

This document is the accepted manuscript version of the following article:  
Weber, P., Bugmann, H., & Rigling, A. (2007). Radial growth responses to drought  
of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *Journal*  
of Vegetation Science, 18(6), 777–792.  
<https://doi.org/10.1111/j.1654-1103.2007.tb02594.x>

## **Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley**

Weber, Pascale<sup>1\*</sup>, Bugmann, Harald<sup>2</sup> & Rigling, Andreas<sup>1</sup>

<sup>1</sup>Swiss Federal Institute for Forest, Snow and Landscape Research, WSL, Zürcherstrasse 111, CH-8903  
Birmensdorf, Switzerland. Email [andreas.rigling@wsl.ch](mailto:andreas.rigling@wsl.ch)

<sup>2</sup>Forest Ecology, Department of Environmental Sciences, Swiss Federal Institute of Technology (ETH), ETH  
Zentrum, CH-8092 Zürich, Switzerland. Email [harald.bugmann@ethz.ch](mailto:harald.bugmann@ethz.ch)

\*Corresponding author; Fax +41 (0) 44 7392 215; Email [pascale.weber@alumni.ethz.ch](mailto:pascale.weber@alumni.ethz.ch)

## Abstract

Question: Lower-montane treeline ecotones such as the inner-Alpine dry valleys are regarded as being sensitive to climate change. In Valais (Switzerland), one of the driest valleys of the Alps, the composition of the widespread low-elevation pine forests is shifting towards a mixed deciduous state. The evergreen sub-boreal Scots pine (*Pinus sylvestris* L.) shows high mortality rates, whereas the deciduous sub-Mediterranean pubescent oak (*Quercus pubescens* Willd.) is spreading. Here, the two species may act as early indicators of climate change. In the present study, we evaluate this hypothesis by focusing on their differences in drought tolerance, which are hardly known, but are likely to be crucial in the current forest shift and also for future forest development.

Methods: We used dendroecological methods to detect species-specific patterns in the growth response to drought. The relationship between radial growth of 401 trees from 15 mixed stands and drought was analysed by calculating response functions using yearly tree-ring indices and monthly drought indices. Principal components analysis (PCA) was applied to the response ratios to discover spatial patterns of drought response.

Results: The results revealed a species-specific response to moisture as well as a sub-regional differentiation of the response patterns. While the oaks showed a response mainly to the conditions of the previous autumn and those of current spring, the pines did not start responding before May, but showed responses throughout the whole summer. Thus, oaks seem to restrict their physiological activity to periods when sufficient soil moisture is available. Moreover, the growth of pines was found to be much more dependent on prior growth.

Conclusions: Given that the climate is changing towards i) longer summer drought periods, ii) higher mean temperatures and iii) shifted seasonality of moisture availability, oak may benefit from being able to adapt better to changing moisture conditions due to a more flexible and summer-drought adapted physiology. In contrast, pine may increasingly face problems related to drought stress as it depends on summer moisture and has a smaller adaptive capacity due to its long-lived photosynthetic tissue.

- 1 *Keywords:* climate change; dendroecology; lower treeline; Principal components analysis
- 2 (PCA); response function
- 3

# 1 Introduction

## 2 *Climate and the abundance of tree species*

3 The distribution of tree species is generally determined by their ecological characteristics, i.e.  
4 by their ability to cope with the prevailing site conditions. Scots pine (*Pinus sylvestris* L.) is  
5 known as the most widely distributed conifer, covering the whole Euro-Siberian range  
6 (Meusel et al. 1965). Pubescent oak (*Quercus pubescens* Willd.) is a typical sub-  
7 Mediterranean broad-leaved tree, with a much smaller ecological range (Meusel et al. 1965).  
8 In Valais, an inner-Alpine dry valley in the southwest of Switzerland (Fig. 1), the ranges of  
9 both species overlap, and oak and pine form mixed stands at altitudes up to 1200 m a.s.l.

10 Here, at the limit of their respective distributions, the two species may therefore act as  
11 early indicators of climate change. The xeric oak-pine forests are mainly found near the  
12 forest-steppe ecotone and constitute the lower treeline. The current forest stands have  
13 developed under changing anthropogenic influences, as well as with natural succession. The  
14 coexistence of pine and oak is partly a result of past forest management, such as goat grazing,  
15 timber harvesting and the selective withdrawal of timber and non-timber forest products. All  
16 these anthropogenic disturbances favoured the early-successional pine forest associations,  
17 which still cover a large part (approx. 12,000 ha) of the low-elevation forests in the Valais.  
18 Most of the traditional management activities have been abandoned to date, particularly in the  
19 second half of the 20<sup>th</sup> century. For this reason, oaks now benefit from less heavy browsing by  
20 goats (Gill 1992, Rigling et al. 2006a), reduced harvesting and better regeneration conditions  
21 (Rigling et al. 2006a). As a more late-successional species, oak is capable of competing  
22 against the pioneer pine species, which consequently suffers stronger suppression.

23 Across the 20<sup>th</sup> century, pine has locally undergone strong decline phases. Until the  
24 1980s, pine decline in Valais was thought to be related partially to fluorine emissions  
25 originating from the aluminium industries (Flühler et al. 1981, Kienast 1982, Kontic et al.  
26 1986). However, the installation of filters stopped pollution, and today the trees are free of  
27 pollution symptoms (Rigling & Cherubini 1999). Furthermore, the areas currently showing  
28 the highest mortality rates (Rigling et al. 2006b) do not correspond to the historically most  
29 polluted areas (Flühler et al. 1981).

30 During the past decades, the successional processes that were induced by the  
31 abandonment of forest uses coincided with climate warming (Begert et al. 2005). Since 1980,  
32 the number of days per summer with a mean temperature above 20° C has more than doubled

(Rebetez & Dobbertin 2004). Degree-day sums play an essential role in determining the length of the growing season (Menzel & Fabian 1999, Defila & Clot 2001) and in modifying the development and the abundance of insect populations (Ayres & Lombardero 2000, Bale et al. 2002, Hodar et al. 2003), phytopathogens (Paine et al. 1997, Lieutier et al. 2004) and mistletoes (Iversen 1944, Dobbertin et al. 2005), which are three factors potentially causing pine decline. Higher temperatures also contribute to increasing drought by boosting evapotranspiration. Additionally, climate data indicate a recent shift in the seasonality of water availability from summer to winter (Begert et al. 2005). This may cause additional periodic drought stress for those tree species that are not adapted to summer drought. So far, however, it is not clear how pine and oak differ in their response to summer drought conditions.

In the low-elevation forests of Valais, a shift in tree-species composition is indeed becoming apparent. A remarkable change from pine towards deciduous tree species has recently been reported. Between 1983 and 1993, the stem numbers of pubescent oak (+30%) and birch (*Betula pendula* Roth) (+27%) have increased, while the stem number of Scots pine (-6%) has decreased (WSL 2001). Also, the repetition of up to 70-year-old vegetation records showed that there has been a significant change towards oak in 30% of the relevés (Kienast et al. 2004).

Forest ecotones such as the lower-montane treeline are regarded as being sensitive to global change (Hansen & di Castri 1992), with consequences ranging from the species to the landscape level (Penuelas & Filella 2001, Theurillat & Guisan 2001, Walther 2002, Penuelas & Boada 2003). Drought-induced shifts in vegetation distribution are expected to be most rapid in semi-arid landscapes (Allen & Breshears 1998) and it is plausible to anticipate drought-induced shifts also for the region studied here. For an estimate of the future growth performance of pine and oak in Valais and other inner-Alpine dry valleys from where comparable processes are reported (Vertui & Tagliaferro 1998), species-specific growth limitations by drought will therefore play an essential role.

## **Growth responses to climate**

Tree growth is influenced by both external and internal factors. Many dendrochronological studies have shown that the external factor *climate* normally explains a relatively large part of the temporal variability in tree-ring width (Fritts 1976, Jacoby et al. 1996, Schweingruber & Briffa 1996, Briffa et al. 2002a, b). At the upper treeline, growth rates contain a strong

1 temperature signal, because temperature mainly limits tree growth in cool-moist climates. In  
2 contrast, the availability of moisture has a considerable impact on tree growth at the lower  
3 (xeric) treeline (Fritts 1976, LaMarche 1978).

4 In general, Scots pine and pubescent oak are known to be relatively well-adapted to  
5 drought (Ellenberg 1988). As a light-demanding pioneer, pine is widely distributed and thus is  
6 not highly specialised with respect to site conditions. Pine has evolved to avoid competition  
7 from other tree species by being capable of growing in extreme conditions, although Pinaceae  
8 are reported to be comparatively vulnerable to xylem embolism at xeric sites (Cochard 1992,  
9 Martinez-Vilalta et al. 2004). The sub-Mediterranean deciduous oak has evolved  
10 physiologically to adapt to drought e.g. by developing a low water potential threshold for  
11 stomatal closure, osmotic adjustment, xeromorphic leaves and a deep rooting system (Epron  
12 & Dreyer 1993, Abrams 1996, Timbal & Aussenac 1996). Thus it seems that the evergreen  
13 pine and the deciduous oak pursue quite different ecological strategies of adaptation and  
14 survival, and one would expect that pine and oak show different growth reactions to the  
15 drought regime in an area such as the Valais.

16 Several studies have investigated the ecological effects of climatic conditions on the  
17 growth of Scots pine and pubescent oak at xeric sites using the method of response function  
18 analysis (Serre-Bachet 1982, Tessier 1986, Kienast et al. 1987, Tessier 1989, von Lürthe  
19 1991, Tessier et al. 1994, Oberhuber et al. 1998, Rigling et al. 2001). Even though such  
20 investigations do not directly measure physiological constraints, the interpretation of the  
21 results can contribute to our knowledge about the autecological characteristics of a given tree  
22 species. Compared to physiological investigations, which are usually short-term, they have  
23 the advantage of allowing for a retrospective analysis of climate-growth relationships over  
24 longer periods.

25 In this study, we analyse how drought influences the radial growth performance of  
26 Scots pine and pubescent oak along five altitudinal gradients. The aim is to estimate  
27 quantitatively and qualitatively how pine and oak are responding to drought. The research  
28 questions are whether we can identify (1) a species-specific drought response, and (2) an  
29 altitudinal gradient in the response to drought. Based on 1) and 2), we discuss the implications  
30 of the differences between the two tree species in the context of climate and land-use change.

## Materials and Methods

### Study sites

The Valais is an inner-Alpine dry valley situated in the southwest of Switzerland (Fig. 1, Sion, 46°13'40'' N, 7°21'35'' E). The climate is fairly continental in the eastern part of the valley and less continental towards the west where humid air reaches from Lake Geneva (cf. Gams Index of Continentality (Gams 1932), Fig. 1).

In this study, we focused on forests below the upper distribution limit of pubescent oak, i.e. below 1200 m a.s.l., that have been described as pine forests belonging to the Ononido-Pinetum, Odontito-Pinetum and Erico-Pinetum associations (Schmid 1936, Plumettaz Clot 1988).

