperature during summer (June–August) 2007 exceeded LTM by 1.3 °C at both plots (Table 1). Difference in air temperature during summer among sites corresponds to a lapse rate of 0.54 °C per 100 m altitude. Mean daily soil temperature throughout April, May and summer (June – August) was consistently c. 11 °C higher within the inner Alpine stand with open canopy compared to largely closed canopy at the timberline site and ranged between 4.4 and 7.6 °C at the latter site (Table 1).

Results

At the inner Alpine site the dormant cambium consisted of 4 cells, when there was no cambial activity from July through March. In early April (95 day of the year) the number of cells in the cambial zone rapidly increased to about 6, whereby maximum values were reached in late April through early May (Fig. 1a). A delayed onset of cambial cell division of c. 3 wk (113 d) was found at timberline, where the dormant cambium consisted of 7 to 8 cells. At timberline the number of cells in the cambial zone rapidly increased to about 13 in early May (122 d) and subsequently steadily decreased. At both plots cambium cell division in 2007 stopped about mid July. Hence, cambial cells in 2007 divided throughout c. 90 days at the inner Alpine site and c. 75 days at timberline (Fig. 1a). Bud break was recorded by the end of March (85 d) and in late April (113 d) at the inner Alpine site and at timberline, respectively. Concurrently or shortly after bud break cambial cell division resumed at both sites. Mean air temperature in April was 13.9 and 6.0 °C at the inner Alpine site and at timberline, respectively, i.e. 6.5 °C above LTM at both sites (Table 1 and data not shown).

Mean onset of wood formation, i.e. first detection of radially enlarging xylem cells in 2007 occurred on 12 April (102 d $\pm$ 9) at the inner Alpine site and 27 April (117 d $\pm$ 5) at timberline (Fig. 1b). While wall thickening and lignification already stopped at the end of August (243 d $\pm$ 9) in *P. sylvestris* at the inner Alpine site, cell differentiation lasted until end of October (301 d $\pm$ 7) in *P. cembra* at timberline. In 2007 mean duration of wood formation, including all developmental phases from cell enlargement to the end of wall thickening and lignification lasted for 141 $\pm$ 8 and 184 $\pm$ 7 days at the inner Alpine site and at timberline, respectively. Hence, growing season length was reduced by about 6 wk at the xeric inner Alpine site compared with the temperature limited timberline site. Correspondingly, the cell production rate amounted to about one and three cells/10 days at the inner Alpine site and at timberline, respectively. Though warm conditions in spring 2007 lengthened the growing season and climate variables recorded during spring and summer were above LTM (cf. Table 1), annual

