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Drought-induced adaptation of the xylem in Scots pine and pubescent oak

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Summary Drought impairs tree growth in the inner-Alpine valleys of Central Europe. We investigated species-specific responses to contrasting water supply, with Scots pine (*Pinus sylvestris* L.), threatened by drought-induced mortality, and pubescent oak (*Quercus pubescens* Willd.), showing no connection between drought events and mortality. The two co-occurring tree species were compared, growing either along an open water channel or at a site with naturally dry conditions. In addition, the growth response of Scots pine to a draining of a water channel was studied. We analysed the radial increment for the last 100 years and wood anatomical parameters for the last 45 years. Drought reduced the conduit area of pubescent oak, but increased the radial lumen diameter of the conduits in Scots pine. Both species decreased their radial increment under drought. In Scots pine, radial increment was generally more dependent on water availability than that in pubescent oak. Irrigated trees responded less negatively to high temperature as seen in the increase in the conduit area in pubescent oak and the removal of the limitation of cell division by high temperatures. After irrigation stopped, tree-ring width for Scots pine decreased within 1-year delay, whereas lumen diameter and cell-wall thickness responded with a 4-year delay. Scots pine seemed to optimize the carbon-per-conduit-costs under drought by increasing conduits diameter while decreasing cell numbers. This strategy might lead to a complete loss of tree rings under severe drought and thus to an impairment of water transport. In contrast, in pubescent oak tree-ring width is less affected by summer drought because parts of the earlywood are built in early spring. Thus, pubescent oak might have gradual advantages over pine in today's climate of the inner-Alpine valley.

Keywords: cell chronology, conduits, dendroecology, forest decline, PDSI, wood anatomy.

Introduction

Climate change is expected to increase the frequency and severity of drought events in Central Europe (Schär et al. 2004, IPCC 2007), and this will strongly affect the physiology, growth and survival of trees of different species. Drought reduces primary production (Ciais et al. 2005, Granier et al. 2007, Reichstein et al. 2007), stem growth (e.g., Schweingruber 1993, Fritts 2001) and the storage of carbohydrates (Bréda et al. 2006). According to the theory of storage depletion, shortage of carbohydrates might be a main cause for drought-induced tree death (Bréda et al. 2006, McDowell et al. 2008), leading to a negative carbon balance as more carbon is needed (e.g., for plant respiration) than the tree is able to take up. As a result, more stored carbohydrates have to be invested, which may, in the long run, lead to tree death by storage depletion (McDowell et al. 2008). Consequently, drought has been frequently discussed as a trigger for forest decline and decline-induced vegetation shifts (Allen and Breshears 1998, Penuelas and Boada 2003, Breshears et al. 2005). But how severely drought affects wood formation has, so far, only been rudimentarily demonstrated (Zweifel et al. 2006, 2007, Sterck et al. 2008).

Inner-Alpine forest ecosystems are regularly exposed to drought, as precipitation is generally low (≈ 600 mm per year), due to the rain shadow of the surrounding high mountain ranges (Rebetez and Dobbertin 2004). During the past decades, climatic conditions in these regions have changed towards increasing summer droughts, exemplarily is the Swiss Rhone valley illustrated by Rebetez and Dobbertin (2004) and Weber et al. (2007). Even though the total amount of precipitation decreased only slightly since 1980, temperature and evapotranspiration significantly increased (Rebetez and Dobbertin 2004), leading, at least seasonally, to a more negative water balance of the trees (Zweifel et al. 2006). In addition, the seasonality of water availability has changed: while water availability has increased in winter it has decreased in summer (Weber et al. 2007). The consequences of these climatic changes for species composition and species survival remain unclear.

The sub-boreal species, Scots pine (*Pinus sylvestris* L., in the following pine), dominates the low elevation forests of the inner-Alpine valleys. In recent decades, unusual high mortality rates of pine have been reported from the Swiss Rhone valley (Dobbertin et al. 2005, Bigler et al. 2006, Dobbertin and Rigling 2006), the Italian Aosta valley (Vertui and Tagliaferro 1998) and the Austrian Inn valley (Oberhuber 2001). In the Swiss Rhone valley, locally almost half of the population of pine has died since 1995 (Rebetez and Dobbertin 2004), with the highest mortality rates at dry sites after drought years (Dobbertin et al. 2005). In the same period, the sub-Mediterranean species, pubescent oak (*Quercus pubescens* Willd., in the following oak), has increased its abundance (Weber et al. 2008) and has not shown an increase in mortality (Dobbertin et al. 2005).

