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# Species-specific stomatal response of trees to drought – a link to vegetation dynamics?

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## Abstract

**Question:** Is stomatal regulation specific for climate and tree species, and does it reveal species-specific responses to drought? Is there a link to vegetation dynamics?

**Location:** Dry inner alpine valley, Switzerland

**Methods:** Stomatal aperture ( $\theta_E$ ) of *Pinus sylvestris*, *Quercus pubescens*, *Juniperus communis* and *Picea abies* were continuously estimated by the ratio of measured branch sap flow rates to potential transpiration rates (adapted Penman-Monteith single leaf approach) at 10-min intervals over four seasons.

**Results:**  $\theta_E$  proved to be specific for climate and species and revealed distinctly different drought responses: *Pinus* stomata close disproportionately more than neighbouring species under dry conditions, but has a higher  $\theta_E$  than the other species when weather was relatively wet and cool. *Quercus* keeps stomata more open under drought stress but has a lower  $\theta_E$  under humid conditions. *Juniperus* was most drought-tolerant, whereas *Picea* stomata close almost completely during summer.

**Conclusions:** The distinct microclimatic preferences of the four tree species in terms of  $\theta_E$  strongly suggest that climate (change) is altering tree physiological performances and thus species-specific competitiveness. *Picea* and *Pinus* currently live at the physiological limit of their ability to withstand increasing temperature and drought intensities at the sites investigated, whereas *Quercus* and *Juniperus* perform distinctly better. This corresponds, at least partially, with regional vegetation dynamics: *Pinus* has strongly declined, whereas *Quercus* has significantly increased in abundance in the past 30 years. We conclude that  $\theta_E$  provides an indication of a species' ability to cope with current and predicted climate.

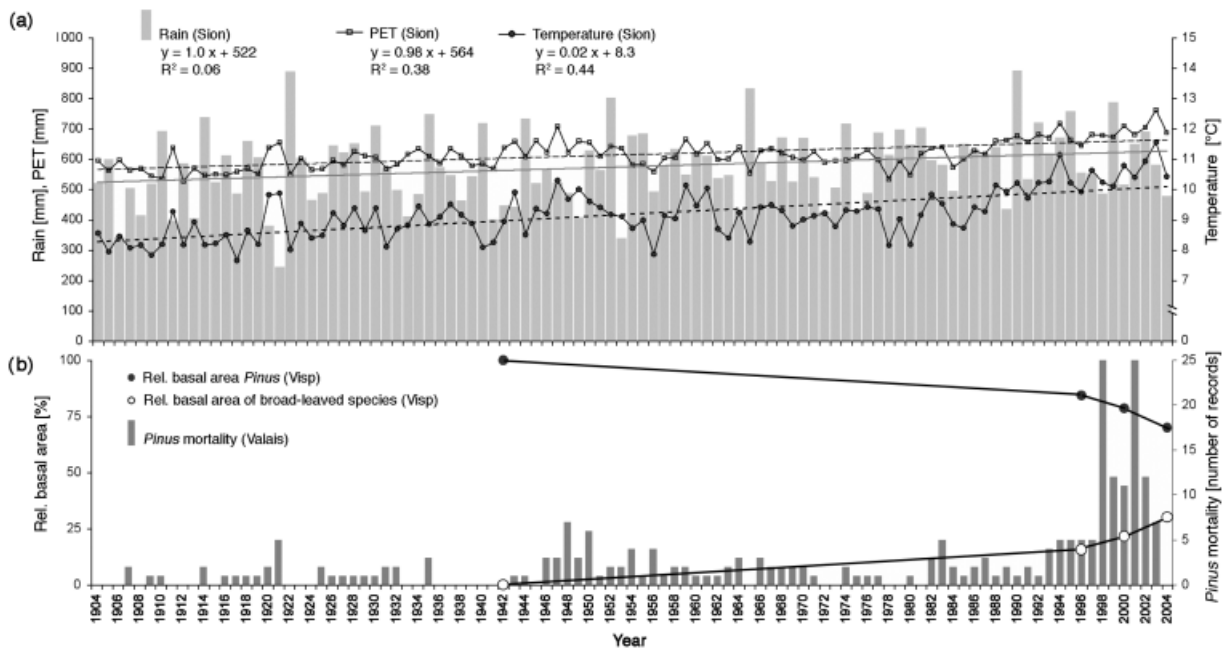
**Keywords:** climate change; species competition; stomatal regulation; tree water relations; vegetation dynamics.