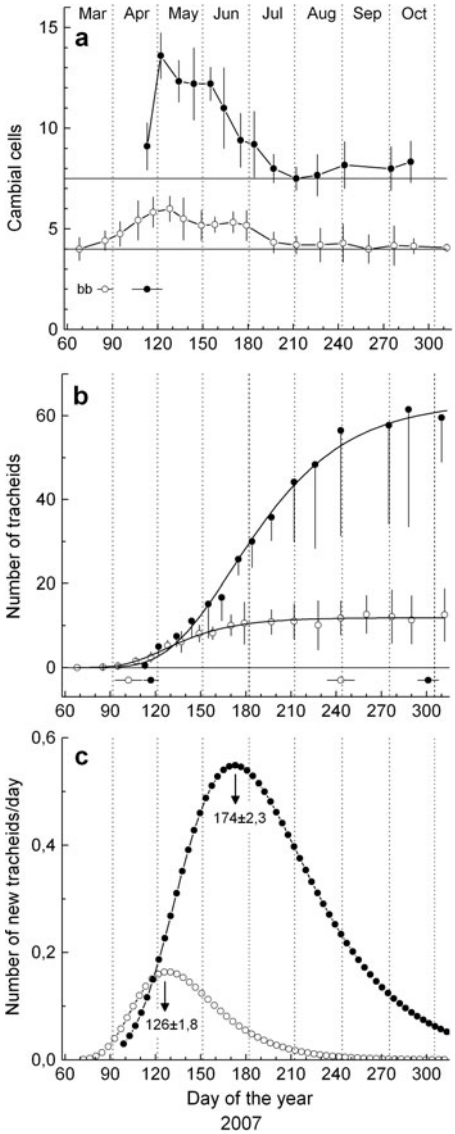

Fig. 1. **a**: Number of cells in the cambial zone **b** Dynamics of xylem growth (including enlarging, wall-thickening, and mature xylem cells) modelled by applying the Gompertz function **c** Daily xylem growth rates calculated on the basis of modelled growth. Inflection points (day of the year ± standard deviation) are indicated. Bars represent standard deviations and horizontal thin lines in **a** indicate the number of dormant cambial cells (bb = time of bud break). In **b**: onset and end of xylem cell differentiation ± standard deviation are shown. Study sites are denoted by open and filled circles for the xeric inner Alpine and timberline site, respectively.

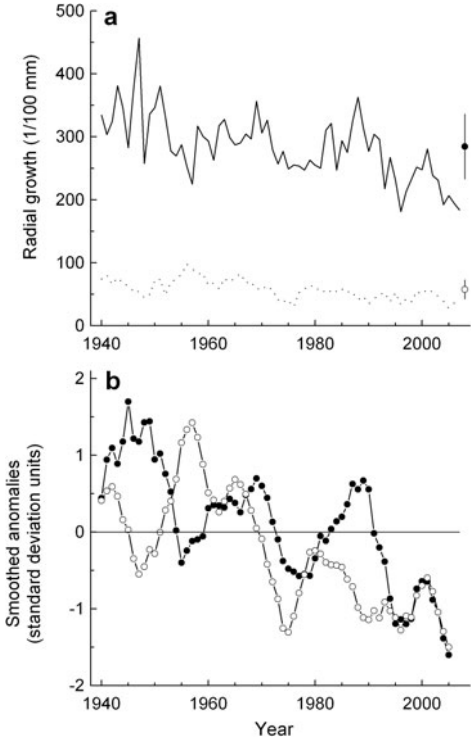

Fig. 2. **a**: Ring width time series of *P. cembra* (solid line) and *P. sylvestris* (dotted line) for the period 1940–2007 (n ≥ 3 trees/site). **b**: Smoothed ring width series. Curves represent *z*-transformed 5-year-running averages with equal weights (see Material and methods). In **a** mean ring width ± standard deviation for the period 1940–2007 are indicated. Symbols as in figure 1.

increments in 2007 were not significantly higher at both study plots compared to previous five years (Table 2). Height and radial growth is much more restricted by environmental factors at the xeric inner Alpine site compared with the timberline site (Table 2). Correspondingly, the total number of new tracheids produced was strikingly higher at timberline (61 ± 11 tracheids) compared to the cell number determined at the inner Alpine site (13 ± 6 tracheids; cf. Fig. 1b). Based on modelled xylem cell number increase by applying the Gompertz function, the maximum cell production rate (tracheids d^{-1}) at the inner Alpine site and at timberline occurred in early May and around summer solstice, respectively (Fig. 1c). Thereafter, daily xylem growth rates decreased at both sites, although growth limiting climate variables, i.e. precipitation and temperature at the xeric inner Alpine site and at timberline, respectively, were more favourable later on (Table 1).

In Figure 2 absolute ring width time series and smoothed anomalies of both species are depicted for the period covered by n ≥ 3 trees (1940–2007). Strikingly wider rings in *P. cembra* at timberline compared with *P. sylvestris* at the inner Alpine site (Fig. 2a) and asynchronous growth fluctuations among both species throughout most of the time period are obvious (Fig. 2b).

Discussion

We compared intra-annual radial growth of two conifers at study sites, where tree growth is limited by different climate factors throughout the year (see Introduction). This becomes obvious in asynchronous growth anomalies depicted in Figure 2b, while the decreasing long-term growth trend evident in tree ring series is related to the inherent effect of tree aging and forest stand development on annual increments (Fritts 1976).

