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Drought alters timing, quantity, and quality of wood formation in Scots pine

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Abstract

Drought has been frequently discussed as a trigger for forest decline. Today, large-scale Scots pine decline is observed in many dry inner-Alpine valleys, with drought discussed as the main causative factor. This study aimed to analyse the impact of drought on wood formation and wood structure. To study tree growth under contrasting water supply, an irrigation experiment was installed in a mature Scots pine (*Pinus sylvestris* L.) forest at a xeric site in a dry inner-Alpine valley. Inter- and intra-annual radial increments as well as intra-annual variations in wood structure of pine trees were studied. It was found that non-irrigated trees had a noticeably shorter period of wood formation and showed a significantly lower increment. The water conduction cells were significantly enlarged and had significantly thinner cell walls compared with irrigated trees. It is concluded that pine trees under drought stress build a more effective water-conducting system (larger tracheids) at the cost of a probably higher vulnerability to cavitation (larger tracheids with thinner cell walls) but without losing their capability to recover. The significant shortening of the growth period in control trees indicated that the period where wood formation actually takes place can be much shorter under drought than the 'potential' period, meaning the phenological growth period.

Key words: Climate change, forest decline, intra-annual tree growth, irrigation experiment, pinning, wood anatomy.

Introduction

The hot and dry summer of 2003 in Europe strongly affected terrestrial ecosystems, not only in the year 2003 but also in the following years (Ciais *et al.*, 2005; Granier *et al.*, 2007; Reichstein *et al.*, 2007). Since the frequency and severity of drought are expected to increase further (IPCC, 2007; Schär *et al.*, 2004), a mechanistic understanding of such impacts of drought on plant growth and plant survival is crucial. In forest ecosystems, drought was shown to decrease primary production (Ciais *et al.*, 2005; Granier *et al.*, 2007; Reichstein *et al.*, 2007), reduce stem growth (Schweingruber, 1993; Fritts, 2001; Rigling *et al.*, 2002; Zweifel *et al.*, 2006) and lower the amount of stored carbohydrates (Bréda *et al.*, 2006). However, not only the amount, but also the timing when carbon is fixed or wood is built might be affected. To what extent still remains unclear.

Due to the strong limitation of tree performance by water shortage, drought has been frequently discussed as a trigger

of vegetation shifts and forest decline (Allen *et al.*, 2010; Breshears *et al.*, 2005; Dobbertin, 2005). Also in inner-Alpine valleys, where precipitation is generally low due to the rain shadow of the surrounding high mountain ranges, drought was found to be the main factor limiting growth (Eilmann *et al.*, 2006, 2009). During the last decades, growth limitation by drought has become more severe, since climatic conditions have changed towards more severe drought during the growth period (Rebetez and Dobbertin, 2004; Weber *et al.*, 2007). Forests at low elevations in this inner-Alpine valleys are naturally dominated by Scots pine (*Pinus sylvestris* L., susequently denoted pine herein), but recently high rates of pine mortality have been observed in many inner-Alpine valleys [e.g. the Aosta valley (Vertui and Tagliaferro, 1998), the Inn valley (Oberhuber, 2001), or the Swiss Rhone valley (Dobbertin, 2005; Zweifel *et al.* 2009)]. Mortality rates were highest on dry sites and after drought

years (Dobbertin *et al.*, 2005). Locally, almost half of the pine population has died since 1995 (Rebetez and Dobbertin, 2004), demonstrating the importance of pine decline for the region. However, even though a clear relationship between drought and pine mortality has been found for the stand level, the processes leading to drought-induced pine decline remain uncertain.

For tree survival at dry sites, the maintenance of an efficient water transport system is of particular importance (Bréda *et al.*, 2006) as it avoids a drought-induced down-regulation of photosynthetic activity (Rennenberg *et al.*, 2006; Zweifel *et al.*, 2007) and keeps xylem water potential above cavitation thresholds (Bréda *et al.*, 2006). Despite the central role of the water transport system for tree performance under drought, only little is known about the effect of chronic drought on the formation of water-conducting stem cells and their geometry (Sterck *et al.*, 2008; Martinez-Vilalta *et al.*, 2009). However, as more negative sap pressure occurs under drought, it would be reasonable to build stronger tracheids with thicker cell walls relative to the span of the cell, for example by building smaller cells with thicker cell walls (Hacke *et al.*, 2001). But concurrently, smaller cells are much less efficient in terms of water conduction, as the hydraulic conductivity decreased by the power of four with decreasing lumen diameter (Hagen Poiseuille law; according to Tyree and Zimmermann, 2002). Thus, trees growing in a dry environment face the dilemma of optimizing between transport efficiency and transport safety of water-conducting cells. Decreasing cell sizes were often observed in periods of water shortage (e.g. Nicholls and Waring, 1977; Sheriff and Whitehead, 1984; Dünisch and Bauch, 1994), which has been discussed as a mechanism to decrease the cavitation risk. However, whether this is also the case under chronic drought with proceeding carbon storage depletion as in inner-Alpine valleys (Eilmann *et al.*, 2010) is unclear.