**Nomenclature:** Aeschimann et al. (2004).

## Introduction

Shifts in the abundance of plant species to higher altitudes (Peñuelas & Boada 2003; Dobbertin et al. 2005a; Walther et al. 2005; Gehrig-Fasel et al. 2007) and towards the poles have been reported for past and current climate warming (Walther et al. 2002; Rebetez & Dobbertin 2004; IPCC 2007; Vittoz et al. 2008). However, studies of the possible species-specific physiological mechanisms underlying such vegetation dynamics are still rare (Zweifel et al. 2007; McDowell et al. 2008). Such mechanisms are of interest because they could provide causal links between climate change and the performance of trees in terms of their ability to benefit from current or predicted conditions. To identify possible mechanisms, we focused on Valais, Switzerland, which is a dry, inner alpine valley. In such valleys unusually distinct vegetation dynamics have been observed over the past 30 years in Austria (Oberhuber 2001), Italy (Vertui & Tagliaferro 1996) and Switzerland (Dobbertin et al. 2005b; Bigler et al. 2006), where the mortality of Scots pine (*Pinus sylvestris* L.) has dramatically increased. The co-occurring broadleaf tree species, particularly pubescent oak (*Quercus pubescens*), have benefited from this situation (Fig. 1). At the same time, a significant increase in mean annual temperature and potential evaporation has occurred, while no significant trend has been found for precipitation in recent decades (Beniston 2004).

Such a shift in species abundance may have been driven by changing climate, as suggested for other regions (Hättenschwiler & Körner 1995; Mueller et al. 2005; Hamann & Wang 2006; Kullman 2007). Several other factors, however, have changed during the same period in this valley: wood pasturing of goats and sheep is now prohibited and no longer plays a role in regeneration; forest litter collection stopped a few decades ago (Gimmi & Bürgi 2007); and lower prices for timber have led



**Fig. 1.** Course of climate conditions and vegetation dynamics in Valais, Switzerland over the past 100 years. **(a)** Temperature<sup>1</sup>, potential evapotranspiration<sup>1,2</sup> ( $PET$ ), and precipitation<sup>1</sup> ( $Rain$ ) have been increasing (linear regressions), however only temperature and  $PET$  show a significant trend (Bigler et al. 2006). **(b)** The abundance<sup>3</sup> of *Pinus sylvestris*, quantified as relative basal area, has decreased, whereas the abundance of broadleaf trees, e.g. *Quercus pubescens*, has markedly increased during the last 20 years (left scale). This corresponds to the documented mortality rates<sup>4</sup> of *Pinus sylvestris* for the entire valley (right scale). <sup>1</sup>Data from the meteo station at Sion (MeteoSwiss). <sup>2</sup> $PET$  calculated according to (Thornthwaite 1948). <sup>3</sup>Data from the Swiss long-term forest ecosystem research plot Visp (Bigler et al. 2006; Dobbertin & Rigling 2006). <sup>4</sup>Historical records on the decline of *Pinus sylvestris* in Valais (Dobbertin et al. 2007).

to changes in harvesting regimes of the forest service. There have also been indirect impacts associated with global warming, such as better breeding conditions for insects (Bale et al. 2003; Wermelinger et al. 2008), increased growth of parasites and hemi-parasites, e.g. mistletoe (Jeffrey & Jeffrey 1996; Dobbertin et al. 2005a), and additional inputs of nitrogen in rain (Rihm & Kurz 2001). Moreover, air pollution ( $NO_x$ , fluorine, etc.) has steadily decreased since the 1980s (Rogora et al. 2006). Any of these factors may have affected development of the species composition and contributed to the observed change in species abundances. This means an indirect approach is needed to determine whether changing climate has influenced the changes in species abundances.

