Effects of water availability on the growth and tree morphology of *Quercus pubescens* Willd. and *Pinus sylvestris* L. in the Valais, Switzerland

U. Sass-Klaassen[1], Md. Q. Chowdhury[1], F.J. Sterck[1] & R. Zweifel[2]
[1]*Forest Ecology and Forest Management Group, Centre for Ecosystem Studies, Wageningen University*
PO. Box 47, 6700 AH Wageningen, The Netherlands
[2]*Institute of Plant Sciences, University of Bern, Altenbergrain 21, CH-3013 Bern Switzerland*
E-mail: ute.sass-klaassenf@wur.nl.

Introduction

Problem statement

Since climate affects forests in many different ways, assessing the impact of climate change on forest ecosystems presents a major scientific challenge. Drought is an important climate factor, which influences tree-growth as well as morphological and functional features of trees (Floret et al. 1990). For the Valais a significant warming during the past century was reported (Rebetez & Dobbertin 2004, Begert et al. 2005). The expected future warming (IPCC 2001) could aggravate a higher frequency and intensity of drought conditions in the Valais, which would have negative effects on the growth and survival of Pubescent oak and Scots pine due to an increased risk of stress to the hydraulic system. Since the end of the last century a high mortality of Scots pine has been observed in the Valais whereas sub-Mediterranean species such as *Quercus pubescens* are spreading (Eilmann et al. 2006).

Approach

To better understand drought-tolerance mechanisms in *Quercus pubescens* and *Pinus sylvestris* in the Valais we studied tree morphology, tree growth, and wood-anatomical features of both species growing at two sub-sites with a different water regime, i.e. along a water channel running through a dry hill with South exposition (wet) and at some distance from the water channel (dry). Tree morphology at the dry and wet site was compared. Classical dendrochronological techniques were applied to trace those weather/climate factors that mainly influence the growth of oak and pine under wet and the dry site conditions in the Valais.

Objective

Tree growth and hydraulic architecture of oak and pine from a dry and a wet site, respectively are determined. Differences are discussed in order to gain (i) a better understanding of the impact of water supply and changes in water supply during the growing season on tree-ring formation (ii) insight into drought response in hydraulic architecture in both species.

Material and Methods

Study area

The study was carried out in the south exposed slopes located in the Rhone valley in Valais Switzerland (Fig. 1). The field data was collected in two sites (*wet,* directly at the water channel and *dry*, far away from the water channel) in Salgesch (46°19'27" N, 7°34'40" E) at an elevation of 975m a.s.l. (Fig.2).