In an irrigation experiment in a mature pine forest (average tree age: 90 years) at a xeric site in the Swiss Rhone valley (Valais) the effect of contrasting water availability (naturally dry conditions versus irrigation) on the growth of pine trees was studied.

Analyses focused on inter- and intra-annual radial increments as well as on intra-annual variation in wood structure (lumen diameter and cell wall thickness).

It was expected that (i) trees adjust their water-conducting system to resource limitation under drought; and (ii) not only the amount and the structure of wood but also the timing of its formation are altered by drought.

Materials and methods

Experimental site and sample trees

The experimental site is located on the valley floor, in the driest central part of the Valais close to the village Susten, (46°18' N, 7°36' E, elevation 615 m). The climate is continental-dry, with a mean annual temperature of 9.2 °C and a mean annual precipitation total of 599 mm (norm period 1961–1990, MeteoSwiss,

weather station Sion, 20 km distance from the experimental site).

The forest at the experimental site can be described as *Erico-Pinetum sylvestri*s. The shallow, skeletal soil (soil depth 60 cm) is a pararendzina characterized by low water retention. The experimental site (~1 ha) was split up into eight plots of 1000 m^2 each, separated by a 5 m buffering strip. Trees on four randomly selected plots were irrigated from June 2003 (referred to in the following as irrigated trees); trees in the other four plots were growing under naturally dry conditions (referred to in the following as control trees). Irrigation water was taken from an adjacent water channel, which is fed by the river Rhone. During the growth period (April–October), irrigation was applied using sprinklers of ~1 m in height. To minimize the water loss and the cooling by evapotranspiration, irrigation took place at night only. Irrigating earlier than April was not possible, due to the risk of equipment damage by late frost. The amount of irrigation corresponded to a supplementary rainfall of ~700 mm year^{-1}. The two years studied were drier compared with the long-term mean precipitation (2004, 477 mm; 2005, 500 mm), leading to a pronounced difference between the control and the irrigated plots.

The growth of six irrigated and six control pine trees were analysed annually for the years 1993 to 2005 and intra-annually for the years 2004 and 2005. Sample trees were classified into three groups according to the defoliation caused by previous drought events (crown transparencies <25%, 25–50% and >50%; for details see Dobbertin et al., 2004). The classification took place in March 2003 before the new shoots emerged and was repeated after 3 years of irrigation (in March 2006). With this sampling design, the treatment effect on tree growth can be analysed with crown transparency as grouping factor.

Sampling and sample preparation

The pinning method was applied on a weekly to biweekly basis to date the timing of wood formation during the growth period 2004 (14 April to 27 October) and 2005 (13 April to 13 October). Pinning means the marking of the cambium by micro-injury using a small needle (diameter 0.6 mm). The resulting wound reaction is used for the exact dating of wood formation (Wolter, 1968; Yoshimura et al., 1981; Nobuchi et al., 1993), as the wound tissue separates cells formed before and after the pinning. At every pinning date, each sample tree was wounded three times at breast height (for details, see Schmitt et al., 2004).

In spring 2006 the trees were harvested. The stem section including the pinning wounds and an additional stem disc from above the stem section were cut and stored at –20 °C to avoid fungal infestation.

Tissue including the pinning wound and tissue unaffected by the wound reaction was extracted from the stem section using a keyhole saw (19 mm) and stored at –20 °C in Strasburger solution [one-third ethanol (95%), one-third glycerol (99%), one-third distilled water]. Using a sliding microtome (Reichert, Germany), thin sections (thickness of 10 μm) were made (i) of the tissue containing the pinning wound, for intra-annual increment measurements; and (ii) of unaffected tissue, for the analysis of the wood structure. For a better contrast between cell wall and cell lumen, thin sections were stained with safranin (1% solution) and astrablue (2% solution). Subsequently the sections were dehydrated in an alcohol concentration gradient (70%, 95%, and absolute ethanol), then in xylol (>98%) and permanently fixed with Canada balsam. Pictures of the thin sections were taken for image analysis (×100 magnification; microscope, Olympus BX41, Japan; camera, ColorView III, Soft Imaging system, Germany).