To analyse the relationship between site conditions and the growth of pine and oak, five dry locations were selected (Fig. 1). At each location three study plots were chosen along an altitudinal gradient (Tab. 1). To provide a rough indication of the between-site differences in the prevailing climatic conditions, air temperature was measured from the beginning of April to the end of October 2003 ( $T_{2003}$ ) (Tab. 1).

Each of the gradients extended across continuous forest with similar stand conditions and consisted of three mixed pine/oak plots, preferably with altitudinal differences between the plots of more than 150 m. Three of the gradients were facing south, one east and the lowest west (Tab. 1). They usually started just above the vineyards, i.e. between 590 and 950 m a.s.l., and ended at 930-1200 m a.s.l., where the proportion of oak decreases markedly and spruce (*Picea abies* (L.) Karst.) starts to occur more frequently. All sampling sites were characterised by steep slopes with an inclination of 93% to 162%, and they differed not only in aspect and altitude, but also in their soil type (cf. Table 1).

Because of the dry climate (Braun-Blanquet 1961, Ozenda 1985) and steep slopes, soils are generally not well developed in the Valais. By means of a soil profile at each of the 15 sampling plots, soil types were classified based on the FAO (1998) nomenclature (Table 1). Soil types were determined as Regosols, Rendzic Leptosols and Distric Cambisols. On xeric sites, soil type plays an important role for determining the available water capacity (AWC). AWC was thus estimated for each plot using data on soil texture, bulk density, content of coarse fragments and depth of each of the recorded soil horizons according to the table in AG Bodenkunde (1982). With values of AWC consistently below 120 mm, the plots exhibit low to very low AWCs (Table 1).

Table 1

Fig. 1

## **Data collection and analysis**

Scots pine and pubescent oak trees from the 15 plots were cored using an increment borer in summer 2002. Two cores were taken at breast height for standard dendrochronological analysis, and one core was extracted at the stem base to determine the age. For each tree, height, diameter at breast height (dbh) and social class (dominant, codominant, subdominant, or suppressed) were recorded. The sampling was designed so as to represent the forest structure at each site, including all social and age classes. In this way, a total of 401 trees were chosen for further analyses.

Tree-ring widths were measured with a Lintab3 measuring system (F. Rinn S.A., Heidelberg, Germany) using the TSAP tree-ring software Version 3.5 (Rinn 1996). Crossdating was done both visually and using standard techniques (Fritts 1976, Cook & Kairiukstis 1990). Cross-dating was verified statistically by using the TSAP and the COFECHA routines (Holmes 1994). A few missing rings due to a lack of cambial activity in extraordinarily dry years had to be inserted in the pine series, mainly in the drought year 1921.

By applying the interval sign test of TSAP, those series with a percentage of sign agreement (Gleichläufigkeit) (Eckstein & Bauch 1969) above 60% were selected for further analysis. This procedure resulted in the exclusion of 56 cores of lower quality, which showed periods of hardly detectable rings due to both slow growth and density fluctuations, or irregular growth structures due to external influences, e.g. wind and rockfall. Between 11 and 53 series per species and plot conformed to our requirements (Table 2). Differences in the number of available tree-ring series between the plots were caused by the variable presence of young or suppressed trees on the sampling plots and by altitudinal effects (fewer tall oaks at higher elevations).

Mean standard and residual chronologies were produced using the ARSTAN software (Cook 1985, Holmes 1994), thereby applying the same standardisation method for each single series to preserve the comparability of chronologies. The final standardisation method as described below was chosen by means of a pre-evaluation of various methods, including double detrending, which was not ideal due to the fact that most series were not showing the typical negative exponential trend. In a first step, the variance of each ring-width series was



1 stabilised by a power transformation (Cook & Peters 1997). In a second step, the series were  
2 standardised by fitting a cubic-smoothing spline with a 50% frequency response of 128 years  
3 (Cook & Peters 1981). By subtracting the expected values given by the spline function from  
4 the power-transformed values, indexed series were produced and finally averaged to 15 pine  
5 and 15 oak standard chronologies (STD) by a robust biweight mean (Fritts 1976, Cook et al.  
6 1990). Residual chronologies (RES) were calculated based on autoregressive modelling.  
7 Although one may argue the chosen spline length was rather long for the many relatively  
8 short series, RES chronologies calculated with a shorter spline (50% frequency response of 60  
9 years, data not shown) were nearly identical to the RES chronologies used here. However, by  
10 using the longer, more conservative spline, we preserved mid-frequency signals in the STD  
11 chronologies, in which we were interested for comparing the explained variance by climate  
12 and prior growth.

13 For quality control, basic chronology statistics (Fritts 1976, Briffa & Jones 1990) such  
14 as mean  $r_{bar}$  (cross-correlation between single series), mean sensitivity (mean percentage  
15 change from each measured annual ring value to the next) and expressed population signal (a  
16 measure for how well single series represent the whole population, Wigley et al. 1984) were  
17 computed for all the RES chronologies for the period 1950-2001 using ARSTAN.

## 19 ***Climate data***

20 Climate data from the regional SMI (Swiss Meteorological Institute, MeteoSwiss) climate  
21 stations of Visp (measurement period 1901-2001) and Sion (measurement period 1864-2001)  
22 were used (Fig. 1). Since the location of both climate stations was moved in the 20<sup>th</sup> century  
23 and temperature data at Visp covered only the last 40 years, climate series had to be corrected  
24 using nearby bridging stations and homogenized as described in Bigler et al. (2006).

25 As we were interested in the functional reaction of tree growth to climate, we used a  
26 drought index (DRI) (Bigler et al. 2006) – the difference between precipitation and potential  
27 evapotranspiration (PET) according to Thornthwaite (1948) – for the statistical analyses.  
28 Values for DRI are positive when precipitation exceeds PET and negative in the case of a  
29 moisture deficit. In a pilot study with other ecologically based indices such as monthly mean  
30 temperature, monthly precipitation sum, length of summer drought periods and minimum  
31 temperature of April and May (late frost), DRI showed the highest correlations with tree-ring  
32 growth. This drought index gives a better estimation of water availability for trees than  
33 precipitation data, since it captures the joint effects of temperature (via PET) and

precipitation. Another advantage of calculating a combined index is that interpretation problems due to the inverse effects of temperature and precipitation can be avoided (Fritts 1976).

### **Statistical analysis**

We used response functions, i.e. a multiple regression after extracting the principal components of the climatic predictors, to evaluate the differences in the reaction of pine and oak to climatic influences. In this way, we avoided the limitations of simple correlations, which may be difficult to interpret due to inter-correlations within the climate data (Fritts 1976, Guiot et al. 1982, Fritts & Guiot 1990). The analysis was performed with the routine PRECON (Fritts et al. 1991) with the RES chronologies as dependent variable, including monthly drought indices (DRI) from June<sub>(i-1)</sub> of the preceding year to September<sub>(i)</sub> of the current year of growth as independent variables. The data of the climate station at Visp were used for Eschwald and Eggerberg, and the climatic data of Sion were used for Salgesch, Lens and Bramois (Fig. 1). Most plots were located in a distance less than 5 km from the climate station used, except for the plots of Salgesch with a distance of approx. 20 km to the climate station of Sion. As most of the tree-ring chronologies covered at least the last 51 years, the period of 1950-2001 was chosen for the analyses. The principal components whose cumulative eigenvalue product (CEP, sometimes also abbreviated as PVP (Principal Vector Product)) was >1 were selected for the regression (Guiot et al. 1982), and in a bootstrap procedure 100 iterations (Guiot et al. 1982, Guiot 1990, Fritts et al. 1991) were calculated to estimate the standard deviation of the response coefficients. The ratio between the response coefficient and its standard deviation was used to estimate the significance of the response (z-test).

A second evaluation was performed to compare the influence of prior growth and climate by using STD chronologies instead of RES chronologies to calculate response functions, and by including not only DRI, but also growth, i.e. STD chronologies up to a lag of -3 years as predictor variables.

Two procedures were established to evaluate the species-specific and the regional response patterns. First, the relationships between moisture availability and tree growth were summarised over all the plots and for the two species separately by recording the percentage of plots exhibiting a significant relationship on the 95% confidence level for each month. The significance of the difference in the response between oak and pine was then tested by a chi-

square test of independence (Sokal & Rohlf 1995). Second, regional response functions were calculated based on regional average tree-ring chronologies.

Finally, the 16 monthly response ratios of all the plots were introduced into a principal components analysis (PCA) (Tessier 1986, 1989) using the statistic software R (R Development Core Team 2003) to detect the relationships between the response functions of the different sites and species. PCA was performed with correlations. The ordination axes are (unrotated) linear combinations of the monthly responses. By applying this method, groups of similar response function patterns were formed and the main grouping factors were identified.

Table 2

## Results

### *Characteristics of the tree-ring chronologies*

For each plot, separate chronologies were produced for both pine and oak. The statistical parameters document that the chronologies are generally of good quality (Table 2). In five chronologies, the number of trees was lower than 10, but this affected the quality only in the case of the chronology egc (6 trees) ( $\text{eps} = 0.78$ ). On the plots leb and bra, both pine and oak did not reach a maximum age of 51 years to cover the common period of analysis. Therefore, those two plots were excluded from further analysis. However, it was decided to keep the oak chronology of plot egb (47 years), since – in contrast to bra and leb – the pine chronology of this plot was long enough (135 years), which gave us another complete pair of chronologies.

### *Dynamics of the drought index*

The intra-annual patterns of the drought index at Visp and Sion illustrate the typical moisture deficit in summer (Fig. 2). Both stations show the tendency of a change in seasonality during the 20<sup>th</sup> century. Average spring March moisture conditions used to be markedly lower between 1941 and 1960 than between 1961 and 2000. Average moisture availability in August used to be noticeably higher between 1941 and 1980 than between 1981 and 2000.

Linear regression revealed that between 1941 and 2000, moisture availability showed a significant positive trend in March (Visp:  $p < 0.05$ , Sion:  $p < 0.05$ ) and May (Visp:  $p < 0.1$ ); on the other hand, moisture availability in August (Visp:  $p < 0.05$ , Sion:  $p < 0.01$ ) decreased significantly.

Fig. 2

## ***Single-plot response to drought***

On all plots, the growth of both tree species was positively correlated with moisture for most months of the period of interest (June<sub>(i-1)</sub> to September<sub>(i)</sub>) (Fig. 3). Separating the single chronologies' response functions in the Visp and the Sion region resulted in a regional differentiation of the patterns (Fig. 3). In the more continental climate of the Visp region, pine and oak showed a more distinct seasonal response pattern than in the Sion region. Furthermore, the single-plot response patterns of the Visp region tended to be more similar to each other than those of the Sion region. Only the oaks of egc, the plot with the highest elevation (1200 m a.s.l.), deviated considerably from the general course. Their responses were lower in November<sub>(i-1)</sub>, February<sub>(i)</sub> and March<sub>(i)</sub>.