In this study, we examine tree growth of pine and oak by analysing tree-ring width over 100 years and a variety of wood anatomical properties for the last 45 years (oak: earlywood vessel size and pine: number, radial lumen diameter and cell-wall thickness of tracheids in earlywood and latewood). This combined approach of dendrochronological and wood anatomical methods enabled us to describe growth limitations by drought more precisely. Particularly, we focused on the growth of oak and pine under contrasting water availability, including temporal dynamics in growth response to climate. The situation that a water channel was falling dry after hundreds of years in use enabled us to analyse how growth parameters developed after this sudden change in water availability. Our research addressed two main questions: (1) are there species-specific responses of wood anatomy to drought in oak and pine and (2) does a change in water availability change the tree species' growth response to drought and temperature?

Materials and methods

Study area and sampling method

The study sites (46°16′ N and 07°26′ E) are located near the village of Lens within the inner-Alpine Swiss Rhone valley (Canton Valais). The climate is continental with a mean annual temperature of 9.2 °C and an annual precipitation of 599 mm for the period 1961–1990 (MeteoSwiss, Sion weather station, 492 m a.s.l., 10 km from the study sites).

The forest with southeast exposition is dominated by oak and pine (*Erico-Pinetum sylvestris*). The soil type can be described as Rendzic, Leptosol with limestone as parent material. At about 1000 m a.s.l. an open irrigation channel runs through the forest. This channel was created in the year 1450 for the irrigation of lower agricultural areas (Crook and Jones 1999). This was carved out of stone or runs in the consolidated soil. The channel is fed from the end of April to the end of October, during winter no water runs through. Due to extensive water loss, a section of the water channel was replaced by a tunnel in 1983, and the former water channel section dried out.

To study adult trees growing under contrasting water supply, oak and pine were chosen at three different sites: (1) an unirrigated control site, 50 m above the irrigation channel (altitude 1050 m a.s.l., slope 90%; in the following called 'control'), (2) an irrigated site along the functioning section of the water channel (altitude 1000 m a.s.l., slope 20–90%; in the following called 'irrigated') and (3) a formerly irrigated, but now dry, site where irrigation stopped in 1983 (altitude 1020 m a.s.l., slope 20–90%; in the following called 'irrigation stop'). As oak was nonexistent at the 'irrigation stop' site only pines were analysed. Apart from water supply, all sites were similar with regard to site conditions.

Sampling and sample preparation

Two cores (diameter: 5 or 10 mm and length: from the bark to the pith) of 15 dominant trees per species were sampled at each of the three sites. To avoid the confounding factor of young cambial age (Vysotskaya and Vaganov 1989, Lei et al. 1996), only trees were sampled that were at least 40 years old in 1960, the first year of cellular analysis.

The cores were planed using a custom-made core-microtome (WSL, Switzerland) to obtain clean surfaces for the analysis of radial increments. Since the cellular measurement in oak was carried out directly on the core surfaces, tyloses had to be removed using a high-pressure water blast (Fonti and García-González 2004). To increase the contrast between cell wall and cell lumen, in a first step, the cell wall was darkened by applying sodium hydroxide (NaOH, 30%) twice with a brush on the core surface. In a second step, the cell lumen was filled by pressing white plasticine (M.creative Plastilin, Switzerland) from the surface into the lumina. For cellular analysis in pine, the cores were subdivided into pieces (length ~ 5 cm) and thin sections (thickness of 10 μm) were cut using a sliding microtome (Reichert, Germany). For a better contrast between cell wall and cell lumen, the thin sections were stained with safranin (1% solution) and astra blue (2% solution), dehydrated with ethanol (70, 95 and 100%) and xylol (> 98%) and fixed with Canada balsam.

Measurements

Tree-ring widths, separated into earlywood and latewood widths, over the last 100 years were measured using a combination of a Lintab digital positioning table and the software TSAP (both Rinntech, Germany). Individual tree-ring series were cross-dated visually and detrended using the software ARSTAN (Holmes 1994) to remove the age-related trend. The tree-ring series were power transformed to stabilize the variance (Cook and Peters 1997) and then were fitted with a negative exponential curve (Fritts 2001).

Cellular characteristics (earlywood vessel area in oak; radial lumen diameter, cell-wall thickness and cell number in pine) were analysed along a 45-year sequence (1960–2004) on four randomly selected trees per species and site. Due to the disparity in xylem composition between oak, with a ring-porous structure, and pine, with a tracheidal structure, no parameters comparable to cell number or cell-wall thickness were measurable in oak. However, conduit size, a key factor for tree performance under drought, was measured in both species (vessel area in oak and radial lumen diameter in pine).

For the cellular analysis in oak, the cores were scanned with a distortion-free scanner (Color Scanner Expression 1000 XL, 12,000 dpi, Epson, CA) and earlywood vessels (minimum area 0.005 mm^2) were measured on the whole core diameter (5 mm) using the software IMAGE PRO PLUS (Media Cybernetics, MD). For the cellular analysis in pine, micro-pictures were taken (100× magnification, microscope: Olympus BX41 and camera: ColorView III, Soft Imaging system, Germany) and radial lumen diameter, cell-wall thickness and cell number in five radial cell rows per tree ring were analysed with the software WINCELL (Regent Instruments Inc., Canada). These measurements were separated into earlywood and latewood based on the Mork index, defining a latewood cell as a cell where the double of the cell-wall thickness exceeds the lumen diameter (Mork 1928), and mean values were calculated. To strengthen the common climate signal in earlywood among the years, only the first 10% of the earlywood tracheids were averaged to a mean, expecting these cells to be equal in the time of their formation. In latewood, no further separation was made, due to the generally small number of latewood cells.