To analyse tree-ring width, the stem discs were sanded (35 μm particle diameter). Tree-ring width was measured on two radii using a combination of a Lintab digital positioning table and the software TSAP (both Rinntech, Germany). These two measurements per tree were averaged to one mean per tree.

Measurement on the intra-annual scale

According to the method of Seo et al. (2007), the intra-annual increment was measured (image analysis software IMAGE PRO PLUS, Media Cybernetics USA) as the distance between the previous tree-ring border and the last matured cell at the time of the pinning (last cells with a secondary wall below the wound; see Fig. 1, white arrow). This last mature cell was determined by polarized light. Mesurement of the intra-annual increment were made on both sides of the needle entry and summed up to an average value. The relative increment, giving the percentage of the entire growth ring built until the pinning date, was calculated by relating the measured intra-annual increment to the total ring width (increment$_{relative}$=increment$_{intra-annual}$ /tree-ring width; see Grotta et al., 2005). Therefore, tree-ring width was measured outside the tissue of the wound reaction.

Cellular parameters (lumen diameter and cell wall thickness) were measured on the samples of unaffected tissue to avoid potential bias by the wound reaction. Measurements were made along 10 radial cell rows per tree-ring using the software WinCell (Regents Instruments Inc., Canada).

Data processing and data analysis

The assignment of measurements to the pinning dates was done in two steps. First, the raw data were normalized to a common length (100 cells) according to the method of Vaganov (1990). This procedure was necessary (i) to avoid a distortion of the mean value at the end of the data set due to varying cell numbers per measurements [see Deslauriers et al. (2008) and Kirdyanov et al. (2003)] and (ii) to prevent a rounding error in the following step. Secondly, all data belonging to the same pinning time frame, according to the relative increment (Grotta et al., 2005; see above), were averaged. For example, if 10% of the tree-ring was built at the date of the first pinning, the lumen diameters of the first 10 cells of the normalized data set were averaged, giving the mean lumen diameter for the first pinning date.
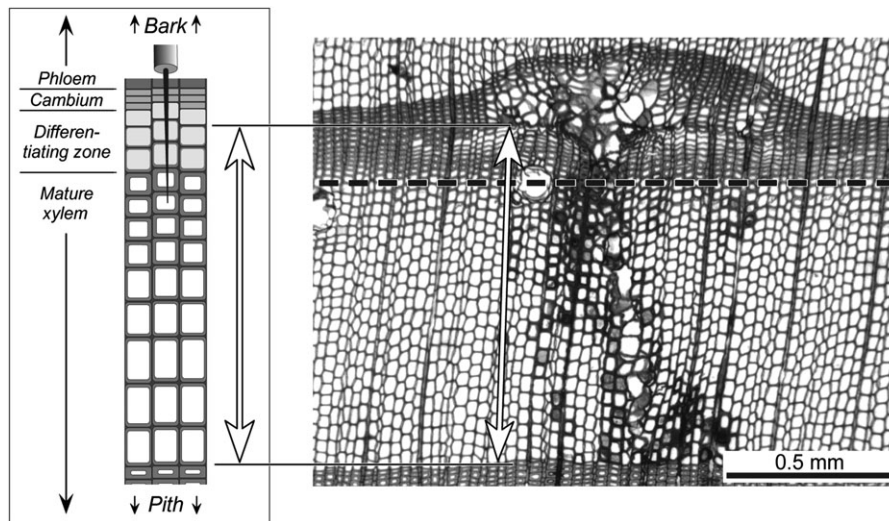