Impact of Temperature on Intra-Annual Dynamic of Cambial Activity and Wood Formation

In 2007, bud break at the xeric inner Alpine site and at timberline was recorded in late March (85 d) and late April (113 d), i.e. about 2–3 wk earlier than in years, when temperatures corresponding to LTM prevailed in spring (own observations). At the low and high altitude study plot timing of onset of cambial activity and cell differentiation processes differed by almost 3 wk suggesting marked effects of early spring temperature on early processes of xylogenesis. That cambial reactivation after winter dormancy is closely related to temperature was demon strated by several authors (e.g. Oribe & al. 2001, Gričar & al. 2006, Moser & al. 2010, Swidrak & al. 2011). Similarly, at several timberline sites warm spring temperatures were found to result in earlier resumption of cambial cell production and xylem differentiation (Rossi & al. 2007, Deslauriers & al. 2008, Gruber & al. 2009). Since results indicate that onset of cambial activity and wood formation at boundaries of tree existence is temperature controlled, a possible shift in climate-growth relationships in response to climate change induced warmer spring temperatures in recent decades (e.g., Menzel & Fabian 1999) has to be considered.

Along the altitudinal transect the timing of maximum cell production in 2007 differed by c. 7 wk, i.e. in early May and in mid June at the inner Alpine montane site and at timberline, respectively. At both sites maximum tracheid production peaked before the occurrence of more favourable growing conditions, i.e. an increase in precipitation and temperature during summer. That the maximum daily growth rate of conifers from cold environments, i.e. at the alpine treeline and in boreal forests peaks around summer solstice was reported by several authors (e.g. Rossi & al. 2006c, Moser & al. 2010). Rossi & al. 2006c hypothesized that in these environ-

ments photoperiodic growth constraint is an adaptation allowing tracheid differentiation to be completed before winter. Instead of considering a timely completion of wood formation as a cause of early decrease in radial stem growth, we suggest that a pronounced internal competition in carbon allocation between aboveground (terminal and radial shoot growth, bud development, foliage growth) and belowground organs (mycorrhiza-associated root system) exists (cf. WARING 1987). That the root system of *P. sylvestris* is a strong sink for carbohydrates is supported by the results of BRUNNER & al. 2009, who reported a lack of increase in fine root biomass in *P. sylvestris* in response to irrigation treatment. Hence, at the xeric inner Alpine site low precipitation and recurring drought periods in spring combined with limited waterholding capacity and nutrient deficiency of shallow stony soils might cause elevated carbohydrate requirements belowground to ensure adequate resource acquisition for shoot growth.

On the other hand, soil temperature is regarded one of the most important limiting factors for root growth (for a review see PREGITZER & al. 2000, ALVAREZ-URIA & KÖRNER 2007) and cold soils, which are developed under closed canopy at timberline (see KÖRNER & PAULSEN 2004) also impair microbial nutrient mineralization rates and nutrient uptake (GILL & JACKSON 2000). Because an increase in fine root biomass with elevation has been reported for trees at treelines (HELMISAARI & al. 2007, LEUSCHNER & al. 2007, HERTEL & SCHÖLING 2011) it needs to be elucidated whether cold soils also exert elevated carbon drain to belowground organs and besides a photoperiodic growth control contribute to early maximum growth rates in *P. cembra* at the Alpine timberline.

Impact of Drought on Xylem Cell Development

Wood formation during 2007 stopped c. 8 wk earlier at the xeric inner Alpine site than at timberline, which resulted in c. 6 wk shorter duration of cell differentiation processes (cell enlargement, wall thickening and lignification) at low altitude. That duration of wood formation in *P. sylvestris* is adversely affected by high water deficits in summer was reported by RIGLING & al. 2003 and THABEET & al. 2009. Extraordinary hot and dry conditions, which prevailed during the growing season 2003 (cf. REBETEZ & al. 2006) also caused an early cessation of cambial activity in *P. sylvestris* at the xeric inner Alpine study plot (PICHLER & OBERHUBER 2007).