The differences between the two regions were also visible in the response curves of the regional average chronologies for Visp and Sion (Fig. 3). The oaks of the Visp region responded most strongly to moisture in autumn of the previous year, whereas the oaks of the Sion region showed the strongest response to May and June moisture. The Visp pines showed significant responses in their growth dating back to August and November of the previous year and had a continuous response during the summer months (June-August) of the current year. In comparison, pines of the Sion region had a peak in their response to moisture in May<sub>(i)</sub>.

Fig. 3

Looking at the significances of the single-chronology responses, the reaction of the oaks was notably more distinct than that of the pines (sub-table in Table 3). Within the oak chronologies, available soil water on the plots (AWC) acted as a sorting criterion for the response patterns. The oaks growing on soils with a low available water capacity (AWC = 36-46) tended to respond to moisture in the autumn of the previous year, while the oaks growing on slightly better soils (AWC  $\geq$  47) responded mainly from March<sub>(i)</sub> to June<sub>(i)</sub>. With the pines, no main sorting factor was evident among elevation, AWC, T<sub>2003</sub>, maximum tree age and tree height.

Table 3

## ***Differences in the response to drought between oak and pine***

The percentage of significantly responding chronologies was calculated for every month to emphasise the different response patterns of the two species (Fig. 4). Months with significant

responses of a large percentage of chronologies stand for a species-specific statistical relationship between radial growth and moisture availability. Significant differences in positive response between the two species were identified in August, September and October of the previous year and in April and July of the current year. Unlike the pine chronologies, a relatively high percentage of oak chronologies responded in a significantly positive manner to moisture in the previous September (38%) and October (46%). In November, both species showed a relatively high response (62% in oak, 38% in pine). During winter (December-February), the response of both species was low. In March, more than twice as many oak (38%) than pine (15%) chronologies recorded positive responses. The highest peak of oak response in the current year was in April (62%). In comparison, pine showed low response (<15%) from early spring to May (54%), when pine reached its maximum response. In July, when 23% of the pine chronologies were still responding, the response of oak dropped to 0%. 54% of the pine chronologies, but none of the oak chronologies, responded in a significantly negative manner to the conditions in June of the previous year.

Fig. 4

### ***Groups of similar response patterns***

The first three axes of the principle components analysis (PCA) explained 46.3%, 12.5% and 10.7% of the total variance (69.5% altogether). The ordination of the first two components resulted in a nearly complete separation of oak and pine (Fig. 5). However, all the chronologies had negative loadings on the first component axis, indicating that the trees were partly affected in a similar way by moisture availability. On the second component axis, the oaks were located mostly in the positive, and the pines mostly in the negative part. The main dividing months in the positive direction were December<sub>(i-1)</sub> (7) and April<sub>(i)</sub> (11). In the negative direction, the main loadings were July<sub>(i-1)</sub> (2), August<sub>(i-1)</sub> (3) and July<sub>(i)</sub> (14).

Fig. 5; Fig. 6

Within the ordination of components 2 and 3, the division into subgroups of similarly responding chronologies was even more apparent (Fig. 6). Most of the pine chronologies were grouped according to the response in summer of both the previous and the current year. The oak chronologies of Eschwald were principally associated with a response to the moisture conditions of the previous autumn. The rest of the chronologies made up a less pronounced group, related to winter and spring responses.

Calculating the PCA for oaks and pines separately (Fig. 7a,b) revealed site-specific response patterns. For both species, the PCA split the response into the sub-regional groups of Eschwald, Eggerberg and Sion (Salgesch, Lens, Bramois). The Eschwald sites, making up a narrow group of arrows, were found to be different from the other sites for both species. In oaks, the discrimination of the plots was related to soil AWC (Fig. 7a). No altitudinal gradient in the response was visible.

Fig. 7a,b

### ***Influence of prior growth***

Additionally, the response functions were calculated for all the STD chronologies to detect the parts of variance in tree-ring width explained by climate and by prior growth. Climate explained significantly more variance in tree-ring width of oaks than of pines ( $p < 0.05$ ). On the other hand, prior growth was significantly more important in pines than in oaks ( $p < 0.05$ ). The total explained variance was high in both species but tended to be higher in pine than in oak, although this difference was not significant (Fig. 8).

Fig. 8

## **Discussion**

### ***Species-specific response to drought***

Our results indicated a species-specific seasonal differentiation of the radial growth response to moisture availability. These differences can be interpreted in the context of the ecological differences between a sub-boreal (pine) and a sub-Mediterranean (oak) tree species. The summarised response patterns of pine and oak (Fig. 4) illustrate the differences best and can be interpreted in terms of ecophysiological adaptations to the extreme site conditions in the Valais, as follows.

The response of pine to moisture in previous August (Fig. 4) is in agreement with many other studies on growth-climate relationships of conifers (Fritts 1974, Gutierrez 1991, Graumlich 1993, Oberhuber et al. 1998, Oberhuber & Kofler 2000, Rigling et al. 2001, Tardif & Stevenson 2001, Rigling et al. 2002, Rigling et al. 2003, Takahashi et al. 2003). One possible ecophysiological explanation for this response was given by Takahashi et al. (2003),

1 who interpreted the response to moisture of the previous August in *Abies veitchii* by  
2 physiological processes concerning bud formation for the following year.

3 The number and size of buds that are formed has a strong influence on the  
4 photosynthetic potential in the current growing season, but also in the following years, since  
5 needles remaining from previous years are still photosynthetically active, as it is the case in  
6 most evergreen species. Therefore, needle loss following drought stress (Pouttu & Dobbertin  
7 2000) reduces photosynthetic capacity in subsequent years. As a result, the growth of pine  
8 was found to be much more dependent on prior growth than that of the deciduous oak (Fig.  
9 8). Thus, this lag effect, which is characteristic for evergreen coniferous tree species in  
10 temperate climates, can obscure the response of pine to current moisture conditions. In Valais,  
11 longer periods of drought (multiple drought years) are apparently causing reduced needle  
12 mass in pines (Pouttu & Dobbertin 2000) and considerable growth decreases followed by a  
13 higher mortality risk (Bigler et al. 2006).

14 Apart from differences in the response to the conditions of the preceding year, our  
15 results pointed to potential differences in the start of the growing season between pine and  
16 oak (Fig. 4). The early growth response of oak in March can be interpreted as the start of  
17 physiological processes related to radial growth, when normally drought is not limiting yet  
18 (Fig. 2). The first differentiated earlywood cells are efficient hydraulic conductors (Abrams  
19 1990), transporting the water to the crown and promoting bud break (Nardini 2002). In  
20 Central European *Quercus petraea*, earlywood vessels were found to be established already  
21 by the end of April (Breda & Granier 1996). In fact, it was found that wood formation in oaks  
22 in Valais started between the end of March and mid April, and most notably around three  
23 weeks earlier in oaks than in pines (Burger & Truniger 2006, Zweifel et al. 2006). By  
24 contrast, the rather late start of the response of pine in May, when conditions are already dry  
25 (Fig. 2), may have implications for the pine's overall growth performance at the limit of its  
26 distribution.

27 While oak seems to minimise its activity in the driest month (no significant response in  
28 July, cf. Table 3), annual radial growth of pine at three sites seemed to partly depend on  
29 moisture conditions in July. As an adaptation to summer drought, oaks probably stop cambial  
30 activity in mid-summer. In 2005, Burger & Truniger (2006) measured the intra-annual  
31 development of oak radial growth in Valais using the pinning method. They found that radial  
32 growth was nearly finished by the end of June and was completed latest by the end of July.  
33 Thus, fast growth in spring and the cessation of cambial activity in July probably represents  
34 the oaks' strategy to avoid cavitation (Tyree & Cochard 1996, Lebourgeois et al. 1998,

1 Nardini & Pitt 1999), comparable to summer dormancy in Mediterranean species (Cherubini  
2 et al. 2003). The physiological activity of pines in July, however, is likely to induce drought  
3 stress, which is connected with an increased risk of cavitation, as pines were found to be more  
4 prone to drought-induced xylem embolism than other conifers (Martinez-Vilalta & Pinol  
5 2002, Martinez-Vilalta et al. 2004).

6 According to the PCA (Fig. 5 and 6), the chronologies can be grouped well into  
7 summer, winter/spring and autumn responders. Most pines belong to the summer responders  
8 (July and August). July is the driest month in the year and therefore drought stress is likely to  
9 occur. Because pines start responding late in the year (peak in May), they appear to be  
10 dependent on summer moisture to grow a wide ring and to produce enough carbon reserves.  
11 The summer moisture dependency of pine found here is in agreement with other studies from  
12 dry, low-elevation sites in Valais, at which growth of pine was found to be correlated  
13 negatively with temperature (Kienast et al. 1987, Rigling et al. 2002) and positively with  
14 precipitation in July and August (Kienast et al. 1987). Furthermore, the PCA results suggest  
15 that oaks are grouped as autumn- (September to November) or winter/spring-responders  
16 (December, March, April). As a sub-Mediterranean tree species, pubescent oak is expected to  
17 be better adapted to summer drought conditions. As a consequence, the oaks probably  
18 concentrate part of their physiological activity on periods when moisture conditions are most  
19 favourable, i.e. during autumn, winter and spring.

20 The positive response to winter conditions may appear surprising in a deciduous tree  
21 species. However, we see two ways to interpret this phenomenon. First, winter precipitation is  
22 needed to refill the soil with water for the next growing season. This effect of moisture  
23 availability in winter would thus be indirect, because deciduous trees do not normally take up  
24 much water until they start photosynthesis in spring. Second, winter moisture can have a  
25 direct positive effect on root growth. Root growth in winter may be advantageous in summer-  
26 dry climates (Cherubini et al. 2003). Oaks have been reported to grow fine roots even in  
27 winter as long as soil temperature is above 0 °C (Hoffmann 1974, Teskey & Hinckley 1981).  
28 Mean monthly soil temperatures below 0 °C are exceptional for Sion and Visp (Defila &  
29 Brändli 1989), and therefore root growth in winter is at least conceivable. Root growth in the  
30 pre-season can be particularly relevant for young trees (as many of the oaks in our sample  
31 are), because they still need to enlarge their root systems (Aussenac & Valette 1982).

32 Generally, frost is a key factor for the distribution of pubescent oak, a species that is  
33 restricted to the sub-Mediterranean area, and in the Valais to elevations below 1200 m a.s.l.  
34 (Burnand 1976). Because of their ring-porous wood anatomy, oak species are susceptible to



winter and spring frosts (Cochard & Tyree 1990, Thomas et al. 2002), and oak seedlings have been found to be particularly damaged by late frost (Chaar & Colin 1999). Thus, oak regeneration is limited to lower elevations. Lower growth rates and less regeneration at higher elevations (Rigling et al. 2006a) could explain that oaks were smaller, thinner and younger at higher altitudes, whereas pines were older and thicker at higher altitudes (Table 1). Thus, higher temperatures due to climate change may lead to a shift in oak distribution to higher altitudes.