Climate–growth correlations

To analyse the climate–growth relationships, Pearson's correlations between climate data (precipitation and temperature, both recorded at the Sion weather station, self-calibrating Palmer drought severity index (PDSI) by van der Schrier et al. (2007)) and the growth parameters for oak and pine at irrigated and control sites were calculated separately. The parameters of the radial increment (earlywood, latewood and tree-ring widths) were correlated with monthly data on precipitation, temperature and the PDSI for the period 1900–2004. PDSI is a measure of regional soil moisture content, based on soil characteristics and records of precipitation and temperature. With the PDSI, the climatic conditions are classified into 11 categories, between extremely wet ($\text{PDSI} \geq 4.0$) and extremely dry ($\text{PDSI} \leq -4.0$).

The cellular parameters were correlated with daily climate data (precipitation and temperature) averaged by a moving window of 10 days for the period 1960–2004. To assure a reliable climate–growth analysis for wood anatomical parameters, characterized by a generally low common signal (correlation between trees r_{bt}) (e.g., Yasue et al. 2000, Fonti and García-González 2004), only growth parameters, having a $r_{bt} > 0.05$ for both treatments (irrigated and control) were included. Hence, climate correlations were only calculated for earlywood vessel area in oak and cell number in pine. To further diminish the risk of statistical artefacts, only climate signals above the 99% significance threshold were considered. The narrow moving window of only 10 days was chosen due to the rapid cell enlargement of earlywood cells (Zasada and Zahner 1969).

Results

Growth responses to irrigation

Irrigated oak and pine showed significantly larger radial increments (width of earlywood, latewood and entire tree ring) than the control trees (Table 1A). The average tree-ring width was almost doubled by the irrigation. In the control trees, the tree rings in oak were smaller due to the narrow latewood, whereas in pine earlywood and latewood they were evenly reduced (Table 1A; Figure 1). In extremely dry years (e.g., 1921 and 1976), the latewood of oak or the entire tree ring of pine were often missing.

The conduit size in oak (area of earlywood vessel) and pine (radial lumen diameter of earlywood tracheids) showed opposite responses to irrigation (Table 1B). Irrigation increased the average vessel area of oak, whereas it decreased the radial lumen diameter of the tracheids of pine. The cell-wall thickness increased in earlywood but showed no significant change in latewood, and the number of cells increased significantly in earlywood and latewood (Table 1B, pine only).

The sudden stop of irrigation in 1983 caused significant changes in nearly all growth parameters studied in pine (Table 2). The additional multiple comparison (Tukey HSD test) between the 'control', 'irrigated' and 'irrigation stop' sites showed that after the 'irrigation stop' all growth parameters significantly differed from those of the still irrigated pine ($P < 0.001$) and were statistically inseparable from those of the control pine. The tree-ring widths of pine at the 'irrigation stop' site were even smaller than the ones at the 'control' site that was never irrigated (Figure 2B). The time lag in growth response to the irrigation stop differed among the growth parameters: tree-ring width (Figure 2A) and cell number (Figure 3) immediately decreased, whereas lumen diameter and cell-wall thickness responded with a 4-year delay.

Response to climate

Independent of the treatment, tree-ring width of pine showed a stronger growth dependence on water availability

Table 1. (A) Response of the radial increment (earlywood, latewood and tree-ring widths; $n = 15$ trees) to water status of oak and pine calculated for the period 1900–2004. P values were calculated with a t test between irrigated and control trees. (B) Response of the cellular parameters (earlywood vessel area for oak, lumen diameter and cell-wall thickness for pine; $n = 4$ trees) to water status of oak and pine calculated for the period 1960–2004. P values were calculated with a t test between irrigated and control trees. Units of measurements: radial increment = 1/100 mm, VA = mm^2, LD and CWT = μm; *, mean lumen diameter and cell-wall thickness of earlywood cells were calculated for the first 10% of earlywood cells only. Abbreviations: SD, standard deviation; r_{bt}, common signal (correlation between trees); radial increment: TRW, tree-ring width; EWW, earlywood width; LWW, latewood width; cellular parameters: VA, vessel area; LD, lumen diameter; CWT, cell-wall thickness; #cell, number of cells; indices: ew, earlywood; and lw, latewood.