Fig. 1. Measurement of intra-annual increment. The scheme (left) shows the tissue at the time of the pinning. The thin section (right) shows the wound reaction found in the tissue 1 year after the pinning. The white arrow marks the distance between the previous tree-ring border and the last cell with secondary wall, which was measured as the absolute intra-annual increment at the time of the pinning. The wound tissue in the thin section corresponds to cambial and enlarging cells in the scheme (first 4–5 cells). The cells above the wound tissue in the thin section were built after the pinning. The horizontal broken line in the thin section shows the earlywood/latewood border.
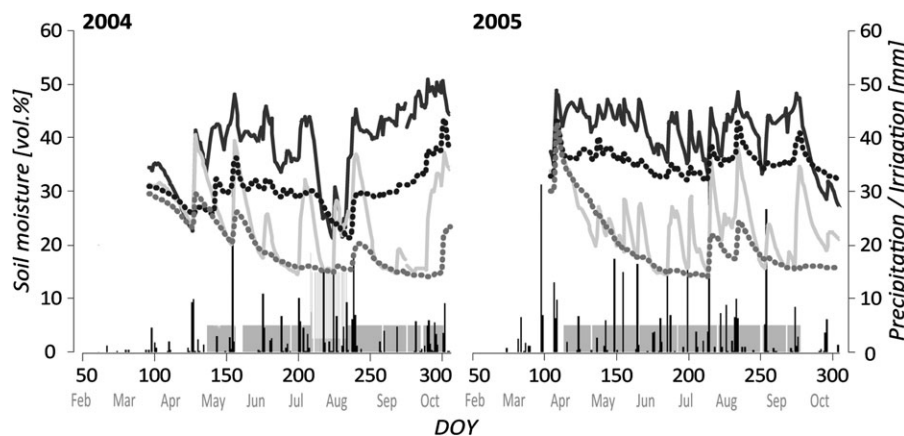

Fig. 2. Soil moisture on the irrigated (black) and the control (grey) plot measured at 10 cm (solid lines) and 60 cm (hatched lines) depth, together with the amount of precipitation (black bars) and irrigation (grey bars) for the years 2004 (left) and 2005 (right). During rainfall no irrigation took place (see breaks in the grey shading).
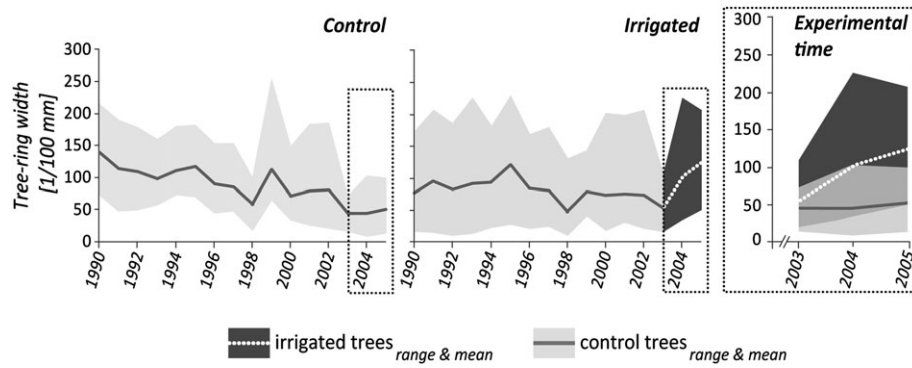
Fig. 3. Development of tree-ring width for the years 1993–2002 in irrigated and control trees. Grey showed the non-irrigated trees/years. The area shows the range of tree-ring width. The irrigated years (2003–2005) are marked by the black shading and the white curve. On the right is shown the tree-ring width of irrigated and control trees in experimental time.
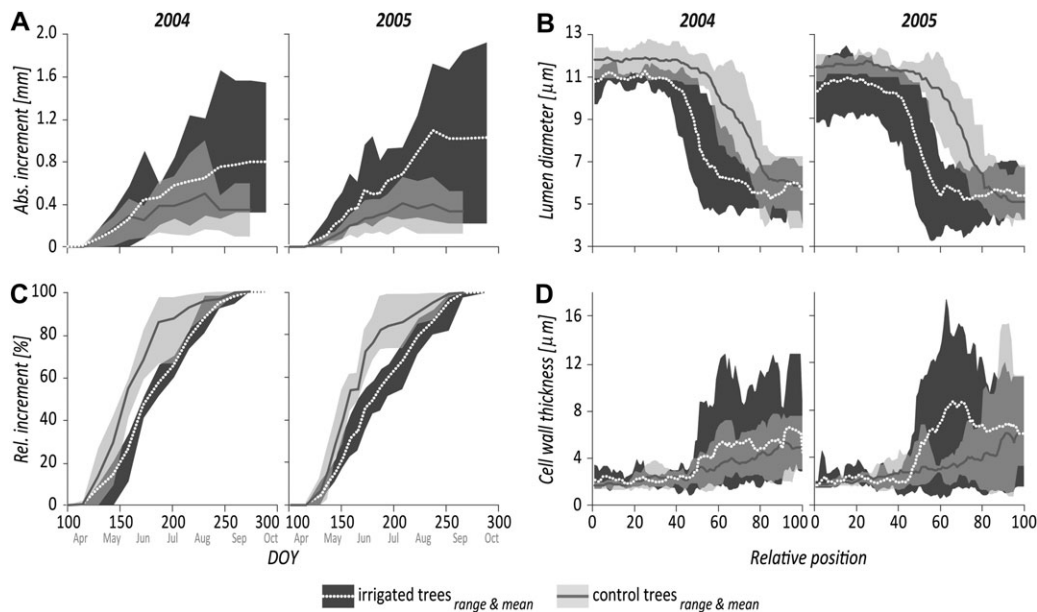
Fig. 4. (A) Absolute and (C) relative radial increment of irrigated (black range, white curve) and control (grey range, dark curve) trees at the pinning dates. (B) Lumen diameter and (D) cell wall thickness of irrigated (black range, white curve) and control (grey range, dark curve) trees standardized to a common length of 100 cells (=relative position).