### ***Sub-regional differentiation***

From our hypothesis, we expected an altitudinal gradient in the response to drought. However, our investigations revealed mainly a sub-regional differentiation in the Visp vs. the Sion area (Fig. 7). Altitudinal effects, if any, were secondary, in that no clear shift was found in drought response with increasing elevation. In both species, the sub-regional differentiation was mainly caused by different responses to differing climatic and soil conditions, as discussed below.

The unique position of the Eschwald gradient (Fig. 7a,b) can be explained by the combination of site factors including 1) very dry soils in summer due to low water holding capacity, 2) the continental dry climate of the side-valley, and 3) the eastern aspect. The characteristic autumn response of oaks at Eschwald can be interpreted physiologically. Trees growing on soils with such low water-holding capacities are limited by drought occurring throughout most of the growing season (at least from May to September, cf. Fig. 2). They thus adapt a strategy to prepare for the growing season in the previous autumn. These preparations may include the storage of metabolic compounds as well as root growth.

The gradients near Sion (Salgesch, Lens and Bramois) were not separated clearly from each other in either species (Fig. 7a,b), even though Bramois is situated on the northwest-facing slope and both Salgesch and Lens on the south-facing slope. Since the gradient of Bramois was located at a lower elevation, we conclude that 200 m in altitude probably compensated for the northwest aspect. In contrast to the gradients of Eschwald and Eggerberg, the soils of the plots around Sion were characterised as rendzic leptosols (except for brb, which was a calcaric cambisol, Table 1). While they all had free carbonate in their topsoil, the soils at Eschwald and Eggerberg were partly decarbonated or carbonate free on silicate. The similarity of the soil types in the Sion area, combined with the presented grouping of the response patterns of this sub-region, suggests that nutrient and water

availability in the soil may be a differentiating factor for tree-growth patterns on xeric sites. For oaks, it seems that the soil type is an important factor for dividing the response patterns into spatial subgroups (Fig. 7a,b). This is also visible from the ranking of the significant responses by AWC (Table 3).

### **Implications in the context of climate and land-use change**

According to Rebetez and Dobbertin (2004), increasing drought due to climate change will lead to increasing pine mortality in the Valais in the future. Increasing temperatures and a change in the seasonality of precipitation towards a more Mediterranean climate with extended summer droughts (Fig. 2) are likely to modify the growth-climate response patterns of oak and pine in the future. On the one hand, oaks may benefit from increasing moisture in spring and autumn (Fig. 4). On the other hand, pines may benefit in May, but are likely to suffer with increasing drought in August (prior and current year). A comparable study of *Quercus petraea* and *Quercus robur* in Germany found a shift in the response to winter precipitation, which was explained by a changing climate (von Lürthe 1991). In contrast, Solberg et al. (2002) observed a shift in the response patterns of *Picea abies* in Norway, where the response to winter precipitation was decreased by a stronger oceanic influence due to climate change. Moving response functions (Biondi & Waikul 2004) could be applied for the Valais to longer chronologies than ours to detect a possible shift in the response pattern. However, below 1200 m a.s.l., old trees, and in particular oaks, are rare in Valais.

Our results imply that oak is better able to adapt to a changing climate regime with longer summer drought periods than pine. Oaks and pines in a Mediterranean forest in the southwestern part of France showed similar differences in their adaptive capacity (Tessier 1986). In a study by Fekedulegn et al. (2003) in the Appalachian mountains, the adaptive capacity to drought of individual *Liriodendron tulipifera* L. trees was interpreted as depending also on their root:shoot ratio, besides the species-specific growth strategy. By analogy, many pine trees that have grown up under earlier, cooler conditions may face additional drought stress in a warmer and drier climate, because their root:shoot ratio may not be adapted to these novel conditions. This view is supported by the sudden breakdown of radial growth that was reported in Valais in pines growing along water channels when irrigation abruptly ceased (Rigling et al. 2003) and in pines on a sinking groundwater table in Germany (Wirtz 2002).

Single (Kienast et al. 1987, Schweingruber 1990) and multiple drought years (Bonn & Worbes 1991, Bigler et al. 2006) can play a very important role in influencing species composition in forest ecotones, such as the one studied here close to the xeric, lower-montane treeline in the Valais. Besides the inter-annual variability of moisture, the intra-annual variability of moisture – i.e. its seasonality (Fig. 2) and the length of single drought periods (Kuhn 1973, Bigler et al. 2006) – contributes to determining radial growth, and has to be considered as well.

Furthermore, the historical and still ongoing reduction in the use of forest resources is altering the competition regime and will consequently change the growth regime at the individual tree level as well. Lower thinning intensities, for example, increase root competition and may thus further decrease the drought resistance of the trees (Sabate et al. 2002, Misson et al. 2003a, Misson et al. 2003b).

In Valais, many factors that are linked to climate and land-use change potentially affect the mortality rates of pines (Rigling & Cherubini 1999, Rigling et al. 2004, Rigling et al. 2006b). This study has revealed that summer drought has a stronger impact on the growth performance of pine than of oak. As a consequence, growth imbalances (lower storage of carbon reserves, needle loss) and a limited adaptive capacity is likely to lead to a high mortality risk for pine (LeBlanc & Foster 1992, Elliott & Swank 1994, Cook et al. 2001, Martinez-Vilalta & Pinol 2002, Bigler et al. 2006). Our results suggest a more flexible reaction and therefore higher drought resistance of oak than of pine. Whether the differences in drought response have consequences for the competitive processes between oak and pine will be the subject of future research.

## Acknowledgements

We thank Jessica Gale, Roger Köchli and the local forest service for their assistance during fieldwork. We are grateful to Felix Kienast, Jacques Tardif and the anonymous reviewers for their helpful comments. We would like to thank the Section of Soil Ecology at WSL for helping us with soil classifications, the Dendro Network at WSL, especially Otto Ulrich Bräker, and Werner Stahel from the Seminar for Statistics at ETH Zürich (Switzerland) for statistical advice. Thanks are also due to our co-researchers in the “Pine project” at WSL and to Roman Zweifel and Lukas Zimmermann at University of Berne (Switzerland) for fruitful discussions. This study was funded by the Velux Stiftung and the Canton of Valais.

## References

- Abrams, M.D. 1990. Adaptations and responses to drought in *Quercus* species of North-America. *Tree Physiol.* 7: 227-238.
- Abrams, M.D. 1996. Distribution, historical development and ecophysiological attributes of oak species in the eastern United States. *Ann. Sci. For.* 53: 487-512.
- AG Bodenkunde. 1982. *Bodenkundliche Kartieranleitung*, 3rd edition. Schweizerbart, Stuttgart.
- Allen, C.D. & Breshears, D.D. 1998. Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climate variation. *PNAS* 95: 14839-14842.
- Aussenac, G. & Valette, J.C. 1982. Comportement hydrique estival de *Cedrus atlantica* Manetti, *Quercus ilex* L. et *Quercus pubescens* Willd. et de divers pins dans le Mont Ventoux. *Ann. Sci. For.* 39: 41-62.
- Ayres, M.P. & Lombardero, M.J. 2000. Assessing the consequences of global change for forest disturbance from herbivores and pathogens. *Sci. Total Environ.* 262: 263-286.
- Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D. & Whittaker, J.B. 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Glob. Change Biol.* 8: 1-16.
- Begert, M., Schlegel, T. & Kirchhofer, W. 2005. Homogeneous temperature and precipitation series of Switzerland from 1864 to 2000. *Int. J. Climatol.* 25: 65-80.
- Bigler, C., Bräker, O.U., Bugmann, H., Dobbertin, M. & Rigling, A. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9: 330-343.
- Biondi, F. & Waikul, K. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comp. & Geosci.* 30: 303-311.
- Bonn, S. & Worbes, M. 1991. Klimaeinfluss und abrupte Zuwachsschwankungen von Fichten (*Picea abies* Karst.) und Kiefern (*Pinus sylvestris* L.) verschiedener Höhenstufen Niedersachsens. *Ber. Forsch.zentrum Waldökosyst., Reihe B* 30: p. 68.
- Braun-Blanquet, J. 1961. *Die inneralpine Trockenvegetation. Von der Provence bis zur Steiermark*. Fischer Verlag, Stuttgart.
- Breda, N. & Granier, A. 1996. Intra- and interannual variations of transpiration, leaf area index and radial growth of a sessile oak stand (*Quercus petraea*). *Ann. Sci. For.* 53: 521-536.
- Briffa, K.R. & Jones, P.D. 1990. Basic chronology statistics and assessment. In: Cook, E.R. and Kairiukstis, L.A. (eds). *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic, Dordrecht, The Netherlands, pp. 137-152.
- Briffa, K.R., Osborn, T.J., Schweingruber, F.H., Jones, P.D., Shiyatov, S.G. & Vaganov, E.A. 2002a. Tree-ring width and density data around the Northern Hemisphere: Part 1, local and regional climate signals. *Holocene* 12: 737-757.
- Briffa, K.R., Osborn, T.J., Schweingruber, F.H., Jones, P.D., Shiyatov, S.G. & Vaganov, E.A. 2002b. Tree-ring width and density data around the Northern Hemisphere: Part 2, spatio-temporal variability and associated climate patterns. *Holocene* 12: 759-789.
- Burger, M. & Truniger, P. 2006. *Das intra-annuelle Wachstum von Waldföhre und Flaumeiche im Pfynwald (Wallis). Eine holzanatomische und dendrochronologische Untersuchung*. Master thesis. ETH Zürich, Zürich.
- Burnand, J. 1976. *Quercus pubescens-Wälder und ihre ökologischen Grenzen im Wallis (Zentralalpen)*. PhD Thesis Nr. 5703. Swiss Federal Institute of Technology Zürich, Zürich.