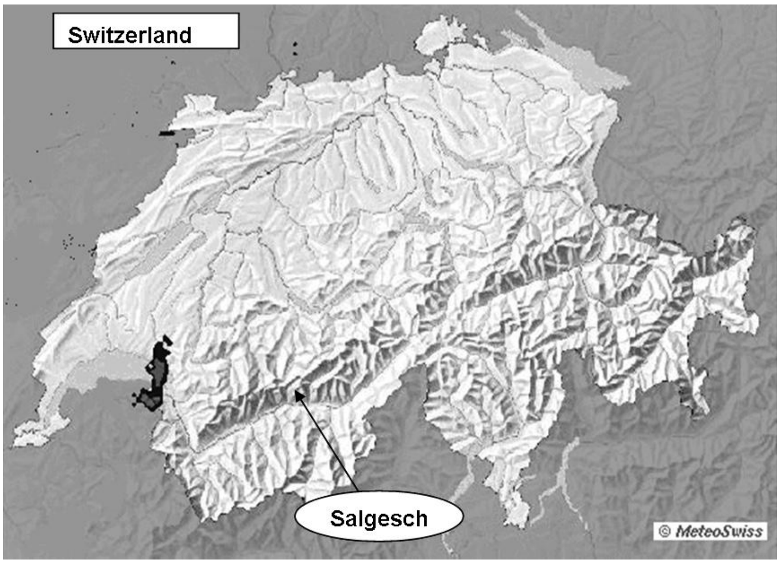

Figure 1: Study area

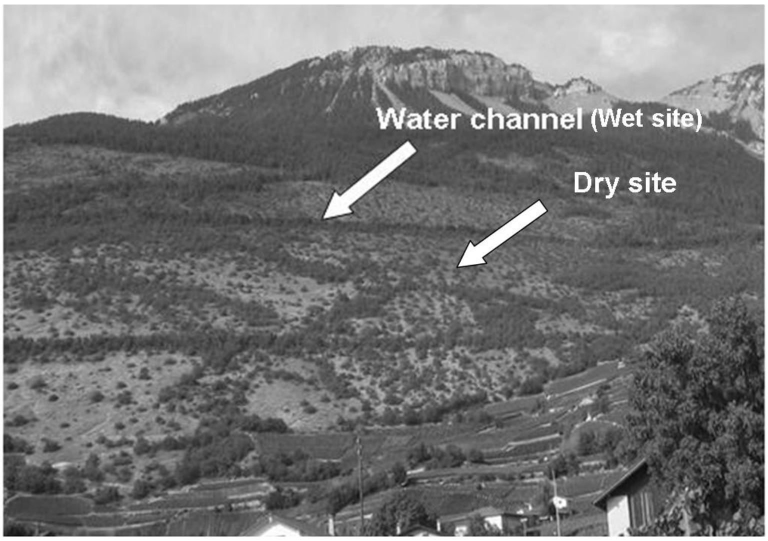

Figure 2: Location of wet and dry sites

The Wallis is an inner-alpine valley with a dry climate because of its East-West direction that prevents it from wet air from the South and the Northwest, the main directions of air streams in the Swiss Alps. According to the FAO classification system the soil of this area is classified as a rendzic leptosol on solid rock limestone and with low water-holding capacity (Rigling et al. 2002).

Climate

Data records were obtained from the meteorological station at Sion, about 20 km from the study site and at an elevation of 547m. Annual precipitation amounts to 664 mm per year with a monthly maximum in summer (Fig.3). The annual mean temperature is 9.7^{0}C. Winter precipitation has great importance on the water regime of the channel (Rigling et al. 2002). Drought periods frequently occur in summer and can last several weeks (Kuhn 1973). At that time even the channel can fall dry. To quantify the drought severity, monthly drought indices are calculated (Bigler et al. c.f. Eilmann et al. 2006). The monthly drought index is defined as the difference between monthly precipitation and the monthly potential evapotranspiration (Thornthwaite 1948). From these monthly indices an annual drought index was calculated by taking the monthly index values from September of the previous year to August of the current year. Drought years are indicated by negative values; mesic years by positive values.

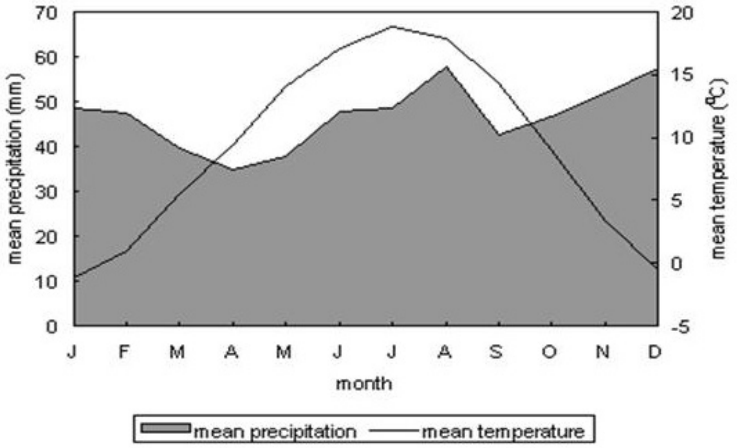

Figure 3. Mean sum of monthly precipitation and mean monthly temperature as recorded at Sion Station, Switzerland (CLIMAP, METEOSWISS).

Study trees and data collection

For this study *Quercus pubescens* (Pubescent oak) were selected as a representative of broadleaved tree species and *Pinus sylvestris* (Scots pine) as a conifer. Twenty individuals of each species (ten from each site) were selected on the basis of similar diameter (DBH). Table 1 gives a survey about the variables that were measured and calculated.