The difference between the parameters in irrigated and control trees was tested for each parameter using a paired Wilcoxon sign rank test with crown transparency as a grouping factor.

Qualitative analysis of wood formation

As for the measurement of the intra-annual increment, attention was also focused on the last matured cell at the time of the pinning to detect the timing of wood formation. Three different phases of tree-ring formation were distinguished (i) if a mature undamaged cell with a secondary wall below the wound was found, wood formation was regarded as having begun; (ii) earlywood/latewood transition was reached if the last mature cells were situated above a tangential line separating earlywood from latewood (Fig. 1, line c); and (iii) the tree-ring was complete if the wound tissue occurred above a continuous band of flattened latewood cells (see Seo *et al.*, 2007).

Intra-annual climate–growth analysis

For the intra-annual climate–growth analysis, data sets were detrended to remove the seasonal growth trend. The trend in the

fortnightly increment was eliminated by trimming the first 5% and the last 10% of the data, where the increment curve usually flattens out. For the detrending of the lumen diameter, a non-linear regression model was adapted to the chronological data and the residuals (=detrended data) between the modelled and the chronological data were calculated. To detrend the cell wall thickness data, the residuals between a linear regression model and assigned data were also calculated. To separate earlywood from latewood, the dates of earlywood/latewood transition found in the qualitative analysis of wood formation were used.

Daily temperature data were monitored at the weather station Sion. Soil moisture was measured every hour at 10, 40, and 60 cm soil depths at two plots on the experimental site using a Time Domain Reflectometry sensor (1502B cable tester, Tektronix, USA) and averaged to a daily mean (see Fig. 3). During 2004 the irrigation was not working for a short period, but only on the plot were the soil moisture measurements took place. This affected only one of the irrigated sample trees. For climate–growth analysis, the soil moisture at 10 cm depth was considered as variation was maximal at this depth (Fig. 3). Daily temperature and soil moisture values were averaged using a moving window of 7 d and

correlated with detrended parameters (lumen diameter and cell wall thickness separated into earlywood and latewood, and the fortnightly increment). To avoid statistical artefacts, the degrees of freedom were corrected depending on the autocorrelation of growth (r_{growth}) and climate ($r_{climate}$) parameters {$df=n\times[(1+r_{growth}\times r_{climate})/(1-r_{growth}\times r_{climate}]$, see De Smith et al. (2007)}, leading to a more conservative evaluation of the correlation. The significance threshold based on the mean degrees of freedom was calculated for each growth parameter.
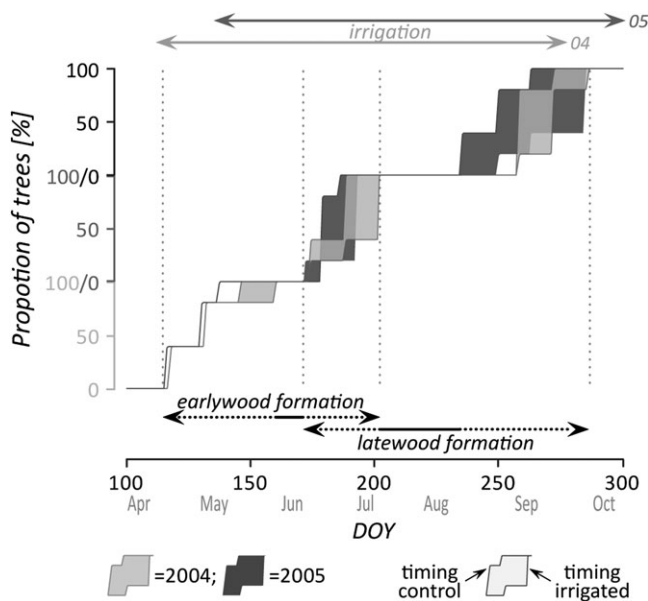

Fig. 5. Timing of wood formation for irrigated and control trees. The curve showed the proportion of trees (0–100%) that started earlywood formation (light grey y-axis), or started (dark grey y-axis) or finished latewood formation (black y-axis). A spanned surface indicates differences in the timing between control and irrigated trees.