- 1 Chaar, H. & Colin, F. 1999. Impact of late frost on height growth in young sessile oak  
2 regenerations. *Ann. Sci. For.* 56: 417-429.
- 3 Cherubini, P., Gartner, B.L., Tognetti, R., Bräker, O.U., Schoch, W. & Innes, J.L. 2003.  
4 Identification, measurement and interpretation of tree rings in woody species from  
5 mediterranean climates. *Biol. Rev.* 78: 119-148.
- 6 Cochard, H. 1992. Vulnerability of several conifers to air-embolism. *Tree Physiol.* 11: 73-83.
- 7 Cochard, H. & Tyree, M.T. 1990. Xylem dysfunction in *Quercus* vessel sizes, tyloses,  
8 cavitation and seasonal changes in embolism. *Tree Physiol.* 6: 393-407.
- 9 Cook, E.R. 1985. *A time series analysis approach to tree-ring standardization*. Dissertation.  
10 University of Arizona, Tucson, Arizona, USA.
- 11 Cook, E.R., Briffa, K.R., Shiyatov, S. & Mazepa, V. 1990. Tree-ring standardization and  
12 growth-trend elimination. In: Cook, E.R. and Kairiukstis, L.A. (eds). *Methods of*  
13 *dendrochronology: applications in the environmental sciences*. Kluwer Academic,  
14 Dordrecht, The Netherlands, pp. 104-123.
- 15 Cook, E.R., Glitzenstein, J.S., Krusic, P.J. & Harcombe, P.A. 2001. Identifying functional  
16 groups of trees in west Gulf Coast forests (USA): A tree-ring approach. *Ecol. Appl.*  
17 11: 883-903.
- 18 Cook, E.R. & Kairiukstis, L.A. 1990. *Methods of dendrochronology: applications in the*  
19 *environmental science*. Kluwer Academic Publishers, Dordrecht, Boston, London.
- 20 Cook, E.R. & Peters, K. 1981. The smoothing spline: a new approach to standardizing forest  
21 interior tree-ring width series for dendroclimatic studies. *Tree-ring b.* 41: 45-53.
- 22 Cook, E.R. & Peters, K. 1997. Calculating unbiased tree-ring indices for the study of climatic  
23 and environmental change. *Holocene* 7: 361-370.
- 24 Defila, C. & Brändli, J. 1989. Bodentemperatur und Verdunstung 1951-1985. *Beih. Ann.*  
25 *Schweiz. Meteorolog. Anst.* 28: 118.
- 26 Defila, C. & Clot, B. 2001. Phytophenological trends in Switzerland. *Int. J. Biometeorol.* 45:  
27 203-207.
- 28 Dobbertin, M., Hilker, N., Rebetez, M., Zimmermann, N.E., Wohlgemuth, T. & Rigling, A.  
29 2005. The upward shift in altitude of pine mistletoe (*Viscum album* ssp. *austriacum*) in  
30 Switzerland - result of climate warming? *Int. J. Biometeorol.* 50: 40-47.
- 31 Eckstein, D. & Bauch, J. 1969. Beitrag zur Rationalisierung eines dendrochronologischen  
32 Verfahrens und zur Analyse seiner Aussagesicherheit. *Holzwissenschaftl. Centralbl.*  
33 88: 230-250.
- 34 Ellenberg, H. 1988. *Vegetation ecology of Central Europe*, 4th edition. Cambridge University  
35 Press, Cambridge UK.
- 36 Elliott, K.J. & Swank, W.T. 1994. Impacts of drought on tree mortality and growth in a mixed  
37 hardwood forest. *J. Veg. Sci.* 5: 229-236.
- 38 Epron, D. & Dreyer, E. 1993. Long-term effects of drought on photosynthesis of adult oak  
39 trees. *Quercus petraea* (Matt) Liebl. and *Quercus robur* L. in a natural stand. *New*  
40 *Phytol.* 125: 381-389.
- 41 Fekedulegn, D., Hicks, R.R. & Colbert, J.J. 2003. Influence of topographic aspect,  
42 precipitation and drought on radial growth of four major tree species in an  
43 Appalachian watershed. *For. Ecol. Manage.* 177: 409-425.
- 44 Flühler, H., Keller, T. & Schwager, H. 1981. Die Immissionsbelastung der Föhrenwälder im  
45 Walliser Rhonetal. *Mitt. Eidg. Anst. forstl. Versuchsw.* 57: 399-414.
- 46 Fritts, H.C. 1974. Relationships of ring widths in arid-site conifers to variations in monthly  
47 temperature and precipitation. *Ecol. Monogr.* 44: 411-440.
- 48 Fritts, H.C. 1976. *Tree Rings and Climate*. Academic Press, London, New York.
- 49 Fritts, H.C. & Guiot, J. 1990. Methods of calibration, verification and reconstruction. In:  
50 Cook, E.R. and Kairiukstis, L.A. (eds). *Methods of dendrochronology: applications in*

- the environmental sciences. Kluwer Academic, Dordrecht, The Netherlands, pp. 163-217.
- Fritts, H.C., Vaganov, E.A., Sviderskaya, I.V. & Shashkin, A.V. 1991. Climatic variation and tree-ring structure in conifers: empirical and mechanistic models of tree-ring width, number of cells, cell size, cell-wall thickness and wood density. *Clim. Res.*: 97-116.
- Gams, H. 1932. Die klimatische Begrenzung von Pflanzenarealen und die Verteilung der hygischen Kontinentalität in den Alpen. *Z. Ges. Erdkunde* 56.
- Gill, R.M.A. 1992. A Review of Damage by Mammals in North Temperate Forests - 1. Deer. *Forestry* 65: 145-169.
- Graumlich, L.J. 1993. Response of tree growth to climatic variation in the mixed conifer and deciduous forests of the Upper Great-Lakes region. *Can. J. For. Res.* 23: 133-143.
- Guiot, J. 1990. Methods of calibration. In: Cook, E.R. and Kairiukstis, L.A. (eds). *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic, Dordrecht, The Netherlands, pp. 165-178.
- Guiot, J., Berger, A.L. & Munaut, A.V. 1982. Response functions. In: Hughes, M.K., Kelly, P.M., Pilcher, J.R. and LaMarche Jr., V.C. (eds). *Climate from tree-rings*. Cambridge University Press, Cambridge, pp. 38-45.
- Gutierrez, E. 1991. Climate tree-growth relationships for *Pinus uncinata* Ram in the Spanish Pre-Pyrenees. *Acta Oecol.* 12: 213-225.
- Hansen, A. & di Castri, F. 1992. *Landscape boundaries: consequences for biotic diversity and ecological flows*. Springer, Berlin, Heidelberg, New York.
- Hodar, J.A., Castro, J. & Zamora, R. 2003. Pine processionary caterpillar *Thaumetopoea pityocampa* as a new threat for relict Mediterranean Scots pine forests under climatic warming. *Biol. Conserv.* 110: 123-129.
- Hoffmann, G. 1974. Beendigung des Wurzelwachstums in der Vegetationsperiode und Zuwachs von Wurzeln im Winter. *Beitr. Forstw.* 3: 38-41.
- Holmes, R.L. 1994. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring b.* 43: 69-78.
- Iversen, J. 1944. *Viscum, Hedera* and *Ilex* as climate indicators. *Geologisk Förenings Förhandlingar Stockholm* 66: 463-483.
- Jacoby, G., D'Arrigo, R. & Luckman, B. 1996. Millennial and near-millennial scale dendroclimatic studies in northern North America. In: Jones, P.D., Bradley, R.S. and Jouzel, J. (eds). *Climatic Variations and Forcing Mechanisms of the Last 2000 Years*. NATO ASI, pp. 67-84.
- Kienast, F. 1982. Jahrringanalytische Untersuchungen in immissionsgefährdeten Waldschadengebieten des Walliser Rhonetales. *Geograph. Helvetica* 3: 143-148.
- Kienast, F., Hadorn, S. & Schütz, M. 2004. Werden Walliser Föhrenwälder zu Eichenwäldern? Eine pflanzensoziologische Studie mit historischen Aufnahmen. *Inf.bl. Forsch.bereich Landsch.* 59: 1-3.
- Kienast, F., Schweingruber, F.H., Bräker, O.U. & Schaer, E. 1987. Tree-ring studies on conifers along ecological gradients and the potential of single-year analyses. *Can. J. For. Res.* 17: 683-696.
- Kontic, R., Niederer, M., Nippel, C.-A. & Winkler-Seifert, A. 1986. *Jahrringanalysen an Nadelbäumen zur Darstellung und Interpretation von Waldschäden (Wallis, Schweiz)*. Eidgenössische Anstalt für das Forstliche Versuchswesen, Birmensdorf.
- Kuhn, N. 1973. Frequenzen von Trockenperioden und ihre ökologische Bedeutung. *Vierteljahrss. Nat.forsch. Ges. Zürich* 118: 257-298.
- LaMarche, V.C. 1978. Tree-ring evidence of past climatic variability. *Nature* 276: 334-338.

- 1 LeBlanc, D.C. & Foster, J.R. 1992. Predicting effects of global warming on growth and  
2 mortality of upland oak species in the midwestern United States - a physiologically  
3 based dendroecological approach. *Can. J. For. Res.* 22: 1739-1752.
- 4 Lebourgeois, F., Levy, G., Aussenac, G., Clerc, B. & Willm, F. 1998. Influence of soil drying  
5 on leaf water potential, photosynthesis, stomatal conductance and growth in two black  
6 pine varieties. *Ann. Sci. For.* 55: 287-299.
- 7 Lieutier, F., Yart, A., Ye, H., Sauvard, D. & Gallois, V. 2004. Variations in growth and  
8 virulence of *Leptographium wingfieldii* Morelet, a fungus associated with the bark  
9 beetle *Tomicus piniperda* L. *Ann. For. Sci.* 61: 45-53.
- 10 Martinez-Vilalta, J. & Pinol, J. 2002. Drought-induced mortality and hydraulic architecture in  
11 pine populations of the NE Iberian Peninsula. *For. Ecol. Manage.* 161: 247-256.
- 12 Martinez-Vilalta, J., Sala, A. & Pinol, J. 2004. The hydraulic architecture of Pinaceae - a  
13 review. *Plant Ecol.* 171: 3-13.
- 14 Menzel, A. & Fabian, P. 1999. Growing season extended in Europe. *Nature* 397: 659-659.
- 15 Meusel, H., Jäger, E.J. & Weinert, E. 1965. *Vergleichende Chorologie der*  
16 *zentraleuropäischen Flora. Text und Karten. Band 1.* VEB Fischer, Jena.
- 17 Misson, L., Antoine, N. & Joel, G. 2003a. Effects of different thinning intensities on drought  
18 response in Norway spruce (*Picea abies* (L.) Karst.). *For. Ecol. Manage.* 183: 47-60.
- 19 Misson, L., Vincke, C. & Devillez, F. 2003b. Frequency responses of radial growth series  
20 after different thinning intensities in Norway spruce (*Picea abies* (L.) Karst.) stands.  
21 *For. Ecol. Manage.* 177: 51-63.
- 22 Nardini, A. 2002. Relations between efficiency of water transport and duration of leaf growth  
23 in some deciduous and evergreen trees. *Trees-Struct. Funct.* 16: 417-422.
- 24 Nardini, A. & Pitt, F. 1999. Drought resistance of *Quercus pubescens* as a function of root  
25 hydraulic conductance, xylem embolism and hydraulic architecture. *New Phytol.* 143:  
26 485-493.
- 27 Oberhuber, W. & Kofler, W. 2000. Topographic influences on radial growth of Scots pine  
28 (*Pinus sylvestris* L.) at small spatial scales. *Plant Ecol.* 146: 231-240.
- 29 Oberhuber, W., Stumbock, M. & Kofler, W. 1998. Climate tree-growth relationships of Scots  
30 pine stands (*Pinus sylvestris* L.) exposed to soil dryness. *Trees-Struct. Funct.* 13: 19-  
31 27.
- 32 Ozenda, P. 1985. *La végétation de la chaîne alpine dans l'espace montagnard européen.*  
33 Masson, Paris.
- 34 Paine, T.D., Raffa, K.F. & Harrington, T.C. 1997. Interactions among scolytid bark beetles,  
35 their associated fungi, and live host conifers. *Annu. Rev. Entomol.* 42: 179-206.
- 36 Penuelas, J. & Boada, M. 2003. A global change-induced biome shift in the Montseny  
37 mountains (NE Spain). *Glob. Change Biol.* 9: 131-140.
- 38 Penuelas, J. & Filella, I. 2001. Phenology - Responses to a warming world. *Science* 294: 793-  
39 795.
- 40 Plumettaz Clot, A.-C. 1988. *Phyto-écologie des pinèdes valaisannes et contribution à la*  
41 *taxonomie du genre pinus.* Dissertation. Université de Lausanne.
- 42 Pouttu, A. & Dobbertin, M. 2000. Needle-retention and density patterns in *Pinus sylvestris* in  
43 the Rhone Valley of Switzerland: comparing results of the needle-trace method with  
44 visual defoliation assessments. *Can. J. For. Res.* 30: 1973-1982.
- 45 R Development Core Team. 2003. *R: a language and environment for statistical computing.*  
46 R Foundation for Statistical Computing, Vienna, Austria. <http://cran.r-project.org/>.
- 47 Rebetez, M. & Dobbertin, M. 2004. Climate change may already threaten Scots pine stands in  
48 the Swiss Alps. *Theor. Appl. Climatol.* 79: 1-9.