Table 1: Measured variables

	Variables
Tree morphology *visual inspection*	DBH, tree height, height of lowest (green) branch, crown radius
Leaf area *Measured with image-analysis system*	Average leaf area (LA), average leaf mass (LM)
Radial tree growth *Measured from cores with dendrochronological equipment*	Tree ring (RW), earlywood (EW) and latewood (LW) width
Wood anatomy *Measured from cores with image-analysis system*	Sapwood area, conduit (vessel, tracheid) area and conduit (vessel, tracheid) density

Tree-morphology variables were measured in the field. Average leaf area was measured from a collection of leaves by using an automated image analysis system and the *Image Tool* software (Version 3.0). Tree-ring width (RW), earlywood width (EW) and latewood width (LW) was measured and analyzed by using standard dendrochronological methods (programs *TSAP,* Rinn 1996, *COFECHA,* Holmes 1983). Wood anatomical features were measured from digital photographs by using *Image Tool, Version 3.0.* Measurements were taken from cross sections prepared with razor blades, soaked with 10% NaOH and chalked. Digital images were taken with a digital camera (*Leica* DFC320). Ten earlywood and 10 latewood conduits (vessels/tracheids) were randomly selected per tree ring and the radial diameter was measured in a sequence of seven consecutive tree rings with *UTHSCSA Image Tool* software (Version 3.0). Earlywood- and latewood conduit density was measured as the numbers of vessels per square millimeter on the transverse section in successive measuring frames of 450 x 2000 µm.

Statistical analysis

To calculate relationships between the tree morphology, leaf area, tree growth and wood anatomy in relation to site conditions, i.e. wet and dry, General Linear Model (GLM) was used (*SPSS for Windows, Version 10.1*).

Statistical characterization of the RW, EW and LW tree-ring series was done by calculating *Mean RW, EW, LW, Mean Sensitivity, and EPS.*

Dendroclimatological analysis was done by using correlation analysis (*DendroClim 2002*; Biondi & Waikul 2004). RW, EW and LW tree-ring chronologies (derived from the single tree-ring series after detrending with a 30-year moving average, *TSAP* program) of oak and pine from the wet and dry sites were compared with monthly mean temperature and monthly sum of precipitation records from the climate station Sion. The reference period was set to 1950 to 2004 and we included temperature and precipitation data from October of the previous year to September of the actual year.

In the wood anatomical analysis the size and density of the conduits was visually compared to the annual drought index (previous September to current August) throughout the 7-year investigation period.

Results and Discussion

Morphological and wood-anatomical variables at wet and dry site

Morphological traits and wood-anatomical variables differ significantly between oaks and pines at the wet and the dry site (Fig. 4). The General Linear Model (GLM) yielded significant values for site effect in both oak and pine for all morphological (trees size, leaf parameters), growth (RW, EW, LW width) and wood-anatomical (sapwood area, conduit size and density) variables.

Oberhuber et al. (1998) and Rigling et al. (2002) observed the same trends in changes of DBH and leaf area for Scots pine in an inner alpine dry valley of Austria and in the Valais. They found that leaf area increased with DBH because larger trees maintain their energy balance for physiological needs by increasing the photosynthetic area. This size differences are most likely related to hydraulic limitations (Ryan & Yoder 1997) in both species due to (temporary) higher water stress at the dry site.

Dendrochronological results

In total 12 tree-ring chronologies (RW, EW and LW chronologies for each species at each site) were constructed for oak and pine. The chronologies of the wet and dry site are very similar for both species (Fig. 5) suggesting that tree growth in both sites is triggered by the same environmental factor(s) (Fig. 6). Mean tree-ring width was smaller in the dry site in comparison to the wet site in both species (Tab. 2). The generally higher growth rate of pine might be related to its phenological characters: pine produces needles which remain between one to five years on the branch (Kurkela & Jalkanen 1990) whereas oak is deciduous and needs to renew its leaves every year.