When comparing the total number of tracheids produced in 2007 among study plots, i.e. c. 13 and 60 tracheids were developed at the xeric inner Alpine site and at timberline, respectively, the importance of tree water status on radial growth becomes obvious. That stem radial growth within dry inner Alpine valleys is limited by precipitation has frequently been stressed (OBERHUBER & al. 1998, RIGLING & al. 2002, ZWEIFEL & al. 2006, OBERHUBER & GRUBER 2010). Several authors also reported a decline

Table 1. Spring (March-May) and summer (June-August) air and soil temperature and precipitation in 2007 throughout the altitudinal transect. Climate data for the inner Alpine site were available from a nearby meteorological station (Oetz, 5 km from the study area) and top of Mt. Patscherkofel (2246 m a.s.l.). Long-term mean values (= LTM) covered the period 1911–2006 and 1967–2004 for the inner Alpine and timberline site, respectively. Mean values ± standard deviation are shown.

Site	Air temperature (°C)				Soil temperature (°C)			Precipitation (mm)			
	Spring		Summer		April	May	Summer	Spring		Summer	
	LTM	2007	LTM	2007				LTM	2007[1])	LTM	2007
Inner Alpine	7.6 ± 1.2	10.3	15.8 ± 1.0	17.1	15.6	16.0	18.7	138 ± 37	148	316 ± 65	403
Timberline	0.6 ± 1.4	4.0	9.3 ± 1.4	10.6	4.4	4.9	7.6	201 ± 55	154	358 ± 63	409

[1]) An extended drought period was recorded from 20 March to 6 May, when total monthly precipitation in April reached < 3 and 8 mm at the inner Alpine and timberline site, respectively. LTM in April was 39 ± 19 and 64 ± 27 mm at the inner Alpine and timberline site, respectively.

Table 2. Characteristics of stands selected for sampling micro-cores (n = 5 trees/site) throughout the altitudinal transect. Mean values ± standard deviation are shown (SDM = stem diameter in c. 1 m height). Statistically significant differences of mean ring width between sites and years are indicated by different letters (P ≤ 0.05, Student's t- test).

Site	Species	Altitude (m a.s.l.)	Aspect	Tree height (m)	SDM (cm)	Age[1]) (yr)	Ring width (mm)	
							2002–2006	2007
Inner Alpine	*Pisy*	750	SW	3–4	29 ± 5	142 ± 27	0.41a ± 0.14	0.36a ± 0.17
Timberline	*Pice*	1950	W	10–14	40 ± 9	80 ± 11	2.13b ± 0.62	1.84b ± 0.72

[1]) Cambial age at sampling height (c. 1 m)

in cambial cell division during drought (ABE & NAKAI 1999, DE LUIS & al. 2007, EILMANN & al. 2009). Besides limited water availability, however, tree growth at the low altitude plot might also be restricted due to inherent low nutrient content and retarded soil development of dolomite parent material (KRAPFENBAUER 1969, cf. AXELSSON & AXELSSON 1986), which is supported by almost twice as wide annual increments of *P. sylvestris* trees of comparable age reported from Valais, an inner Alpine dry valley in Switzerland (RIGLING & al. 2002). On the other hand, photoperiod is regarded to control ending of xylogenesis in conifers at timberline (ROSSI & al. 2007, LÜTTGE & HERTEL 2009, MOSER & al. 2010), where soil water availability is regarded as being of minor importance for tree growth (WIESER 2004). GRUBER & al. 2009 also found no significant relations between precipitation and tracheid production at timberline on Mt. Patscherkofel. The missing growth response of *P. cembra* to the extended and warmer than average growing season in 2007, which corresponds to the weak growth response of *P. cembra* to the 2003 summer heat-wave (OBERHUBER & al. 2008), might be caused by the finding of several authors that besides summer temperature other climate variables, like temperature in previous fall, winter precipitation, and weather extremes (late frost) are influencing radial growth of *P. cembra* at timberline (e.g., FRENZEL & MAISCH 1981, OBERHUBER 2004, PFEIFER & al. 2005, CARRER & al. 2007).