From a system analytic point of view, a change in species abundance can only be attributed to changing climate if the associated species have clearly distinguishable physiological responses to the same climatic environment. A potential physiological process that can be measured under field conditions and reflects how well a plant benefits from the predominant climatic environment is sto-

mat regulation (Hetherington & Woodward 2003). Stomata respond to a combination of climatic and physiological conditions (Leuning et al. 2003) and play a key role in controlling the metabolic activity of a tree. There is strong evidence from several field investigations that stomata of different tree species respond species-specifically to microclimate (Larcher 2003; Mediavilla & Escudero 2004; Zweifel et al. 2007). Open stomata allow for potentially high rates of gas exchange. Closed stomata represent a limiting situation because they not only reduce transpiration, but also reduce photosynthesis and thus total tree metabolism (Larcher 2003), especially at dry sites (Hsiao & Acevedo 1974; Rambal et al. 2003). Stomatal aperture ( $\theta_E$ ) in combination with light is an indirect measure of photosynthesis and therefore for the potential C income of a tree (Farquhar & Sharkey 1982). In other words,  $\theta_E$  reflects the climate-related physiological performance of a tree as a percentage, and can be compared across species. The average  $\theta_E$  of trees can be estimated from the ratio between measured sap flow and estimated potential transpiration of branches (Zweifel et al. 2002). This ratio is taken as a

measure of down-regulation of transpiration and thus the degree of stomatal opening. An advantage of measuring  $\theta_E$  instead of stomatal conductance of leaves is that all necessary factors such as sap flow rates and microclimatic conditions can be automatically and continually recorded at a high temporal resolution.

In this study, we compared stomatal regulation patterns of field-grown mature trees at a 10-min resolution to microclimatic conditions in air and soil over four seasons (May–September), including the exceptionally hot and dry summer of 2003 (Beniston 2004; Schär et al. 2004). We tested (i) whether the four co-occurring tree species showed distinguishable stomatal responses to certain microclimatic conditions, (ii) whether the resulting physiological species profiles reveal different strategies for coping with drought, and (iii) then compared our physiological results with reported changes in climate and species composition for the region. Of particular interest was the question of whether the observed decline in pine in Valais, Switzerland, can at least partially be attributed to a changing climate.

## Materials and Methods

### Study sites and trees

Central Valais, Switzerland, is an inner alpine valley characterized by a dry climate mainly caused by inner valley shielding that repels wet air masses from the west and south. The two study sites, Salgesch (46°19'27"N, 7°34'40' E, 975 m a.s.l.) and Jeizinen (46°19'21"N, 7°43'30" E, 1270 m a.s.l), have similar oak-pine vegetation, which primarily differs in tree height, soil depth and crown cover at the two sites (Fig. 2). At Salgesch, the vegetation patches are shrub-like and surrounded by grass and bare rock, with tree heights < 5 m, whereas at Jeizinen the same species grow as larger trees (5–15 m) forming a closed canopy. Details of tree individuals and number of individuals per species investigated are listed in Table 1. Soil at Salgesch is shallow, with a maximum depth of 0.1–0.3 m, whereas the soil at Jeizinen reaches depths of 0.5–1.3 m (rendzic leptosol on solid rock limestone).

The two sites are 11 km apart and both located on a south-exposed slope (25°–30°). Pubescent oak



**Fig. 2.** The two south-exposed sites investigated at Salgesch (left), 975 m a.s.l., and Jeizinen, 1270 m a.s.l., in Valais, a dry inner alpine valley of Switzerland. Both sites are dominated by *Pinus sylvestris* and *Quercus pubescens*.