Mean sensitivity was higher for the tree-ring (RW, EW, LW) chronologies of oak and pine at the dry site which indicates a stronger relation to annually changing environmental conditions such as precipitation. This fits the assumption that the oaks and pines at the wet site profit from the effect of ample water supply from the water channel buffering the effect of precipitation. As can be expected from high values of mean sensitivity the autocorrelation was generally low in both species and at both sites. Interestingly, the autocorrelation was slightly higher at the dry site for both oak and pine. This is most likely due to the occurrence of prolonged growth depressions in both oak and pine at the dry site in response to drought years or drier periods (Fig. 5). The *Expressed Population Signal* (EPS) of the pine and oak chronologies indicates that the number of study trees is well chosen to represent the tree collectives (Briffa & Jones 1990). If comparing the ‘signal strength’ of the RW, EW and LW chronologies in *Q. pubescens* it is striking that mean sensitivity of the EW chronologies is in the same range as for RW and LW. Together with high values in EPS this indicates that annual changes in EW width reflect a strong environmental signal. This phenomenon has also been observed by Eilmann et al. (2006). *Q. robur* and *Q. petraea* from temperate sites in NW Europe are known to show a low mean sensitivity and only weak ‘common ´signal´ in EW time series (Eckstein & Schmidt 1974).

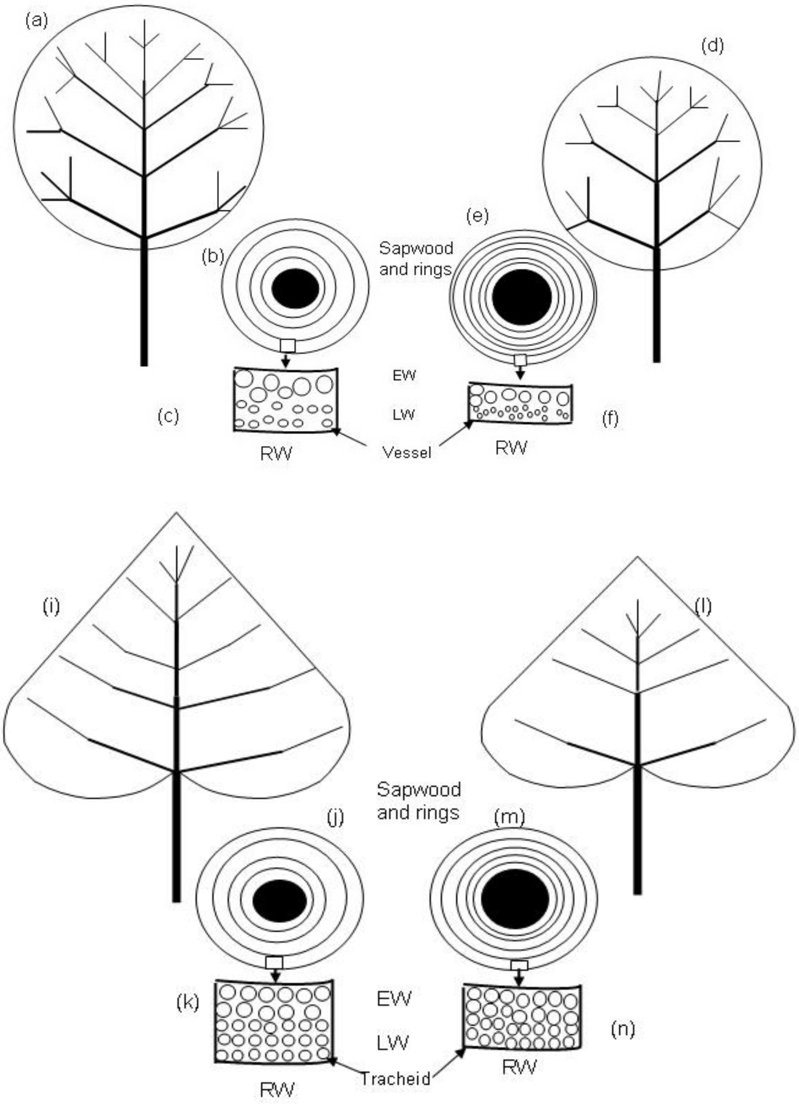

Figure 4: Difference in morphological and anatomical traits (a) oak wet, (d) oak dry, (i) pine wet and (l) pine dry; sapwood area and sapwood rings, (b) oak wet, (e) oak dry, (j) pine wet and (m) pine dry; RW, EW, LW, vessel and tracheid, (c) oak wet, (e) oak dry, (k) pine wet and (n) pine dry.