Conclusions

This study demonstrates that although mild temperatures in spring 2007 caused early onset of cambial activity and wood formation in *P. sylvestris* and *P. cembra* at low and high altitude, respectively, a lengthened and warmer than average growing season does not concurrently result in increased tree growth due to compensating effects of climate variables and/or biological preconditioning in previous years. Furthermore, we suggest that the early decrease in tracheid production found in late spring at the inner Alpine valley site and around summer solstice at Alpine timberline is due to an early switch of carbon allocation to belowground organs as an adaptation to cope with extreme environmental conditions prevailing at these boundaries of tree existence. Hence, in future studies concentrating on tree growth response to climate variability, interactions between aboveground and belowground processes including carbon allocation, root growth and turnover and nutrient availability need to be considered more closely.

Acknowledgements

This work was supported by the Austrian Science Fund (FWF Project Nos. P19563-B16 “Dynamics of cambial activity and wood formation of Scots pine (*Pinus sylvestris* (L.) exposed to soil dryness” and P18819-B03 “Temperature dependence of

Pinus cembra (L.) stem growth and respiration along an altitudinal transect"). We greatly acknowledge Hydrographischer Dienst, Innsbruck, and Zentralanstalt für Meteorologie und Geodynamik, Innsbruck, for providing us the climate data.

References

ABE H. & NAKAI T. 1999. Effect of the water status within a tree on tracheid morphogenesis in *Cryptomeria japonica* D. Don. – Trees 14: 124–129.

ALVAREZ-URIA P. & KÖRNER C. 2007. Low temperature limits of root growth in deciduous and evergreen temperate tree species. – Funct. Ecol. 21: 211–218.

AXELSSON E. & AXELSSON B. 1986. Changes in carbon allocation patterns in spruce and pine trees following irrigation and fertilization. – Tree Physiol. 2: 189–204.

BRUNNER I., PANNATIER E. G., FREY B., RIGLING A., LANDOLT W., ZIMMERMANN S. & DOBBERTIN M. 2009. Morphological and physiological responses of Scots pine fine roots to water supply in a dry climatic region in Switzerland. – Tree Physiol. 29: 541–550.

CAMARERO J. J., OLANO J. M. & PARRAI A. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. – New Phytol. 185: 471–80.

CARRER M., NOLA P., EDUARDS J.L., MOTTA R. & URBINATI C. 2007. Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps. – J. Ecol. 95: 1072–1083.

DE LUIS M., GRIČAR J., ČUFAR K. & RAVENTOS J. 2007. Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. – IAWA J. 28: 389–404.

DESLAURIERS A., MORIN H. & BEGIN Y. 2003. Cellular phenology of annual ring formation of *Abies balsamea* in the Quebec boreal forest (Canada). – Can. J. For. Res. 33: 190–200.

DESLAURIERS A., ROSSI S., ANFODILLO T. & SARACINO A. 2008. Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. – Tree Physiol. 28: 863–871.

EILMANN B., ZWEIFEL R., BUCHMANN N., FONTI P. & RIGLING A. 2009. Drought-induced adaptation of the xylem in Scots pine and pubescent oak. Tree Physiology 29: 1011–1020.

FAO. 1998. World reference base for soil resources. – FAO, Rome.

FRENZEL B. & MAISCH I. 1981. Klimatische Analyse der Jahrringbreitenschwankungen an der alpinen Waldgrenze. – Mitt. Forstl. Bundes-Vers.anst. Wien 142: 399–416.

FRITTS H. C. 1976. Tree rings and climate. – Academic Press, London, UK.

GILL R. A. & JACKSON R. B. 2000. Global patterns of root turnover for terrestrial ecosystems. – New Phytol. 147: 13–31.