- 1 Rigling, A., Bräker, O.U., Schneiter, G. & Schweingruber, F. 2002. Intra-annual tree-ring  
2 parameters indicating differences in drought stress of *Pinus sylvestris* forests within  
3 the Erico-Pinion in the Valais (Switzerland). *Plant Ecol.* 163: 105-121.
- 4 Rigling, A., Brühlhart, H., Bräker, O.U., Forster, T. & Schweingruber, F.H. 2003. Effects of  
5 irrigation on diameter growth and vertical resin duct production in *Pinus sylvestris* L.  
6 on dry sites in the central Alps, Switzerland. *For. Ecol. Manage.* 175: 285-296.
- 7 Rigling, A. & Cherubini, P. 1999. Wieso sterben die Waldföhren im "Telwald" bei Visp? Eine  
8 Zusammenfassung bisheriger Studien und eine dendroökologische Untersuchung.  
9 *Schweiz. Z. Forstwes.* 150: 113-131.
- 10 Rigling, A., Dobbertin, M., Bürgi, M., Feldmeyer-Christe, E., Gimmi, U., Ginzler, C., Graf,  
11 U., Mayer, P., Zweifel, R. & Wohlgemuth, T. 2006a. Baumartenwechsel in den  
12 Walliser Föhrenwäldern. *Forum für Wissen* 2006: 23-33.
- 13 Rigling, A., Dobbertin, M., Gimmi, U., Graf Pannatier, E., Gugerli, F., Heiniger, U.,  
14 Polomski, J., Rebetez, M., Rigling, D., Weber, P., Wermelinger, B. & Wohlgemuth, T.  
15 2006b. *Verdrängen Flaumeichen die Walliser Waldföhren? Merkblatt für die Praxis*  
16 *41*. Eidg. Forschungsanstalt WSL Birmensdorf.
- 17 Rigling, A., Waldner, P.O., Forster, T., Bräker, O.U. & Pouttu, A. 2001. Ecological  
18 interpretation of tree-ring width and intraannual density fluctuations in *Pinus sylvestris*  
19 on dry sites in the central Alps and Siberia. *Can. J. For. Res.* 31: 18-31.
- 20 Rigling, A., Weber, P., Cherubini, P. & Dobbertin, M. 2004. Bestandesdynamik zentralalpiner  
21 Waldföhrenwälder aufgezeigt anhand dendroökologischer Fallstudien aus dem Wallis,  
22 Schweiz. *Schweiz. Z. Forstwes.* 155: 178-190.
- 23 Rinn, F. 1996. *TSAP - Reference manual. Version 3.5*. Rinntech, Heidelberg, Germany.
- 24 Sabate, S., Gracia, C.A. & Sanchez, A. 2002. Likely effects of climate change on growth of  
25 *Quercus ilex*, *Pinus halepensis*, *Pinus pinaster*, *Pinus sylvestris* and *Fagus sylvatica*  
26 forests in the Mediterranean region. *For. Ecol. Manage.* 162: 23-37.
- 27 Schmid, E. 1936. Die Reliktföhrenwälder der Alpen. *Beiträge zur geobotanischen*  
28 *Landesaufnahme der Schweiz* 21.
- 29 Schweingruber, F. 1990. Identification, presentation and interpretation of event years and  
30 pointer years in dendrochronology. *Dendrochr.* 8: 9-38.
- 31 Schweingruber, F.H. & Briffa, K.R. 1996. Tree-ring density networks for climate  
32 reconstructions. In: Jones, P.D., Bradley, R.S. and Jouzel, J. (eds). *Climatic Variations*  
33 *and Forcing Mechanisms of the Last 2000 Years*. NATO ASI, pp. 43-66.
- 34 Serre-Bachet, F. 1982. Analyse dendroclimatologique comparée de quatre espèces de pin et  
35 du chêne pubescent dans la région de la Gardiole près Rians (Var, France). *Ecol.*  
36 *mediterr.* 8: 167-183.
- 37 Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in*  
38 *biological research*, Third edition. W. H. Freeman and Company, New York.
- 39 Solberg, B.O., Hofgaard, A. & Hytteborn, H. 2002. Shifts in radial growth responses of  
40 coastal *Picea abies* induced by climatic change during the 20th century, central  
41 Norway. *Ecoscience* 9: 79-88.
- 42 Takahashi, K., Azuma, H. & Yasue, K. 2003. Effects of climate on the radial growth of tree  
43 species in the upper and lower distribution limits of an altitudinal ecotone on Mount  
44 Norikura, central Japan. *Ecol. Res.* 18: 549-558.
- 45 Tardif, J. & Stevenson, D. 2001. Radial growth-climate association of *Thuja occidentalis* L. at  
46 the northwestern limit of its distribution, Manitoba, Canada. *Dendrochr.* 19: 179-187.
- 47 Teskey, R.O. & Hinckley, T.M. 1981. Influence of temperature and water potential on root  
48 growth of white oak. *Physiol. Plant.* 52: 363-369.



- 1 Tessier, L. 1986. Approche dendroclimatologique de l'écologie de *Pinus sylvestris* L. et  
2 *Quercus pubescens* Willd. dans le Sud-Est de la France. *Acta Oecol.-Oecol. Plant.* 7:  
3 339-355.
- 4 Tessier, L. 1989. Spatio-temporal analysis of climate tree-ring relationships. *New Phytol.* 111:  
5 517-529.
- 6 Tessier, L., Nola, P. & Serre-Bachet, F. 1994. Deciduous *Quercus* in the Mediterranean  
7 region - Tree-ring/Climate relationships. *New Phytol.* 126: 355-367.
- 8 Theurillat, J.P. & Guisan, A. 2001. Potential impact of climate change on vegetation in the  
9 European Alps: A review. *Clim. Change* 50: 77-109.
- 10 Thomas, F.M., Blank, R. & Hartmann, G. 2002. Abiotic and biotic factors and their  
11 interactions as causes of oak decline in Central Europe. *Forest Pathol.* 32: 277-307.
- 12 Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geogr.*  
13 *Rev.* 38: 55-94.
- 14 Timbal, J. & Aussenac, G. 1996. An overview of ecology and silviculture of indigenous oaks  
15 in France. *Ann. Sci. For.* 53: 649-661.
- 16 Tyree, M.T. & Cochard, H. 1996. Summer and winter embolism in oak: Impact on water  
17 relations. *Ann. Sci. For.* 53: 173-180.
- 18 Vertui, F. & Tagliaferro, F. 1998. Scots pine (*Pinus sylvestris* L.) die-back by unknown  
19 causes in the Aosta Valley, Italy. *Chemosphere* 36: 1061-1065.
- 20 von Lürthe, A. 1991. Dendroökologische Untersuchungen an Kiefern und Eichen in den  
21 stadtnahen Berliner Forsten. *S.reihe Fachbereich Landsch.entw. TU Berlin* 77.
- 22 Walther, G.R. 2002. Weakening of climatic constraints with global warming and its  
23 consequences for evergreen broad-leaved species. *Folia Geobot.* 37: 129-139.
- 24 Wigley, T.M.L., Briffa, K.R. & Jones, P.D. 1984. On the average value of correlated time-  
25 series, with applications in dendroclimatology and hydrometeorology. *J. Clim. Appl.*  
26 *Meteorol.* 23: 201-213.
- 27 Wirtz, M. 2002. Die Reaktion im Jahrringmuster von Kiefern (*Pinus sylvestris*) auf eine  
28 Grundwasserabsenkung im Naturschutzgebiet Lüneburger Heide. *Stuttgarter*  
29 *Geograph. Studien* 133: 73-82.
- 30 WSL. 2001. *Schweizerisches Landesforstinventar LFI. Spezialauswertung der Erhebung*  
31 *1993-1995 vom 20. August 2001.* Eidgenössische Forschungsanstalt für Wald, Schnee  
32 und Landschaft WSL, Birmensdorf.
- 33 Zweifel, R., Zimmermann, L., Zeugin, F. & Newbery, D.M. 2006. Intra-annual radial growth  
34 and water relations of trees - implications towards a growth mechanism. *J. Exp. Bot.*  
35 57: 1445-1459.
- 36  
37  
38

Table 1. Site characteristics of the 15 sampling plots. T2003 = measured mean temperature for April-October 2003. AWC = available water capacity of soils. Age, dbh (diameter at breast height), height: mean of the 10 tallest pine/oak trees.