Table 2. Descriptive statistics of ring width (RW), earlywood width (EW) and latewood width (LW)

Species	*Site*	*variables*	*Mean [mm]*	*mean sensitivity*	*autocorrelation*	*EPS*
Oak	wet	RW	1.00	0.42	0.26	0.85
		EW	0.55	0.45	0.08	0.83
		LW	0.45	0.44	0.34	0.86
	dry	RW	0.71	0.39	0.36	0.86
		EW	0.30	0.37	0.29	0.85
		LW	0.41	0.51	0.30	0.83
Pine	wet	RW	1.19	0.35	0.20	0.88
		EW	0.71	0.36	0.20	0.86
		LW	0.48	0.39	0.11	0.85
	dry	RW	1.10	0.40	0.28	0.87
		EW	0.50	0.43	0.27	0.85
		LW	0.60	0.44	0.15	0.82

Dendroclimatological results

The ring width (RW) chronologies of both oak and pine (Fig. 5) indicate severe drought years in 1921, 1934, 1944, 1949, 1964, 1972, 1976, and 1998 as reflected by a sharp reduction of ring width in these years. Rigling et al. (2002), Eilmann et al. (2006) and Zweifel et al. (2006) found the same climate-growth response in oak and pine from the same area in the Valais.

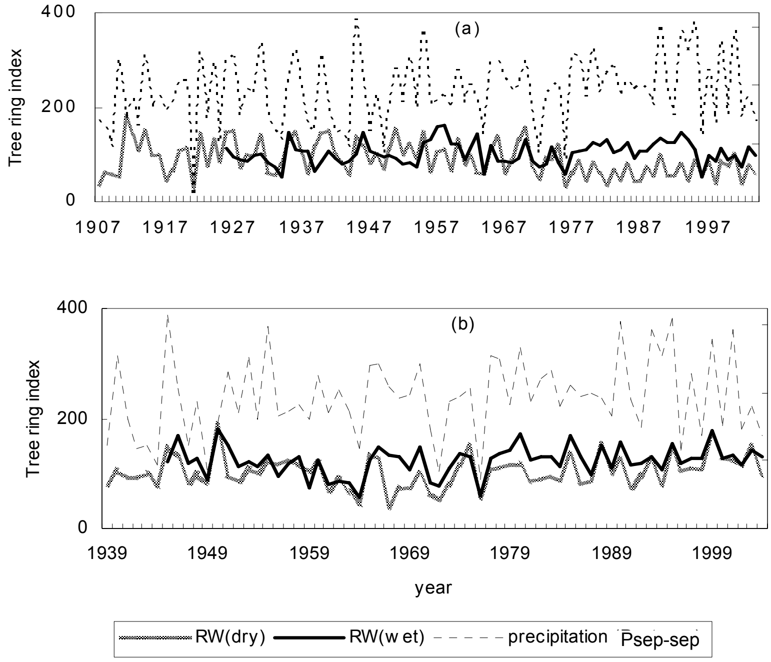

Figure 5: Ring width chronologies of oak (a) and pine (b) with the sum of precipitation from previous September to current October (dashed line).