Since the climate impact on cell growth was studied for 2 years only, the analysis focuses on general trends. Therefore, mainly the direction of significant responses (i.e. positive or negative) was interpreted but not the timing of the individual correlation peaks, as the impact of the individual years on the timing is unclear. Correlations with growth parameters of irrigated trees were not performed for soil moisture but for non-manipulated temperature only as (i) soil moisture was drastically manipulated by the irrigation treatment, leading to a more balanced soil moisture regime (Fig. 3); and (ii) trees need several years to adjust their whole metabolism including needle mass and the size of the root system to changing water supply (Eilmann et al., 2009; Dobbertin et al., 2010).

Results

Effects of water availability on the different growth parameters: Irrigation started in June of the drought year 2003, when most of the annual increment was expected to be already completed (compare with Fig. 4D, control trees). Therefore, all trees investigated showed a drought-induced decrease of tree-ring widths, independent of treatment (Fig. 3). In control trees, radial increments remained low in the following year, even though 2004 and 2005 were less dry than 2003 (annual precipitation 2003, 426 mm; 2004, 477 mm; 2005, 500 mm). In contrast, irrigated trees recovered from the 2003 drought year and increased tree-ring widths in 2004 and 2005.

At the intra-annual scale, improved water supply by irrigation led to significant changes in all growth parameters: absolute radial increment ($P <0.001$, Fig. 4A) and cell wall thickness ($P <0.001$, Fig. 4D) increased, while lumen diameter decreased ($P <0.001$, Fig. 4B). The wood formation rate in irrigated trees was very constant over the years
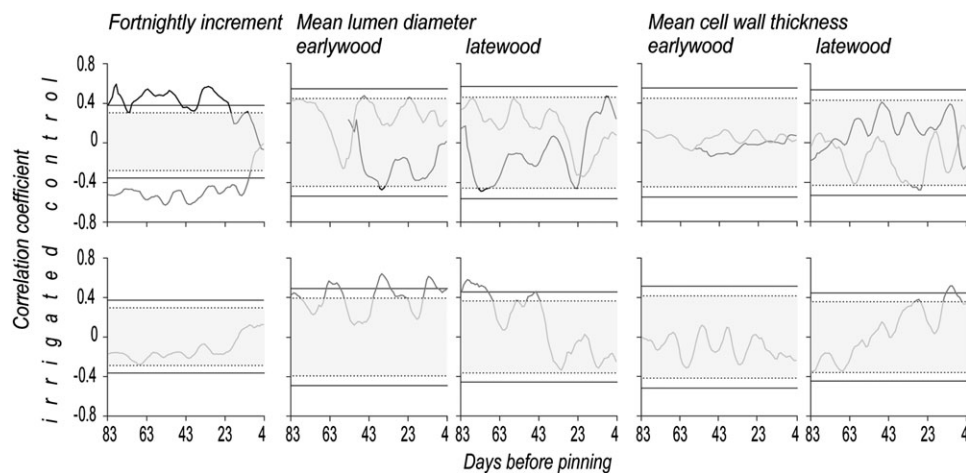
Fig. 6. Moving window correlations between the intra-annual growth parameters (fortnightly increment, lumen diameter, and cell wall thickness, the latter two separately for earlywood and latewood cells) and temperature (grey curve) or soil moisture (black curve; for growth parameters of the control plot only) calculated for the years 2004 and 2005 for trees of all crown density classes. Data on the x-axis give the central number around which the 7 d mean of climatic data for the moving window correlation was calculated. The horizontal lines mark the significance thresholds (broken line for $P <0.01$, solid line for $P <0.001$) for an autocorrelation-corrected mean degree of freedom. Non-significant correlations are located in the shaded area. The correlation between earlywood growth parameters in control trees and soil moisture was calculated for a period <83 d due to missing soil moisture data during the winter.

Table 1. Principal tree characteristics (mean ±SD)

Tree-ring width was calculated for the 10 years before irrigation started (1993–2002). The crown transparency value shows the estimates of March 2003, before the start of irrigation (=before) and March 2006 (=after), after two and a half years of irrigation. Tree height, steam diameter, crown length, and crown diameter were measured during sampling (spring 2006).