GRACE J., BERNINGER F. & NAGY L. 2002. Impacts of climate change on the tree line. – Ann. Bot. 90: 537–544.

GRIČAR J., ZUPANČIČ M., ČUFAR K. & PRIMOŽ O. 2006. Regular cambial activity and xylem and phloem formation in locally heated and cooled stem portions of Norway spruce. – Wood Sci. Technol. 41: 463–475.

GRUBER A., BAUMGARTNER D., ZIMMERMANN J. & OBERHUBER W. 2009. Temporal dynamic of wood formation in *Pinus cembra* along the alpine treeline ecotone and the effect of climate variables. – Trees 23: 623–635.

GRUBER A., STROBL S., VEIT B. & OBERHUBER W. 2010. Impact of drought on the temporal dynamics of wood formation in *Pinus sylvestris*. – Tree Physiol. doi: 10.1093/treephys/tpq003.

HELMISAARI H.-S., DEROME J., NÖJD P. & KUKKOLA M. 2007. Fine root biomass in relation to site and stand characteristics in Norway spruce and Scots pine stands. – Tree Physiol. 27: 1493–1504.

HERTEL D. & SCHÖLING D. 2011. Norway spruce shows contrasting changes in below- versus above-ground carbon partitioning towards the Alpine treeline: evidence from a central European case study. – Arctic, Antarctic Alpine Res. 43: 46–55.

KÖRNER C. 1998. A re-assessment of high elevation treeline positions and their explanation. – Oecologia 115: 445–459.

KÖRNER C. & PAULSEN J. 2004. A world-wide study of high altitude treeline temperatures. – J. Biogeogr. 31: 713–732.

KRAPFENBAUER A. 1969. Böden auf Dolomit und Serpentin in ihrer Auswirkung auf die Waldernährung. – Centralbl. Ges. Forstw. 86: 189–219.

LEUSCHNER C., MOSER G., BERTSCH C., RÖDERSTEIN M. & HERTEL D. 2007. Large altitudinal increase in tree root/shoot ratio in tropical mountain forests of Ecuador. – Basic Appl. Ecol. 8: 219–230.

LÜTTGE U. & HERTEL B. 2009. Diurnal and annual rhythms in trees. – Trees 23: 683–700.

MÄKINEN H., SEO J.-W., NÖJD P., SCHMITT U. & JALKANEN R. 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. – Eur. J. For. Res. 127: 235–245.

MENZEL A. & FABIAN P. 1999. Growing season extended in Europe. – Nature 397: 659.

MOSER L., FONTI P., BÜNTGEN U., ESPER J., LUTERBACHER J., FRANZEN J. & FRANK D. 2010. Timing and duration of European larch growing season along altitudinal gradients in the Swiss Alps. – Tree Physiol. 30: 225–233.

NEUWINGER I. 1970. Böden der subalpinen und alpinen Stufe in den Tiroler Alpen. – Mitt. Ostalpin-Dinarische Ges. Veg.kde 11: 135–150.

OBERHUBER W. 2001. The role of climate in the mortality of Scots pine (*Pinus sylvestris* L.) exposed to soil dryness. – Dendrochronologia 19: 45–55.

OBERHUBER W. 2004. Influence of climate on radial growth of *Pinus cembra* within the alpine timberline ecotone. – Tree Physiol. 24: 291–301.

OBERHUBER W. & GRUBER A. 2010. Climatic influences on intra-annual stem radial increment of *Pinus sylvestris* (L.) exposed to drought. – Trees, doi:10.1007/s00468-010-0458-1.

OBERHUBER W., STUMBÖCK M. & KOFLER W. 1998. Climate-tree-growth relationships of Scots pine stands (*Pinus sylvestris* L.) exposed to soil dryness. – Trees 13: 19–27.

OBERHUBER W., KOFLER W., PFEIFER K., SEEBER A., GRUBER A. & WIESER G. 2008. Long-term changes in tree-ring-climate relationships at Mt. Patscherkofel (Tyrol, Austria) since the mid-1980s. – Trees 22: 31–40.