Gradient	Plot acronym	Aspect	Slope [%]	Elevation [m a.s.l.]	T2003 [°C]	Soil type (FAO)	AWC [mm]	Age [yr] (pine/oak)	Dbh [cm] (pine/oak)	Height [m] (pine/oak)
Eschwald	esa	e	100	710	15.7	calcaric regosol	46	77.8 / 91.5	29.3 / 23.6	15.3 / 14.5
	esb	e	102	865	15.4	dystic regosol	36	84.1 / 62.6	22.3 / 18.0	9.7 / 12.9
	esc	e	162	960	15.5	dystic regosol	37	67.2 / 59.6	19.5 / 16.1	8.9 / 8.1
Eggerberg	ega	sw	125	950	15.8	dystic regosol	41	85.7 / 60.6	29.5 / 23.0	10.7 / 10.0
	egb	s	93	1075	14.9	dystic cambisol	69	65.3 / 42.4	25.8 / 16.4	11.3 / 9.5
	egc	s	93	1200	13.9	dystic cambisol	83	78.4 / 42.9	29.0 / 16.4	10.5 / 8.1
Salgesch	saa	s	105	825	15.3	rendzic leptosol	61	105.9 / 75.1	21.0 / 12.9	7.6 / 9.5
	sab	s	132	980	15.2	rendzic leptosol	97	110.6 / 109.4	23.0 / 15.6	8.9 / 10.5
	sac	s	117	1120	14.5	rendzic leptosol	75	63.3 / 79.6	20.8 / 14.2	8.8 / 7.4
Lens	lea	s	117	695	16.4	rendzic leptosol	91	78.0 / 103.5	18.45 / 15.3	9.6 / 11.1
	leb	sse	129	935	15.8	rendzic leptosol	36	35.4 / 39.7	22.4 / 14.5	9.6 / 10.1
	lec	se	140	1150	14.6	rendzic leptosol	73	119.2 / 68.5	25.6 / 12.5	10.1 / 6.7
Bramois	bra	n	97	590	16.4	rendzic leptosol	71	41.7 / 49.3	18.0 / 15.5	13.4 / 16.8
	brb	w	84	735	15.9	calcaric cambisol	47	95.2 / 89.0	25.1 / 26.7	13.7 / 13.2
	brc	w	112	930	14.8	rendzic leptosol	114	107.5 / 99.1	23.3 / 17.7	12.6 / 10.9

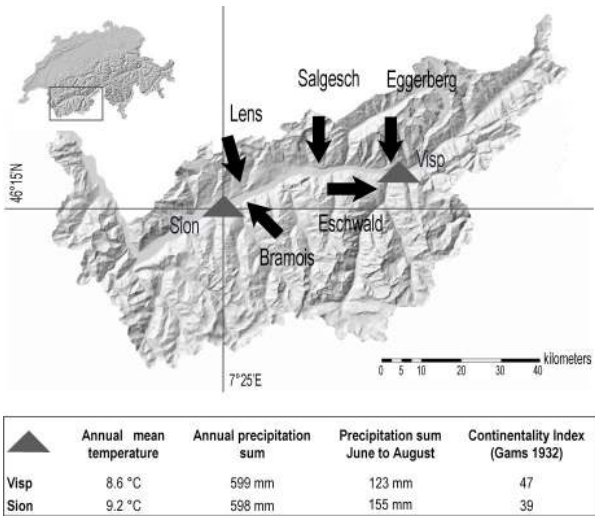


Fig. 1. Map of the inner-Alpine dry valley Valais (inset shows outline of Switzerland; © 2005 BFS GEOSTAT/swisstopo). 5 altitudinal gradients were chosen (black arrows) consisting of 3 single plots each. Climate stations (grey triangles) are situated at Visp (640 m a.s.l.) and Sion (482 m a.s.l.). Listed climate data for Visp and Sion belong to the norm period 1961-1990.

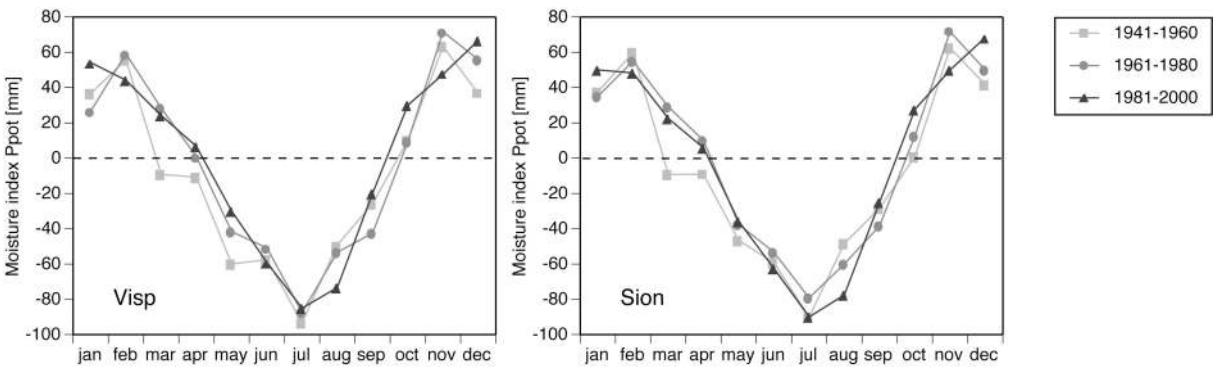


Fig. 2. Mean intra-annual course of the drought index DRI (= Precipitation - Potential Evapotranspiration, Thornthwaite 1948) for three periods in the 20<sup>th</sup> century. Both moisture regimes show a dry period from May to September.

Table 2. Characteristics of tree-ring chronologies: N of cores, N of trees, maximum, mean and minimum age at coring height, mean radial growth ( $G_{\text{mean}}$ ) and its standard deviation ( $G_{\text{std}}$ ), cross-correlation between single series (mean rbar), mean sensitivity of single series (mean S) and expressed population signal (eps) of the residual chronologies of all 15 plots for oak and pine.

chronology	N cores	N trees	Max. age	Mean age	Min. age	$G_{\text{mean}}$ [mm]	$G_{\text{std}}$ [mm]	mean rbar	mean S	eps
esa.oak	53	27	105	78	43	0.92	0.53	0.36	0.33	0.97
esa.pine	39	23	75	61	45	0.98	0.57	0.27	0.31	0.93
esb.oak	46	26	85	47	33	1.07	0.50	0.42	0.31	0.96
esb.pine	26	14	94	55	36	1.15	0.67	0.50	0.38	0.95
esc.oak	36	18	131	49	30	0.94	0.52	0.42	0.37	0.95
esc.pine	20	11	93	56	32	1.26	0.71	0.46	0.33	0.93
ega.oak	22	11	71	52	35	1.69	0.82	0.37	0.34	0.91
ega.pine	20	10	136	76	51	1.56	0.86	0.36	0.32	0.91
egb.oak	42	26	47	37	31	1.45	0.72	0.21	0.33	-
egb.pine	22	11	135	57	34	1.78	0.87	0.29	0.29	0.87
egc.oak	11	6	51	38	30	1.11	0.53	0.28	0.36	0.78
egc.pine	18	11	109	75	42	1.63	0.89	0.27	0.29	0.86
saa.oak	29	17	81	59	17	0.63	0.29	0.45	0.30	0.96
saa.pine	19	10	157	83	41	1.00	0.55	0.40	0.34	0.92
sab.oak	38	19	112	88	53	0.56	0.31	0.41	0.32	0.96
sab.pine	23	14	196	97	59	0.67	0.44	0.34	0.33	0.92
sac.oak	24	13	103	70	50	0.74	0.41	0.45	0.31	0.95
sac.pine	16	8	104	58	36	1.26	0.63	0.51	0.33	0.92
lea.oak	20	12	187	110	26	1.26	0.63	0.48	0.30	0.94
lea.pine	18	9	89	64	40	1.17	0.77	0.45	0.36	0.93
leb.oak	20	10	39	35	28	1.46	0.72	0.59	0.37	-
leb.pine	24	12	34	31	26	2.77	1.88	0.51	0.43	-
lec.oak	16	8	129	54	27	1.06	0.46	0.39	0.35	0.86
lec.pine	18	9	187	107	19	1.34	0.59	0.46	0.27	0.93
bra.oak	25	13	48	42	36	1.48	0.62	0.45	0.31	-
bra.pine	26	13	38	35	29	1.91	0.93	0.49	0.39	-
brb.oak	16	10	108	84	57	1.42	0.69	0.61	0.38	0.96
brb.pine	20	10	102	83	55	1.22	0.68	0.50	0.33	0.95
brc.oak	19	10	106	88	48	0.78	0.46	0.36	0.28	0.91
brc.pine	20	10	109	83	52	1.04	0.54	0.43	0.28	0.94

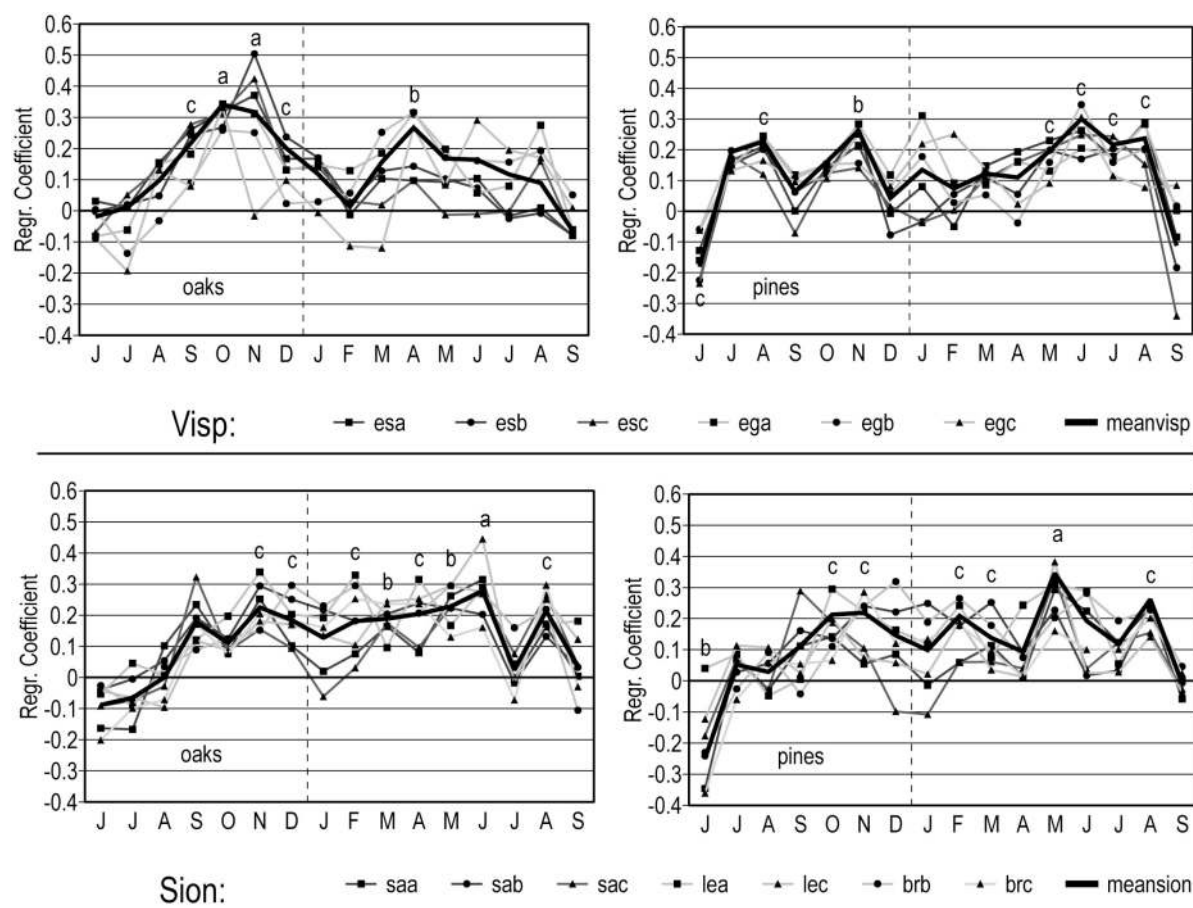


Fig. 3. Response function coefficients for 13 oak (left) and 13 pine (right) chronologies from June of the previous year to September of the current year. The response function was calculated with yearly tree-ring width (residual chronologies) as the dependent and monthly drought indices DRI as the independent variables for the period 1950-2001. Regional responses (meanvisp, meansion) were calculated from the regional average chronologies. Significances of the regional responses are given: a =  $p < 0.001$ ; b =  $p < 0.01$ ; c =  $p < 0.05$ .