	Crown transparency (%)		Age (years)	Tree-ring width (mm)	Tree height	Stem diameter (cm)	Crown length (m)	Crown diameter (m)
	Before	After						
Irrigated	33	29	97±28	0.79±0.56	11.3±1.1	25.9±3.7	4.0±0.8	4.7±1.3
Control	34	51	97±27	0.67±0.30	10.6±1.0	23.1±3.4	3.7±1.1	4.1±0.7

2004 and 2005 with little variation between the trees (see range in Fig. 4C). In contrast, control trees showed more variation in the rate of increment towards the end of the growth period. In addition, the increment curves of control trees flattened ~1 month earlier than those of the irrigated trees.

Effects of water availability on the timing of wood formation: Water availability influenced the timing of wood formation (Fig. 5). Irrigation led to a prolongation of the growth period as the cessation of cell production occurred up to 5 weeks later in irrigated trees compared with control trees. In addition, the earlywood/latewood transition occurred ~2–4 weeks later in irrigated trees than in control trees. Therefore, the period of earlywood and latewood formation was prolonged due to irrigation. In contrast, the beginning of wood formation was not affected by irrigation.

Intra-annual climate–growth correlations: While the fortnightly radial increments of control trees decreased under high temperature and low soil moisture (Fig. 6), a limiting effect of high temperatures was not found for the irrigated trees. However, high temperature led to an increase in lumen diameter in early- and latewood of both control trees and irrigated trees, with pronounced responses for irrigated trees. Lumen diameter in control trees also increased under low soil moisture.

Cell wall thickness in earlywood of irrigated and control trees showed no response to climate conditions at all. Nevertheless, in latewood, cell wall thickness responded differently to temperature between treatments: it decreased in control trees but increased in irrigated trees under high temperatures.

Discussion

Growth responses to drought

Irrigation significantly altered all of the examined growth parameters, emphasizing the importance of drought as a limiting growth factor under natural conditions in the Valais.

Lumen diameters were significantly smaller in irrigated trees compared with control trees (Fig. 4B). This is in accordance with the results of Eilmann *et al.* (2009) studying the growth of Scots pine along an open water channel in comparison with tree growth under naturally dry conditions during four decades in the Valais. In addition, Maherali and DeLucia (2000) also reported larger lumen diameter for ponderosa pine at a semi-arid site (Great Basin) compared with trees on a moderate mountain site (Sierra Nevada) in the USA. Increasing lumen diameters under dry conditions are thought to compensate for the disadvantage of the decreasing conductive area of the tree-ring (decreasing ring increment, Fig. 4), as the volume flow, which will establish depending on the water potential, increases by the power of four with increasing lumen diameter (Hagen Poiseuille law; according to Tyree and Zimmermann, 2002). Hence, with larger lumen diameter less tissue has to be invested to reach a given water conductivity, thus higher rates of transpiration can be tolerated (Sperry, 2003). However, in contrast to the present results, increasing lumen diameters with increasing water availability were reported (Jenkings, 1974; Nicholls and Waring, 1977; Sheriff and Whitehead, 1984; Sterck *et al.*, 2008). However, the lumen diameters observed in the present study were at the lower end of lumen diameters ever measured. The mean earlywood lumen diameter in this study was control=10.9μm, irrigated=9.9μm, whereas in other studies, earlywood lumen diameter ranged from 14.4μm to 40.3μm (Jenkings, 1974; Nicholls and Waring, 1977; Sheriff and Whitehead, 1984; Castro-Diez *et al.*, 1998; Decoux *et al.*, 2004; Eilmann *et al.*, 2006; Kilpelainen *et al.*, 2007; Sterck *et al.*, 2008). These low values underline the strong restriction of cell enlargement due to the chronic drought in Valais, which is in accordance with Eilmann *et al.* (2009) and Maherali and DeLucia (2000).