**Table 1.** Size characteristics of the trees investigated at Salgesch and Jeizinen.

Species	Site	Number of trees	Range of tree heights (m)	Range of stem diameters (cm)
<i>Pinus sylvestris</i>	Salgesch	2	3.5–5.0	11.9–23.2
	Jeizinen	3	8–15.0	27.3–53.2
<i>Quercus pubescens</i>	Salgesch	6	3.5–4.0	7.2–9.5
	Jeizinen	5	5.0–12.0	12.9–25.3
<i>Juniperus communis</i>	Salgesch	3	0.8–1.4	1.8–2.2
<i>Picea abies</i>	Jeizinen	2	5.5–17.0	13.0–38.5

**Table 2.** Mean daytime values (06:00-20:00 h) of microclimatic factors at Salgesch (Sa) and Jeizinen (Je), Switzerland: temperature ( $T$ ), solar radiation ( $Rad$ ), vapour pressure deficit ( $VPD$ ), soil water potential ( $\Psi_{Soil}$ ) (seasonal minimum in brackets) and total precipitation ( $Rain$ ) (24 h) over the vegetation period (1 May-30 September).

	$T$ (°C)		$Rad$ (W m <sup>-2</sup> )		$VPD$ (kPa)		$\Psi_{Soil}$ (kPa)		$Rain$ (mm)	
	Sa	Je	Sa	Je	Sa	Je	Sa	Je	Sa	Je
2001	18.2	–	402	–	0.86	–	–74 (–167)	–	289	–
2002	18.6	–	376	–	0.83	–	–77 (–283)	–	456	–
2003	22.4	19.6	409	399	1.38	1.09	–188 (–448)	–138 (–451)	228	183
2004	19.5	16.9	381	386	1.06	0.83	–135 (–324)	–114 (–327)	233	170

(*Quercus pubescens* Willd.) and Scots pine (*Pinus sylvestris* L.) are the most abundant tree species, and juniper (*Juniperus communis* L. and *J. sabina* L.) the most abundant woody shrub in the vegetation of both sites. Norway spruce (*Picea abies* L. Karst.) only grows at Jeizinen. Tree age was measured as between 70 and 110 years for *Quercus* and between 100 and 150 years for *Pinus* at Salgesch. At Jeizinen, dendrochronological measurements of selected trees showed that mature *Quercus* and *Pinus* there were not only larger but also older than at Salgesch (between 100 and 250 years). Continuous climate and vegetation data were analysed from 1 May to 30 September in 2001-2004 at Salgesch and in 2003-2004 at Jeizinen (Table 2).

#### Meteorological data

Meteorological data were collected with solar-powered logging and steering systems (CR10X, Campbell, UK). Details of the sensor types and installation can be found in Zweifel et al. (2006). For the analyses, mean daytime (06:00-20:00 h) values for the different climate factors were used, with the exception of precipitation, which was summed over 24 h. In addition to measurements at the sites, climate data from the nearby (about 20 km away) national meteorological station at Sion (MeteoSwiss) were used to analyse the climate history of the past 100 years.

#### Stomatal aperture

The average stomatal aperture ( $\theta_E$ ) of individual north- and south-exposed branches was estimated from continuous measurements of branch sap flow ( $F_{Transp}$ ) (SGB15-35, Dynamax, USA), and computed maximum transpiration values ( $F_{Pot}$ ) from the microclimatic conditions and branch-specific geometric properties.  $\theta_E$  is the ratio between  $F_{Transp}$  and  $F_{Pot}$ . The model for  $F_{Pot}$  is based on an adapted single leaf model (Penman 1948; Monteith 1965) that takes the boundary layer conditions of

individual branches into account, and calculates maximum transpiration rates for fully open stomata.  $\theta_E$  does not account for differences between stomatal patchiness and heterogeneously more open or closed stomata, but is rather an integrated mean value for the stomatal aperture of a tree species. The parameterization procedure and further details can be found in Zweifel et al. (2002). For the analyses, mean daytime (06:00-20:00 h) values of  $\theta_E$  were used. The 10-min values of the individual twigs were averaged per species.