A

Parameter	Treatment	Mean	SD	r_{bt}	P value control versus irrigated
pubescent oak					
TRW	Control	64	21	0.210	< 0.001
	Irrigated	145	42	0.372	
EWW	Control	25	3	0.092	< 0.001
	Irrigated	46	6	0.164	
LWW	Control	38	19	0.234	< 0.001
	Irrigated	99	38	0.456	
Scots pine					
TRW	Control	76	23	0.469	< 0.001
	Irrigated	133	42	0.234	
EWW	Control	53	16	0.431	< 0.001
	Irrigated	89	29	0.413	
LWW	Control	20	8	0.435	< 0.001
	Irrigated	43	14	0.330	

B

Parameter	Treatment	Mean	SD	r_{bt}	P value control versus irrigated
pubescent oak					
VA_{ew}	Control	0.03	0.004	0.078	< 0.001
	Irrigated	0.04	0.003	0.121	
Scots pine					
LD_{ew}*	Control	11.4	0.6	0.023	< 0.001
	Irrigated	10.4	0.5	−0.050	
LD_{lw}	Control	5.9	0.5	0.037	ns
	Irrigated	5.8	0.4	0.042	
CWT_{ew}*	Control	1.0	0.2	0.043	< 0.001
	Irrigated	1.2	0.2	−0.064	
CWT_{lw}	Control	4.7	1.1	0.035	ns
	Irrigated	4.9	1.2	0.024	
$\#cell_{ew}$	Control	9	3	0.225	< 0.001
	Irrigated	19	4	0.234	
$\#cell_{lw}$	Control	6	2	0.202	< 0.001
	Irrigated	20	5	0.241	

(i.e., precipitation and PDSI) than that of oak. In other words, to produce a wide tree ring in pine more months with high water availability are needed than in oak (Table 3).

At the control site, radial increment of oak and pine responded differently to water availability (i.e., precipitation and PDSI) over time (Table 3). Radial increment of oak increased with high winter precipitation and latewood width increased with high precipitation in summer. In contrast, the radial increment of pine growing on the control site showed no significant correlations with winter precipitation. But high precipitation at the beginning of the growth period had a positive effect on radial increment. Furthermore, earlywood and tree-ring width increased with high precipitation in the previous fall. High summer precipitation also promoted the latewood growth. Temperature, taken as an isolated factor, did not significantly determine tree-ring width at any time of the year (except for latewood of pine and July temperature, data not shown). However, the radial increment of control trees strongly respond to the water availability index (PDSI), linking precipitation and temperature. The radial increment of oak increased with high water availability (high values of the PDSI) in the previous December until August. Radial increment in pine even responded to high water availability from the previous October to September.

In contrast to the control trees, the radial increment of irrigated trees was less affected by climatic conditions (Table 3). Growth response to precipitation, temperature and PDSI, was reduced, as seen in the earlywood and tree-ring width of pine or even nonexistent, as in oak and the latewood width of pine.

On the cellular level, in contrast to the tree-ring level, the growth dependence on the climate of the earlywood vessel area of oak increased with irrigation (Figure 4). The irrigated oak trees responded positively to the temperature in August of the previous year and in January, March, April and May of the current year. Precipitation in January and February had a negative effect on earlywood vessel area in irrigated oak trees. The earlywood vessel area in control oak trees only responded to precipitation in August of the previous year.

Pine showed the same general response to irrigation on the cellular level as on the tree-ring level, as the growth dependence on climate was lower in irrigated than in control pine trees (Figure 4). Although the cell number in pine was highly correlated with radial increment ($r_{irrigated} = 0.77$ and $r_{control} = 0.84$), the cell number