ORIBE Y., FUNADA R., SHIBAGAKI M. & KUBO T. 2001. Cambial reactivation in locally heated stems of evergreen conifer *Abies sachalinensis* (Schmidt) Masters. – Planta 212: 684–691.

PFEIFER K., KOFLER W. & OBERHUBER W. 2005. Climate related causes of distinct radial growth reductions in *Pinus cembra* during the last 200 yr. – Veg. Hist. Archaeobot. 14: 211–220.

PICHLER P. & OBERHUBER W. 2007. Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. – For. Ecol. Manage. 242: 688–699.

PREGITZER K. S., KING J. S., BURTON A. J. & BROWN S. E. 2000. Responses of tree fine roots to temperature. – New Phytol. 147: 105–115.

REBETEZ M., MAYER H., DUPONT O., SCHINDLER D., GARTNER K., KROPP J. P. & MENZEL A. 2006. Heat and drought 2003 in Europe: a climate synthesis. – Ann. For. Sci. 63: 569–577.

RIGLING A., BRÄKER O. U., SCHNEITER G. & SCHWEINGRUBER F. H. 2002. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Erico-Pinion in the Valais (Switzerland). – Plant Ecol. 163: 105–121.

RIGLING A., BRÜHLHART H., BRÄKER O. U., FORSTER T. & SCHWEINGRUBER F. H. 2003. Effects of irrigation on diameter growth and vertical resin duct production in *Pinus sylvestris* L. on dry sites in the central Alps, Switzerland. – For. Ecol. Manage. 175: 285–296.

ROSSI S., DESLAURIERS A. & MORIN H. 2003. Application of the Gompertz equation for the study of xylem cell development. – Dendrochronologia 21: 33–39.

ROSSI S., ANFODILLO T. & MENARDI R. 2006a. Trephor: a new tool for sampling microcores from tree stems. – IAWA J. 27: 89–97.

ROSSI S., DESLAURIERS A. & ANFODILLO T. 2006b. Assessment of cambial activity and xylogenesis by microsampling tree species: an example at the Alpine timberline. – IAWA J. 27: 383–394.

ROSSI S., DESLAURIERS A., ANFODILLO T. & CARRARO V. 2007. Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. – Oecologia 152: 1–12.

ROSSI S., DESLAURIERS A., ANFODILLO T., MORIN H., SARACINO A., MOTTA R. & BORGHETTI M. 2006c. Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. – New Phytol. 170: 301–310.

SAXE H., CANNELL M. G. R., JOHNSEN Ø., RYAN M. G. & VOURLITIS G. 2001. Tree and forest functioning in response to global warming. – New Phytol. 149: 369–400.

SWIDRAK I., GRUBER A., KOFLER W. & OBERHUBER W. 2011. Effects of environmental conditions on onset of xylem growth in *Pinus sylvestris* under drought. – Tree Physiol. 31: 483–493.

THABEET A., VENNETIER M., GADBIN-HENRY C., DENELLE N., ROUX M., CARAGLIO Y. & VILA B. 2009. Response of *Pinus sylvestris* L. to recent climatic events in the French Mediterranean region. – Trees 23: 843–853.

WARING R. H. 1987. Characteristics of trees predisposed to die. – Bioscience 37: 569–574.

WIESER G. 2004. Seasonal variation of soil respiration in a *Pinus cembra* forest at the timberline in the Central Austrian Alps. – Tree Physiol. 24: 475–480.

WIESER G., MATYSSEK R., LUZIAN R., ZWERGER P., PINDUR P., OBERHUBER W. & GRUBER A. 2009. Effects of atmospheric and climate change at the timberline of the Central European Alps. – Ann. For. Sci. 66: 402.

ZWEIFEL R., ZIMMERMANN L., ZEUGIN F. & NEWBERRY D. M. 2006. Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. – J. Exp. Bot. 57: 1445–1459.