The climate-growth relationships (Figs. 5 & 6) illustrate a strong positive correlation between the tree-ring width chronologies and the sum of precipitation from previous September to current October in both sites and for both species. The relation with temperature (not shown) was generally negative during the growing season and significantly negative during the summer month in the dry site for both oak and pine. This proves a negative impact of hot and dry (=drought) conditions in summer. Figure 5 shows similarities between time series of RW and precipitation from previous September to current October. The correlation coefficients calculated for the period from 1950 to 2004 are: oak r_{wet} =0.43, r_{dry} =0.48; pine $r_{wet=}$ 0.42 and r_{dry} =0.46. In the dry site, chronologies showed a slightly closer relation to precipitation than in the wet site. In detail, oak on both sites reveals a positive correlation with the precipitation of the current year whereas pine at the dry site also shows a strong response to the autumn precipitation of the previous year (Fig. 6d). Together with the low response to precipitation in summer (Fig. 6d) this might indicate that pine at the dry sites generally stops growing early in the growing season. A surplus of assimilates that is produced under wet weather conditions in late summer is thus not invested in LW production but stored and invested in growth of the next growing season. Nevertheless, at the wet site LW of pine is significantly related to precipitation at the end of the growing season, i.e. in August and September (Fig. 6c). This indicates that the cambium is still active and sensitive in late summer and assimilates are invested in LW. Oak, however, seems to use another strategy: in the wet site, the relation with precipitation is less concentrated on single months, instead a positive 'precipitation signal' from previous December to actual October is visible (Fig. 6a). A strong impact of the March precipitation i.e. the period just before or at the start of the growing season (see Zweifel et al. 2006) is evident and strongly determines RW, EW and (to a lesser extend LW), respectively. A second 'block' with high positive correlations with LW occurs in late summer, in August and September LW (Fig. 6b). This strong late-summer precipitation impact was surprising and disagrees with the results by Zweifel et al. (2006) who found that 90 % of the annual increment in both oak and pine is already finished between the end of June and beginning of July.

It can be summarized that RW (and EW) of oak and pine on both the wet and dry site are positively correlated with the precipitation just before and/or at the beginning of the growing season. Good starting conditions are thus of major importance for tree growth throughout the growing season (Zweifel et al. 2006).