#### Selection of days

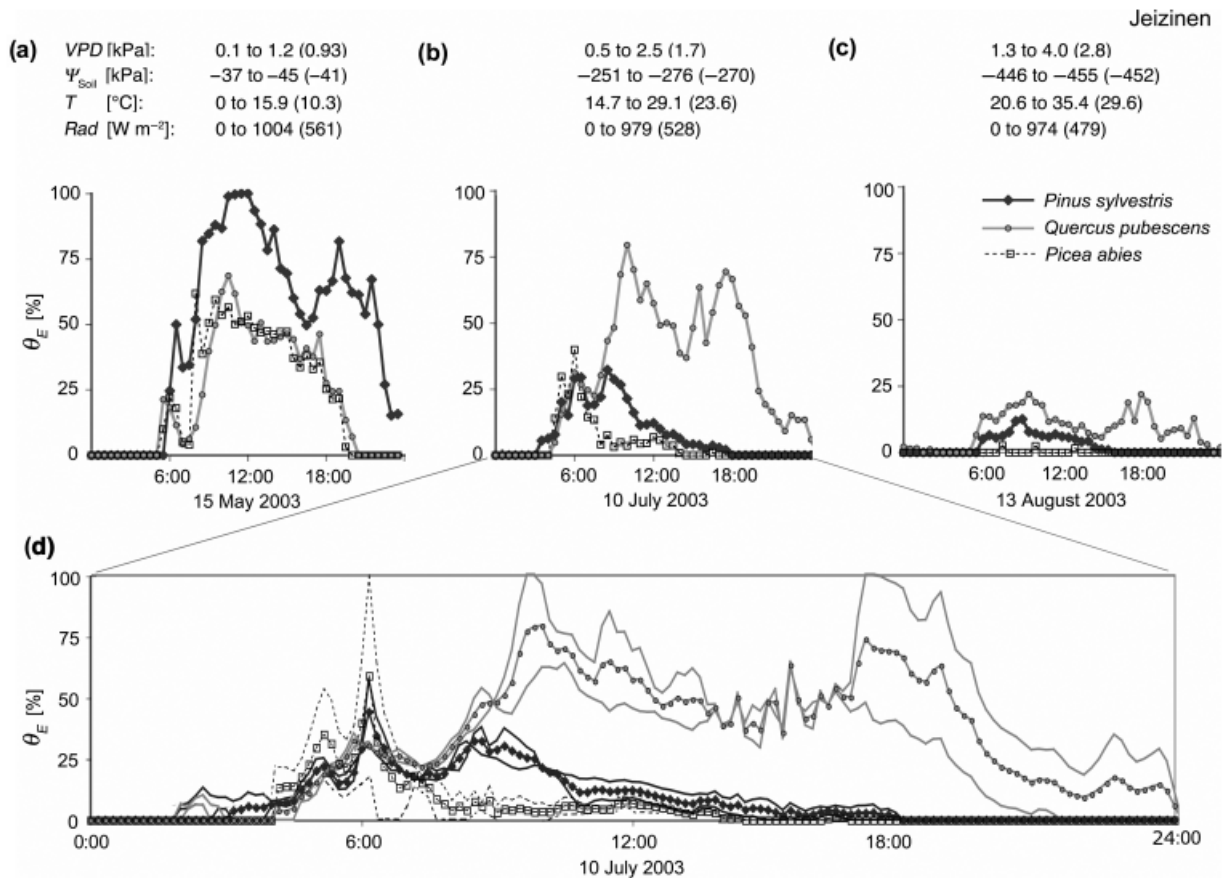
The 20% most extreme days with the most positive or negative deviations from average  $\theta_E$  of all co-occurring species were selected as out-performance days (*out*) or underperformance days (*under*) for each species. The mathematical procedure for this selection is described in App. A.