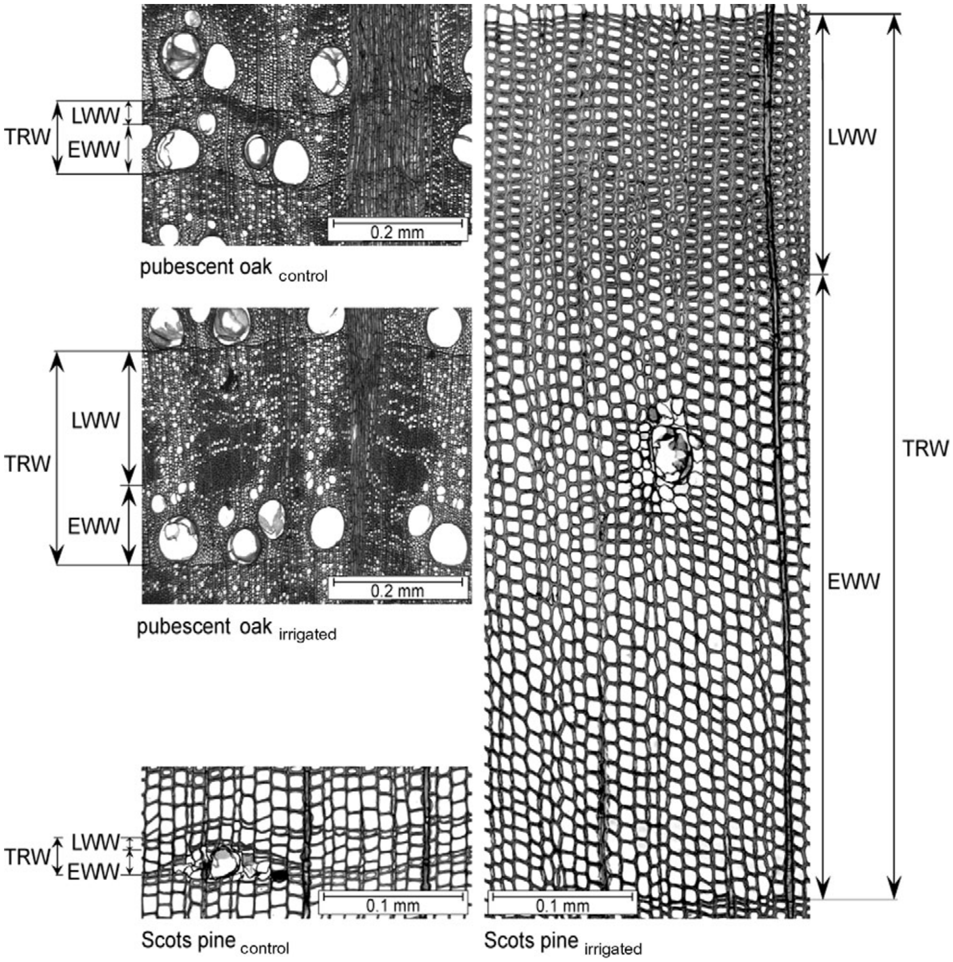

Figure 1. Tree rings of the drought year 1976 in control and irrigated pubescent oak and Scots pine. Abbreviations: TRW, tree-ring width; EWW, earlywood width; and LWW, latewood width.

showed unlike radial increment, a high negative correlation with temperature in addition to precipitation signals. High temperatures during the previous August, in late winter (January to March) and in the months before and during their formation (April to June) led to a decline in the number of earlywood cells. The number of latewood cells decreased with high temperatures during the previous August and during the months before and during their formation (March to August). In addition, low precipitation in winter (December and January) and spring (March and May) reduced the number of latewood cells in pine.

Discussion

Growth adaptation to drought: tree-ring level

Under drought, both species need to economize carbon in short supply as the photosynthesis and thus assimilate availability are low (Ciais et al. 2005, Granier et al. 2007, Reichstein et al. 2007). Both species reduced their radial increments (Table 1A) supporting the 'carbon allocation hierarchy' theory postulated by Waring (1987), with stem growth being of lower priority than bud formation and root growth. Other studies from regions with a similar environment also found that tree-ring width was reduced under drought (Tessier et al. 1994, Oberhuber et al. 1998, Rigling et al. 2002, 2003, Bigler et al. 2006, Weber et al. 2007).

Oak mainly reduced latewood width under drought, while pine evenly reduced earlywood and latewood. These trends culminated in missing latewood in oak and even entirely missing tree rings in pine during severe drought years. Due to these species-specific differences the impact of multiple drought years should be different for oak versus pine. In ring-porous oak, the bulk water transport takes place in the big earlywood vessels of the youngest outermost tree rings (Ellmore and Ewers 1985). Each spring at least one new tangential row of earlywood vessels is added (e.g., Eckstein and Schmidt 1974, Nola 1996). Thus, oak has the chance to regenerate its maximal conductivity every spring, which is a successful strategy in summer-dry climates. However, latewood vessels are also important for water transport in oak. They represent the emergency system in water conduction of ring-porous species as they provide the water transport together with the tracheids in case of cavitation of the earlywood vessels (Granier et al. 1994). Therefore, a repeated missing or strong reduction of latewood under severe drought, as shown by our data,

Table 2. Growth parameters of pine before (1961–1982) and after (1983–2004) irrigation cessation (given as 'time period'). *P* values were calculated with a *t* test between the growth parameters before and after irrigation stop. Unit of measurements: radial increment = 1/100 mm, VA = mm^2, LD and CWT = μm; *, mean lumen diameter and cell-wall thickness of earlywood cells were calculated for the first 10% of earlywood cells only. Abbreviations: SD, standard deviation; radial increment: TRW, tree-ring width; EWW, earlywood width; LWW, latewood width; cellular parameters: LD, lumen diameter; CWT, cell-wall thickness; #cell, number of cells; indices: ew, earlywood; and lw, latewood (radial increment: $n = 15$ trees and cellular parameters: $n = 4$ trees).