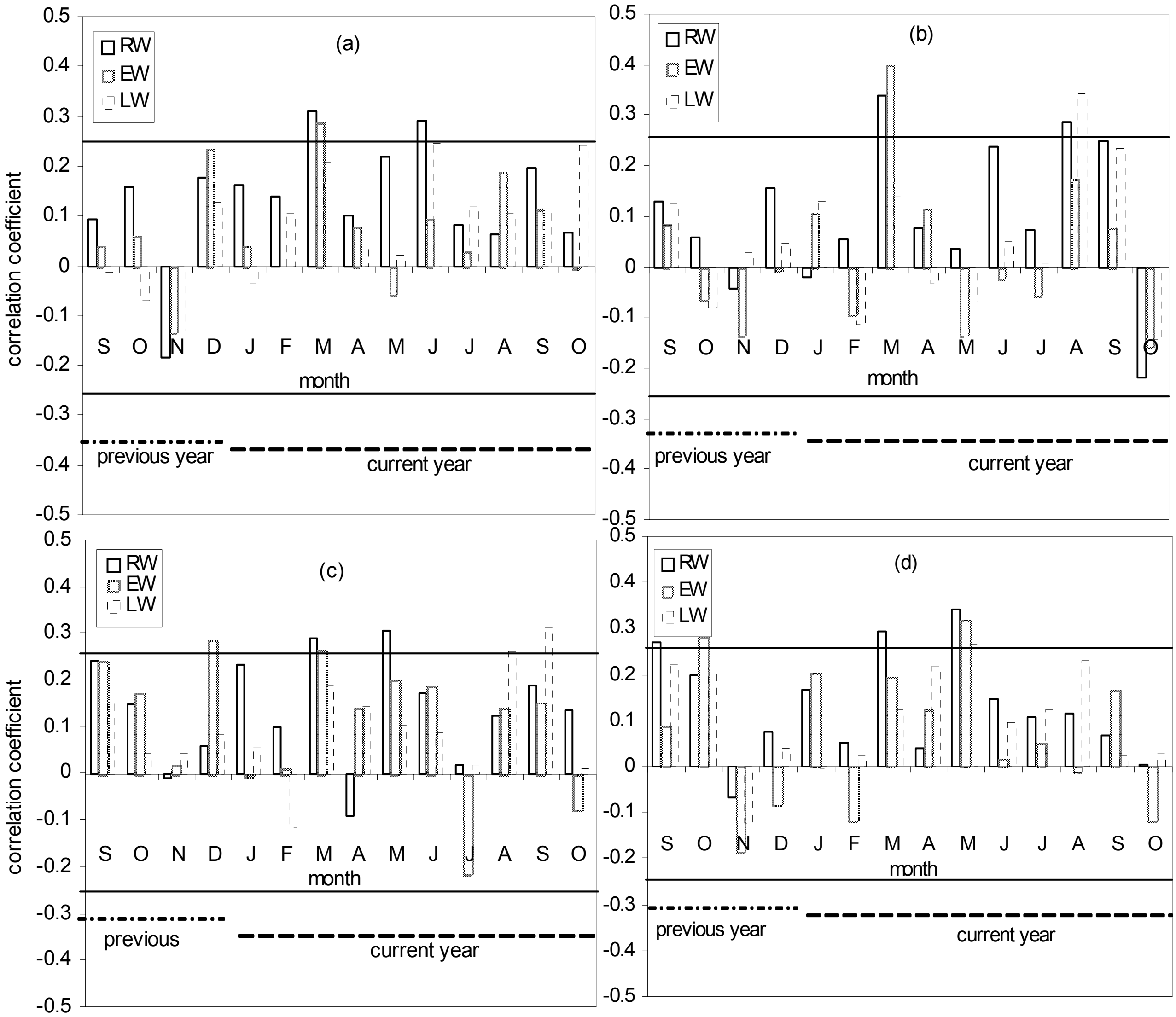

Figure 6: Correlation values of chronologies with monthly precipitation from (1950-2004); oak wet (a) and oak dry (b); pine wet (c) and pine dry (d); horizontal lines indicate the significance level (p=0.05).

Wood anatomy and drought index

The impact of water availability (expressed as drought index) on annual changes in conduit size and density of oak and pine is evident (Fig. 7). The visual comparison with the annual drought index (calculated from previous September to current August) shows a remarkable synchrony: years with high values for the drought index (=wet years) correspond with wider vessels and tracheids in EW and LW and a lower vessel and tracheid density and *vice versa*. Even if the investigation period includes seven years only this is a strong indication that variation in conduit size and density are a strong indicator for changes in water supply. Figure 7 also illustrates that annual changes in conduit size and density are occurring in trees at the wet and the dry site respectively – with somewhat higher amplitude at the wet site. Hence it is obvious that oak and pine show elastic growth behaviour (RW, EW, LW) and are able to adapt to both, local (site specific) as well as temporal changes in water availability.

Conduit size and density have earlier proved to be good indicators of changing environmental conditions (Dünisch & Bauch 1994, Sass & Eckstein 1995, Garcia-Gonzales & Eckstein 2003) and provide the potential for studying the relation between water availability and wood anatomy with a high temporal resolution.