## Results

### Species-specific stomatal regulation

In general, stomata of the four tree species at these dry sites were most open in relatively cool weather conditions with moderately humid soil, and closed when climatic conditions became hotter and drier. Besides this overall trend in  $\theta_E$ , there were distinct climate-related differences between the species investigated on both a daily (Fig. 3) and a seasonal time scale (Fig. 4).

On a daily time scale, the course of  $\theta_E$  of all species increased at sunrise and showed species-specific variations during the day (Fig. 3). On a relatively wet day,  $\theta_E$  of *Pinus* was usually higher than  $\theta_E$  of the associated species. Under drier conditions, *Quercus* (or *Juniperus* at Salgesch, Fig. 4) had the highest  $\theta_E$ . Under high drought conditions, all species greatly reduced their  $\theta_E$ . However,  $\theta_E$  of *Quercus* at Jeizinen was still higher than that of the



**Fig. 3.** Average day courses of stomatal aperture ( $\theta_E$ ) reflecting the species-specific responses to different drought conditions at Jeizinen: **(a)** wet and cool day in May 2003, **(b)** dry day in July 2003, and **(c)** extremely hot and dry day in August 2003. Climate values are listed over 24 h, and average daytime value from 06:00 to 20:00 h (in brackets). **(d)** A more detailed view on July 10 shows, in addition to the average, the range of  $\theta_E$  recorded from south-exposed and north-exposed branches of the same species (different individuals).

two other associated species (Fig. 3). On a seasonal time scale, the course of  $\theta_E$  of *Pinus* always followed the degree of drought (soil water potential  $\Psi_{\text{Soil}}$  and vapour pressure deficit  $VPD$ , e.g. Fig. 4a and e) more closely than that of *Quercus*. *Picea* stomata closed almost completely during summer.

Differences were also found between the two investigated sites (Fig. 4). At Salgesch,  $\theta_E$  of all species dropped almost completely in July 2003, whereas  $\theta_E$  of *Quercus* at Jeizinen remained over 25% until the end of September. This is in accordance with the average lower air temperature (2.7°C), lower  $VPD$  (0.26 kPa) and higher  $\Psi_{\text{Soil}}$  (36 kPa) at Jeizinen than at Salgesch (Table 2, Fig. 5).