However, concurrently with the increase in transport efficiency, transport safety might be jeopardized, as the vulnerability of a water-conducting cell to cavitation is expected to increase with increasing lumen diameter (Mauseth, 1988). Moreover, this negative effect on transport safety is further aggravated by the fact that the cell walls were significantly thinner in control trees (Fig. 4D) due to the reduced carbohydrate availability under chronic drought (Eilmann *et al.*, 2010). This combination of larger cell size and thinner cell walls results in a reduction of wood density (Bodig and Jayne, 1993) which might reduce the bending strength of the water-conducting cells, with again negative consequences on the resistance to drought-induced cavitation (Hacke *et al.*, 2001; Pittermann *et al.*, 2006). Therefore, it is expected that the wood tissue in control trees is more vulnerable to

cavitation than that of irrigated trees. However, keeping in mind that the cell size observed in this study is amongst the smallest ever found (see above), it is expected that the cavitation risk of Scots pine in Valais is not significantly higher compared with Scots pine at other sites, which is in accordance with the results of Martinez-Vilalta et al. (2009) comparing Scots pine vulnerability towards cavitation all over Europe. Thus, all in all, the present results on the wood anatomical level suggest that pine trees under naturally dry conditions built a 'cheaper' (in terms of carbon investment) and more effective (in terms of conductivity), but at the same time potentially more vulnerable, water-conducting system under naturally dry conditions than under moderate conditions.

Radial increment was significantly lower in control pine trees compared with the irrigated pines (Fig. 5A), probably due to the direct control of cambial activity by water availability, as suggested by Zweifel et al. (2006) and Steppe and Lemeur (2007). In addition lower photosynthetic activity under drought (Ciais et al., 2005; Reichstein et al., 2007) will also lead to low carbon availability and allocation for cell division.

Impact of drought on the timing of wood formation

The present study showed that control trees finished wood formation earlier compared with irrigated trees, as the periods both of earlywood and of latewood formation were terminated ∼2–5 weeks earlier in control trees compared with irrigated trees (Fig. 5). Similar results were also found for red pine or spruce in the case of the premature earlywood/latewood transition (Zahner et al., 1964; Whitmore and Zahner, 1966; Dünisch and Bauch, 1994) and for spruce in the case of the early cessation of cell formation under drought (Dünisch and Bauch, 1994). In contrast to this 'realized' growth period, the phenological growth period in the Northern hemisphere, determining the beginning and the end of the growth period, was shown to have become longer in the past decades, mainly due to an earlier occurrence of spring events as a result of increasing temperatures (Menzel and Fabian, 1999; Defila and Clot, 2001; Menzel et al., 2006). However, in accordance with the present results, other studies also showed that net carbon uptake and therefore annual increments of trees do not necessarily increase (Dunn et al., 2007), due to increased drought stress during summer and higher respiratory losses during autumn. In fact, the ecophysiological growth period, the period of carbon uptake, tended to be shorter in the last 20 years, due to an early cessation of carbon uptake in autumn (Piao et al., 2008). These and the present results indicate that the prolongation of the phenological growth period might be superimposed by the negative consequences of drought on the duration of the growth period. The difference between the phenological growth period and the actually realized growth period might become even more pronounced in the future as the importance of drought as a liming growth factor is expected to increase (Schär et al., 2004; IPCC, 2007).

Climate impact on intra-annual growth

The climate–growth relationships correspond to the intra-annual tree growth under contrasting water supply (Fig. 4). Dry soil conditions led to reduced intra-annual increment and cell wall thickness (latewood) but to increased lumen diameter (Fig. 6) for the control trees. Generally, low soil moisture and high temperatures acted in parallel, either due to the amplification of drought under high temperature by increasing evapotranspiration or due to direct reduction of cambial activity under high temperatures (Antonova and Stasova, 1993; Jenkings, 1974).

Irrigation led to a decoupling of wood formation from climate conditions, as no growth response to temperature was found in the fortnightly increments of irrigated trees, which is in accordance with the results of tree-ring studies by Eilmann et al. (2009) and Rigling et al. (2003) on irrigated trees close to the plots investigated in the present study. However, the response of lumen diameters to temperature became more important due to irrigation as high temperature was shown to promote the formation of cells with a large lumen diameter. Thus, removing the growth limitation by drought causes temperature to gain in importance with regard to cell enlargement.

Conclusion

According to our first hypothesis, pine trees adjusted their water-conducting system to drought. They build a more effective and economic water-conducting system under natural dry conditions with larger cells but less carbon investment due to reduced cell number and cell wall thickness. This growth strategy might enable trees to transport more water if available. However, it entails risks if water is limited as concurrently the water-conducting system might be more vulnerable against cavitation due to decreasing wood density. Therefore, this strategy might be seen as a sign for the strong growth limitation of wood formation under the current site conditions.

In addition to the negative effect on the amount and structure of wood built, drought also noticeably shortened the period of wood formation as assumed in our second hypothesis. This indicates that the actual realized growth period might be shorter than the potential phenological growth period due to the strong limitation of tree growth by drought.

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