Table 3. Significance of responses to the drought index DRI, for 13 plots, a) for oak, b) for pine and the overall explained variance by climate. Chronologies are sorted according to the available water capacity of the soil on the plot (AWC).

a) *Quercus pubescens*

AWC	chronology	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	explained variance
36	esb				⊕	⊕	⊕⊕⊕	⊕	⊕									0.60
37	esc				⊕⊕	⊕⊕	⊕⊕⊕											0.55
41	ega				*	⊕⊕⊕	⊕⊕⊕		*		*	⊕⊕⊕	⊕⊕			⊕		0.68
46	esa				⊕	⊕⊕	⊕⊕⊕		*									0.51
47	brb							⊕⊕	⊕	⊕⊕	⊕⊕	⊕	⊕⊕	⊕⊕	*	⊕		0.66
61	saa				⊕		⊕						⊕	⊕⊕				0.53
69	egb					⊕	⊕				⊕⊕	⊕				*		0.51
73	lec						*				⊕⊕	⊕	⊕⊕	⊕⊕⊕		⊕		0.65
75	sac				⊕⊕								*	⊕		⊕		0.46
83	egc					⊕						⊕		⊕				0.44
91	lea						⊕	*		⊕⊕⊕		⊕⊕		⊕⊕			*	0.61
97	sab				*		⊕	⊕		*	⊕	⊕	⊕	⊕				0.53
114	brc	<					*			⊕	⊕⊕	⊕				⊕⊕		0.53

b) *Pinus silvestris*

AWC	chronology	J	J	A	S	O	N	D	J	F	M	A	M	J	J	A	S	explained variance
36	esb	∠ ∠		⊕			⊕						⊕		⊕		<	0.52
37	esc	∠ ∠										*	*	⊕	⊕		∠ ∠ ∠	0.59
41	ega	∠		⊕⊕		*	⊕⊕		⊕⊕⊕			*		*	⊕	⊕⊕		0.67
46	esa						*						⊕	*		⊕		0.54
47	brb	∠					*	⊕⊕		⊕⊕	⊕		*	⊕⊕	*	*		0.63
61	saa	∠ ∠ ∠											⊕⊕	⊕		⊕		0.51
69	egb		*	⊕					*					⊕	*	*		0.54
73	lec					*							⊕⊕					0.40
75	sac				⊕	*							⊕⊕					0.39
83	egc						⊕⊕		*	⊕⊕				⊕				0.50
91	lea					⊕				⊕		⊕	⊕	⊕				0.55
97	sab	∠					⊕	⊕	⊕	*	⊕⊕		⊕			⊕⊕		0.61
114	brc	∠ ∠					⊕			*						*		0.44

Level	significantly positive	oak	pine	significantly negative	oak	pine
0.1 %	⊕⊕⊕	8	1	∠ ∠ ∠	-	2
1 %	⊕⊕	18	13	∠ ∠	-	3
5 %	⊕	31	26	∠	-	3
10 %	*	13	20	<	1	1
≤ 10 %		70	60		1	9

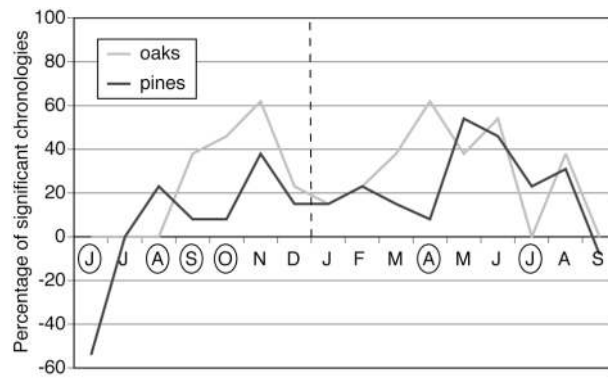


Fig. 4. Summarised growth response to the monthly drought index DRI. Percentage of chronologies with a significant ( $p < 0.05$ ) negative or positive response of pines and oaks from June<sub>(i-1)</sub> to September<sub>(i)</sub> are shown. 100% = 13 chronologies. Circles indicate significant differences in the responses between oak and pine ( $p < 0.05$ ).



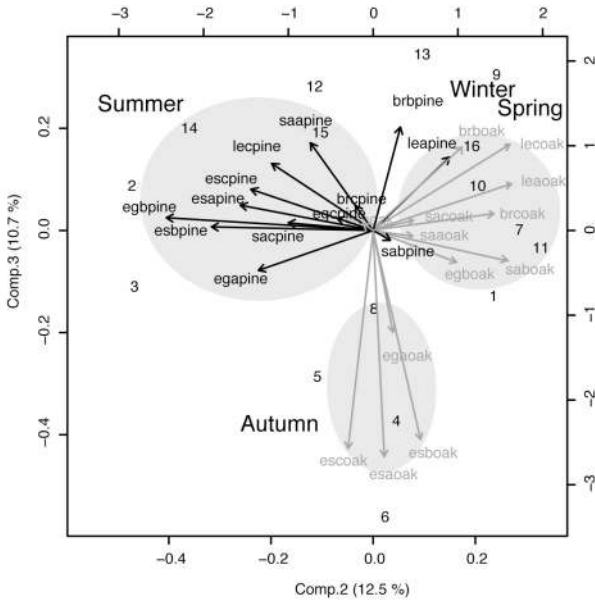
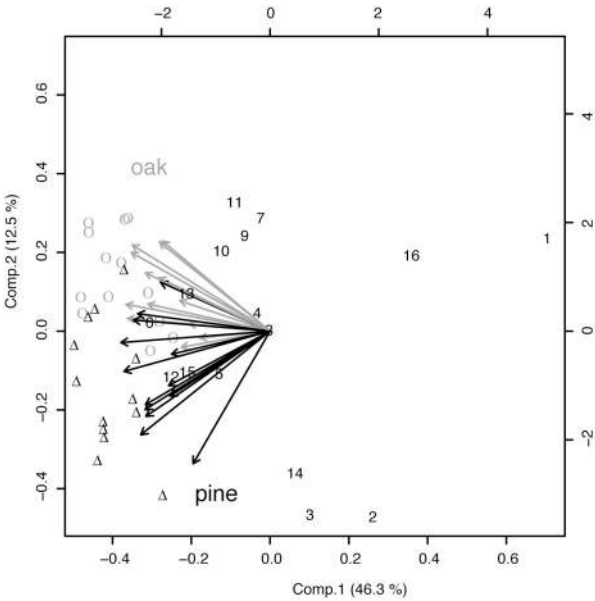


Fig. 5. PCA with response ratios to drought index DRI (first and second component axes). Numbers 1-16 stand for the months from June<sub>(i-1)</sub>=1 to September<sub>(i)</sub>=16; January<sub>(i)</sub>=8. O and grey arrows: oaks; Δ and black arrows: pine.

Fig. 6. PCA with response ratios to drought index DRI (second and third component axes). Numbers 1-16 stand for the months from June<sub>(i-1)</sub>=1 to September<sub>(i)</sub>=16; January<sub>(i)</sub>=8. Grey arrows: oaks; black arrows: pine.

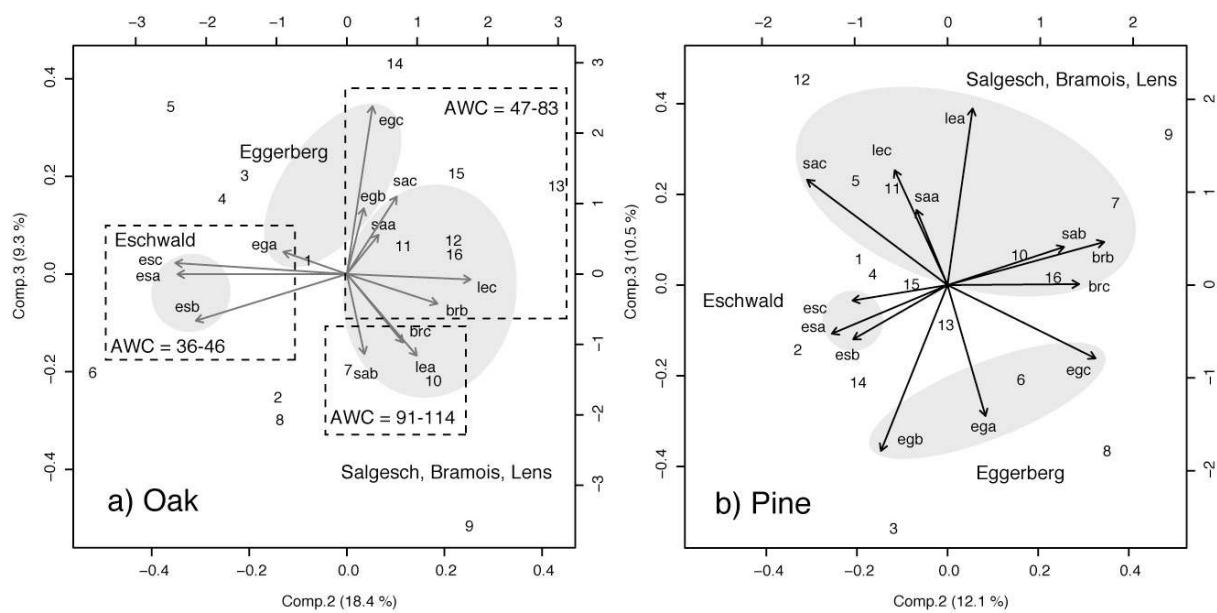


Fig. 7. PCA with response ratios to drought index DRI for oak (Fig. 7a) and pine (Fig. 7b) (second and third component axes). Eschwald and Eggerberg belong to the Visp region, Salgesch, Lens and Bramois belong to the Sion region. Numbers 1-16 stand for the months from June<sub>(i-1)</sub>=1 to September<sub>(i)</sub>=16; January<sub>(i)</sub>=8. AWC = available water capacity of the soil.

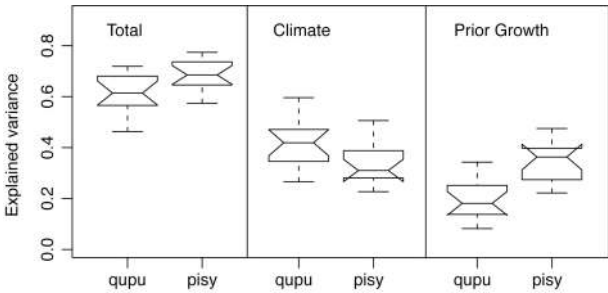


Fig. 8. Notched boxplot of explained variance in the response functions of oak and pine. If the notches of two plots do not overlap, the medians are significantly different ( $p < 0.05$ ). Response functions of STD chronologies, including the STD chronologies up to a lag of  $-3$  years as independent variables.  $N=15$  for each oak and pine.