Parameter	Time period	Mean	SD	*P* value before versus after irrigation stop
TRW	Before	144	28	< 0.001
	After	53	21	
EWW	Before	99	21	< 0.001
	After	39	15	
LWW	Before	45	8	< 0.001
	After	13	8	
LD_{ew}*	Before	10.6	0.5	< 0.001
	After	11.2	0.5	
LD_{lw}	Before	6.5	0.4	ns
	After	6.7	0.6	
CWT_{ew}*	Before	1.1	0.1	< 0.001
	After	0.9	0.2	
CWT_{lw}	Before	3.8	1.1	ns
	After	3.5	0.9	
$\#cell_{ew}$	Before	29	8	< 0.001
	After	10	4	
$\#cell_{lw}$	Before	19	5	< 0.001
	After	6	4	

might in the long run hinder efficient water transport after cavitation of earlywood vessels.

Compared to oak, water transport in pine takes place in many more tree rings. Therefore, a single missing tree ring might be compensated. But multiple narrow tree rings due to severe drought years would significantly reduce water transport as pine relies on individual tree rings much longer than oak.

Growth adaptation to drought: cellular level

Focussing on the conduit sizes, diverging species-specific adaptation patterns to drought were found (Table 1B). In oak, significantly smaller earlywood vessels were formed in control trees than in the irrigated ones. This is in accordance with other studies (Sass and Eckstein 1995, Steppe and Lemeur 2007, Sterck et al. 2008) and might be a strategy to decrease vessels' vulnerability to cavitation (Hacke and Sperry 2001). In contrast, pine trees significantly increased their earlywood conduits under drought (Table 1B). Increasing lumen diameter might be an adaptation to compensate for the reduction in conducting area (reduced tree-ring widths) under drought, as hydraulic conduction is proportional to the fourth power of the conduit 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, and higher rates of transpiration can be tolerated (Sperry 2003). Larger lumen diameters under drought are also found by Maherali and DeLucia (2000) reporting higher specific hydraulic conductivity (K_s) due to larger lumen diameter in ponderosa pine growing at a semi-arid site than in those of a moderate mountain site. They discussed the increase in K_s as a way to improve whole-tree hydraulic conductivity without increasing carbon costs. However, other studies reported decreasing lumen diameters under warm and dry conditions (Jenkings 1974, Nicholls and Waring 1977, Sheriff and Whitehead 1984, Sterck et al. 2008). It is important to realize that the lumen diameters we observed were among the smallest (mean earlywood lumen diameter; irrigated = 10.4 μm and control = 11.4 μm) compared to other studies (range of earlywood lumen diameter = 14.4–40.3 μm), indicating a very strong restriction of cell enlargement under the prevailing site conditions at our site in Valais.

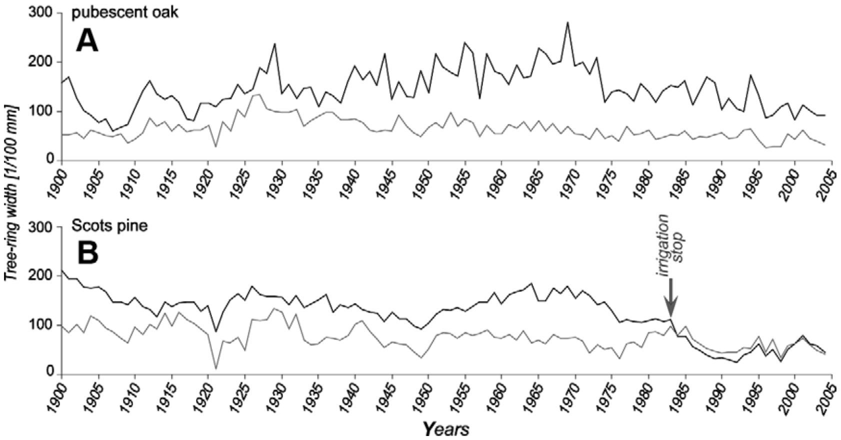

Figure 2. Tree-ring width chronologies ($n = 15$) of control and (at least temporarily) irrigated oak and pine. Black, trees of the irrigation or irrigation stop site; grey, trees of the control site; and arrow, the year irrigation stopped.

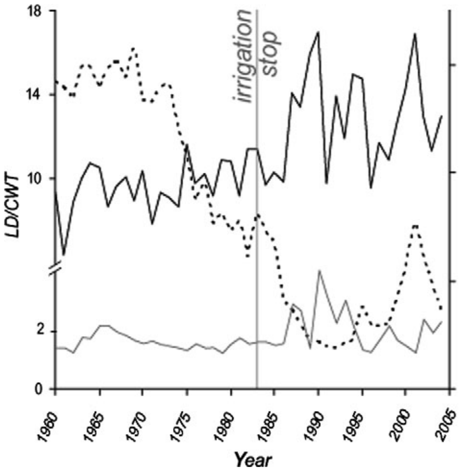

Figure 3. Cellular growth reactions of pine to irrigation stop in 1983. Solid lines, ratio of lumen diameter to cell-wall thickness; black, earlywood; and grey, latewood. Dashed line, annual number of cells. Vertical line, the year irrigation stopped. Abbreviations: LD/CWT, lumen diameter to cell-wall thickness ratio; and #cell, number of cells.