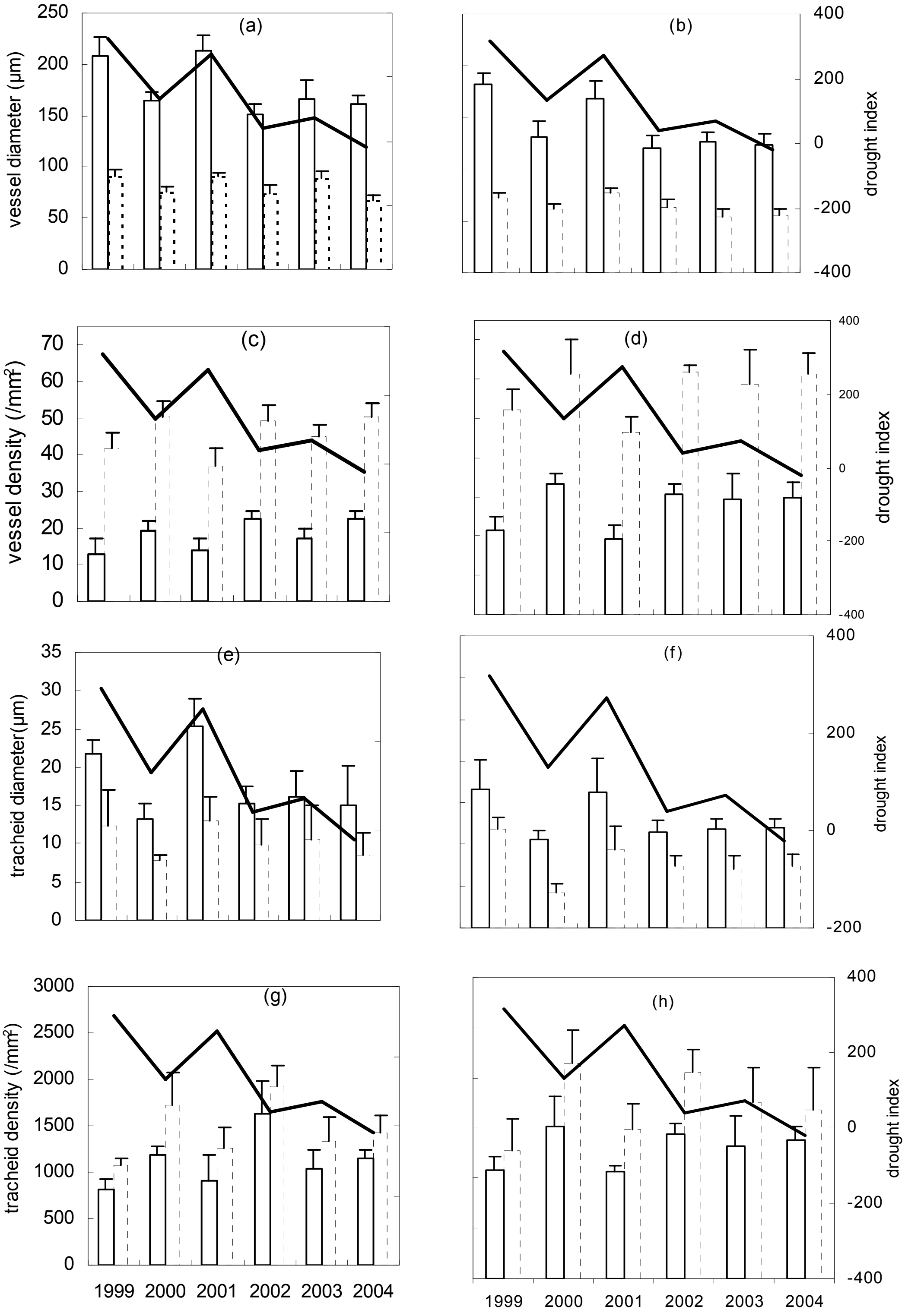

Figure 7: Variation of average conduit size and conduit density from 1999 to 2004 in EW (closed boxes) and LW (dashed boxes) and the relation to the annual drought index (black line); a+c =oak wet, b+d =oak dry, e+g =pine wet, f+h=pine dry .

Conclusions

This study on Pubescent oak and Scots pine growing under harsh weather conditions with frequent summer droughts in the Valais indicated that:

(1) both species, Pubescent oak and Scots pine, strongly respond to the specific water regime at the dry and the wet site which is reflected by significant differences in morphological factors (DBH, tree height, crown radius, leaf area, leaf mass), growth (RW, EW, LW) and wood anatomy (sapwood area, conduit size and density). All components of the hydraulic architecture, i.e. the continuous water-conducting system, were significantly different with generally smaller trees developing under conditions with lower water availability (Fig. 4). Future studies are planned involving the roots as well in order to get a complete picture about adaptation patterns in hydraulic architecture.

(2) Despite differences in water availability at the wet and dry site, growth and wood anatomy of both species is strongly influenced by the amount of rainfall during the growing season and prior to it. Additional water supply by the channel significantly reduces the impact of water shortage during summer droughts. The climate-growth relationships suggest that cambial activity of pine at the dry site ceases early. This means that LW and RW of a certain year are mainly related to rainfall conditions during the prior year(s) and at the beginning of the growing season. In oak from the dry site, however, LW formation is strongly influenced by water supply from precipitation during late summer. This assumption of a different response of both species to cope with summer drought has to be supported by additional studies on the intra-annual dynamics of cambial activity.

Hence it can be concluded that Pubescent oak and Scots pine are able to adapt their morphology and wood anatomy to long-term (site specific) and short-term (temporal) changes in water availability. We found no indication of a reduced growth activity during the last years in our sample trees.

Acknowledgements

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