Besides the efficiency, the safety of the conducting system is important for tree survival. As mentioned before, larger conduits are more vulnerable to cavitation than smaller ones (Sperry 2003). In addition, the vulnerability to cavitation depends on the mechanical strength of the conduits as in wood with a greater density, more negative pressure is needed to induce 50% loss of hydraulic conductivity. Thus, especially in dry environments with more negative sap pressure, strong tracheids, having a thicker double cell wall relative to its span, are required (Hacke and Sperry 2001). However, our data showed that pine reduced the thickness-to-span ratio under drought, as cell-wall thickness significantly decreased while lumen diameter increased (Table 1B). Thus, pine built a more effective water conducting system with lower construction costs in terms of carbon investment under drought, but at the expense of safety.

Growth response of pine to irrigation stop

After irrigation stop (Table 2), tree growth approached that of the control pine trees (Table 1). The time lag between irrigation stop and the growth reaction varied among growth parameters, indicating differences in their dependence on water availability. The immediate decrease in radial increment (Figure 2) and cell number (Figure 3) point to a direct control of cambial activity by water availability, as suggested by Zweifel et al. (2006) and Steppe and Lemeur (2007). In contrast, the delayed reaction of lumen diameter and cell-wall thickness (Figure 3) indicates an indirect impact of drought on cell differentiation, probably via the amount of assimilates. Assimilates are crucial not only for the synthesis of cell-wall products but also for maintaining turgor pressure (via osmotic potentials) in the enlarging cells (e.g., Ray et al. 1972, Larcher 2003). The drop in photosynthesis due to reduced water availability might have been buffered by a mobilization of stored carbohydrates as demonstrated by Högberg et al. (2001) and Bhupinderpal-

Table 3. Pearson's correlation between the radial increment (earlywood, latewood and tree-ring widths) and monthly data of precipitation, temperature and the PDSI. Climate correlations with the earlywood width of oak were only calculated for the period August of the previous year to May of the current year. For the earlywood width in pine, climate correlations were only calculated for the period August of the previous year to July of the current year. Positive correlation: $+P < 0.01$, $++P < 0.001$. No negative correlation was found. Abbreviations: TRW, tree-ring width; EWW, earlywood width; and LWW, latewood width.

	pubescent oak														Scots pine													
Precipitation	A	S	O	N	D	J	F	M	A	M	J	J	A	S	A	S	O	N	D	J	F	M	A	M	J	J	A	S
$TRW_{control}$					+										+							+		++				
$EWW_{control}$					+										+							+		++				
$LWW_{control}$					++							+										+		++		++	+	
$TRW_{irrigated}$																								+				
$EWW_{irrigated}$															+									+				
$LWW_{irrigated}$																												
PDSI	A	S	O	N	D	J	F	M	A	M	J	J	A	S	A	S	O	N	D	J	F	M	A	M	J	J	A	S
$TRW_{control}$						+	+	++	+	++	++	+	+				+	++	++	+		+	+	++	++	+		
$EWW_{control}$										+							+	+	+					+	+			
$LWW_{control}$					+	+	+	++	++	++	++	+					++	+	++	++	+	++	++	++	++	++	++	++
$TRW_{irrigated}$																												
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$LWW_{irrigated}$																												

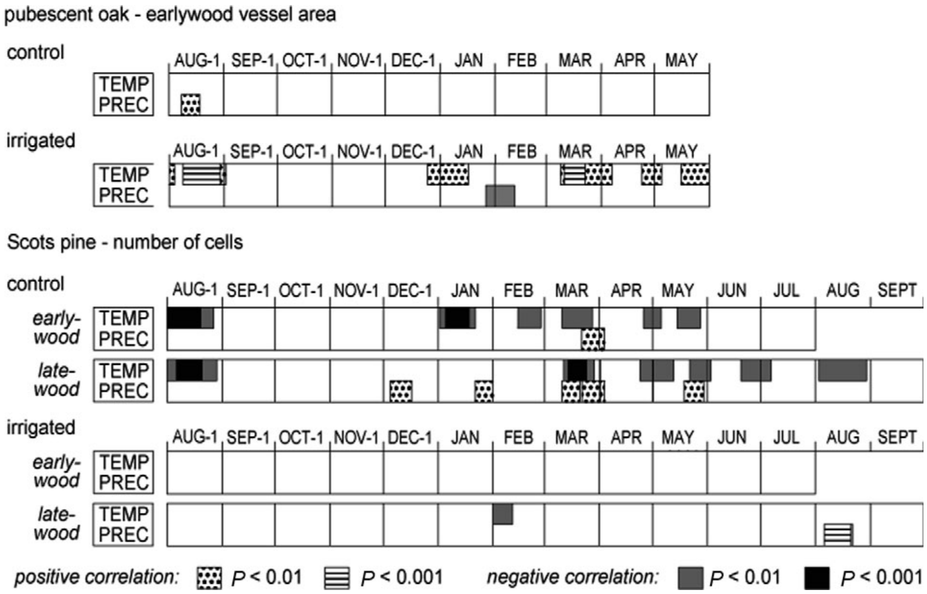

Figure 4. Moving-window correlation between climate data and earlywood vessel area of oak (top), and cell number of pine (bottom). Climate data were averaged by a moving window of 10 days. Earlywood-vessel formation in pubescent oak takes place in April and May, thus climate correlations for this parameter were only calculated for the period August of the previous year to the end of May of the current year. As earlywood in Scots pine is built from April to July, the climate correlations with the number of earlywood cells were calculated for the period August of the previous year to the end of July of the current year. The number of latewood cells were correlated with climate data from August of the previous year to September of the current year, as latewood formation takes place from July to September. Months of the previous year are labelled with the suffix −1. Different fillings represent positive and negative correlations at two significance levels. Abbreviations: TEMP, correlation with temperature; PREC, correlation with precipitation.

Singh et al. (2003). These authors measured still high soil respiration rates after girdling pine trees, due to the usage of mobilized carbohydrates until storage depletion 1 year later. The 4-year delay in the growth response to the irrigation stop that we observed might be due to reduced but still ongoing photosynthesis, providing assimilates for tree growth, and to the accessibility of the above-ground carbohydrate pools via xylem and phloem.

Climatic control of tree growth under naturally dry conditions

The analysis of climate impact on the radial increment of the control trees growing under naturally dry conditions revealed both clear species-specific and common growth responses of oak and pine to climate. The radial increment in pine showed a stronger growth dependence on water availability than in oak, as seen in the strong positive precipitation signals in spring and summer as well as in the PDSI signals (Table 3). This is in line with the observation that pine closed its stomata sooner than oak when drought increased (Zweifel et al. 2007). Thus, pine might be more strongly affected by changing climate conditions in Valais, especially since the seasonality of water availability changed towards increasing summer drought (Weber et al. 2007), which will strongly reduce radial increment in pine but will affect that of oak less.

Besides the species-specific differences, strong common positive responses of radial increments of oak and pine to precipitation and the PDSI were observed (Table 3). Radial increments in both species did not show any relevant temperature signals, indicating no temperature limitation at this site.

Irrigation alters climate dependence of tree growth

Irrigated trees of oak and pine responded negatively to high temperatures compared to the control trees as seen in the increase in conduit area in oak (Figure 4, top) and the elimination of the limitation of cell division by high temperatures (see cell number; Figure 4, bottom). This might be because water is no longer the limiting factor and therefore, higher transpiration rates under high temperatures can be tolerated. In irrigated oak trees, the earlywood vessel area increased under higher temperatures (Figure 4), while earlywood vessels of the control oak trees showed hardly any climate signal at all. This low growth dependence of the control oak trees on climate might be evidence that not only the formation (Eckstein and Schmidt 1974, Nola 1996) but also the enlargement of earlywood vessels is endogenously controlled if drought was sufficiently severe.

In both species, growth dependence on climate in terms of the radial increment was pronouncedly reduced with irrigation (Table 3). However, species-specific differences in climate dependence exist as radial increments in irrigated oak showed no climate dependence at all, while irrigated pine still depended on high precipitation in May and in the previous August. In addition, the cell formation in pine depended on additional water supply by precipitation during August (see cell number; Figure 4, bottom), even though irrigation was still ongoing. Thus, irrigation was obviously not sufficient to completely decouple radial growth from precipitation.

Conclusions

Species-specific differences between pine and oak became apparent after analysing the adaptation of the water conducting system to drought. Oak showed a stress avoidance strategy with decreasing conduit size under drought leading to a reduction in water-conducting capacity and a lower risk of cavitation. But the additional reduction in latewood width and, therefore, in the number of latewood vessels might create higher susceptibility to drought. Thus, even oak might soon reach the limits of its physiological capacity in this area if the frequency of drought years increases, leading to frequently missing latewood. In contrast, pine reduced carbon costs for the water conducting system under drought by decreasing the number and the cell-wall thickness of conduits, while increasing their lumen diameter. As a result, the efficiency of water conduction might increase, but at the expense of decreasing safety. Climate–growth analysis revealed a stronger need for water in pine compared to oak. Assuming a hotter and drier climate in the future, a further decrease in cell numbers in pine must be expected with negative effects on water transport in the stem. Due to this, the future efficiency of the water conducting system is at risk, which might together with the low safety of water transport further amplify the risk of pine mortality in Valais, at the dry distribution limit of pine.

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