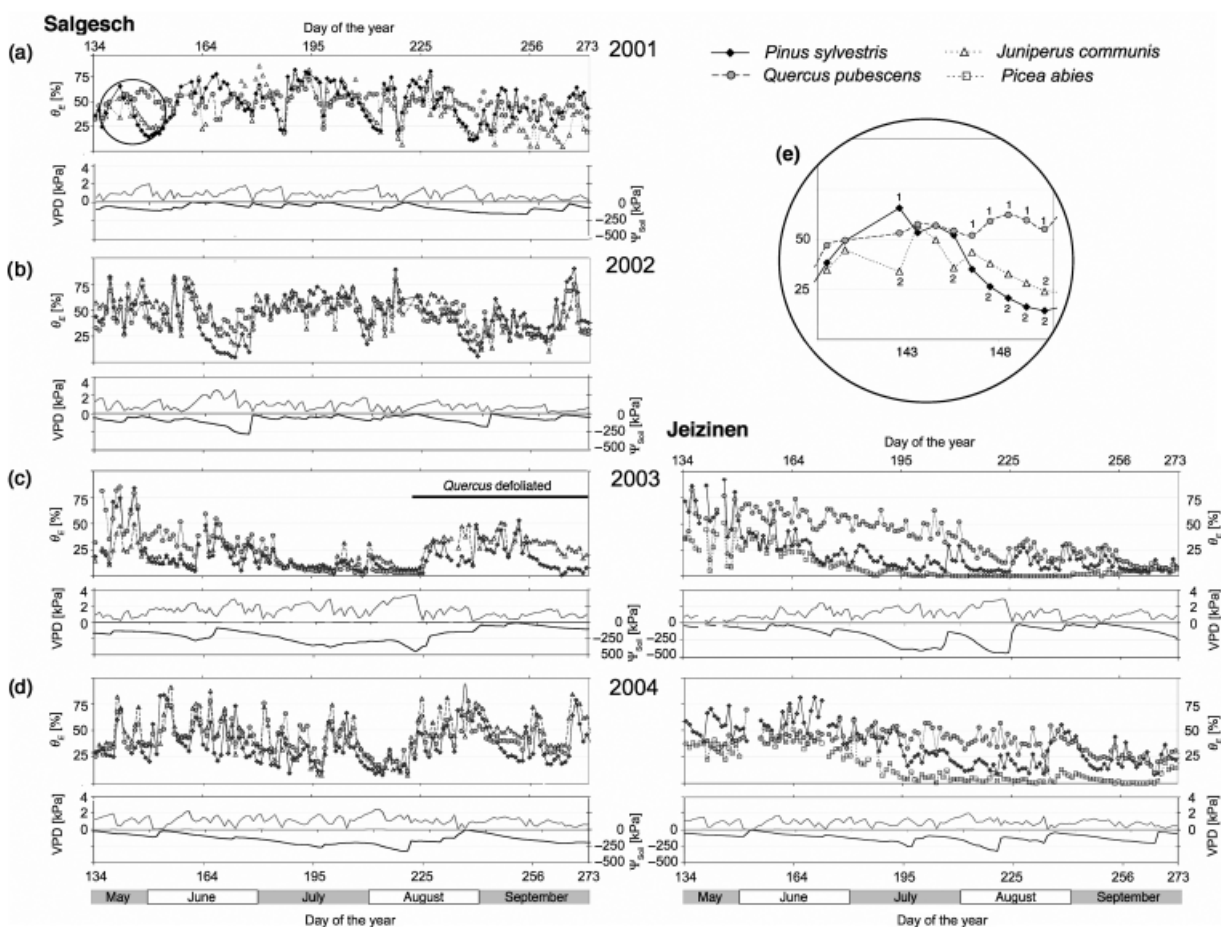
#### Selection of days with out- and underperformance of $\theta_E$

To test whether exceptionally high or low  $\theta_E$  values were related to specific climate conditions,

days with outperformance (*out*) and underperformance (*under*) were selected according to Eqs. A1-A4. When *out* was significantly different from *under* (double-sided *t*-test, Table 3), the corresponding  $\theta_E$  patterns were assumed to be strongly determined by the particular climate factor.  $\Psi_{\text{Soil}}$ ,  $VPD$  and precipitation within the past 48 h (*Rain*) were found to be most distinctive for  $\theta_E$ , followed by air temperature ( $T$ ). Solar radiation ( $Rad$ ) had the least explanatory power. Noteworthy is the relative stomatal response of *Quercus* to  $\Psi_{\text{Soil}}$  at Salgesch, since the group of *under* was split into two extremes: very low and very high  $\Psi_{\text{Soil}}$  led to underperformance for this species (Table 3).

#### Climatic preferences of the four investigated species

Frequency distributions of differences between the number of *out* and *under* days ( $\Delta N_{\text{out} - \text{under}}$ ) were calculated in relation to climatic gradients for all



**Fig. 4.** (a) Seasonal courses of stomatal aperture ( $\theta_E$ ), vapour pressure deficit ( $VPD$ ) and soil water potential ( $\Psi_{Soil}$ ) of the four tree species investigated at Salgesch and Jeizinen in (a) 2001, (b) 2002, (c) 2003 and (d) 2004. (e) The inset of (a) illustrates how both high  $\theta_E$  values (1 = outperformance) and low  $\theta_E$  values (2 = underperformance) were selected according to Eqs. A1-A4. All values in the graphs are mean daytime values measured between 06:00 and 20:00 h.

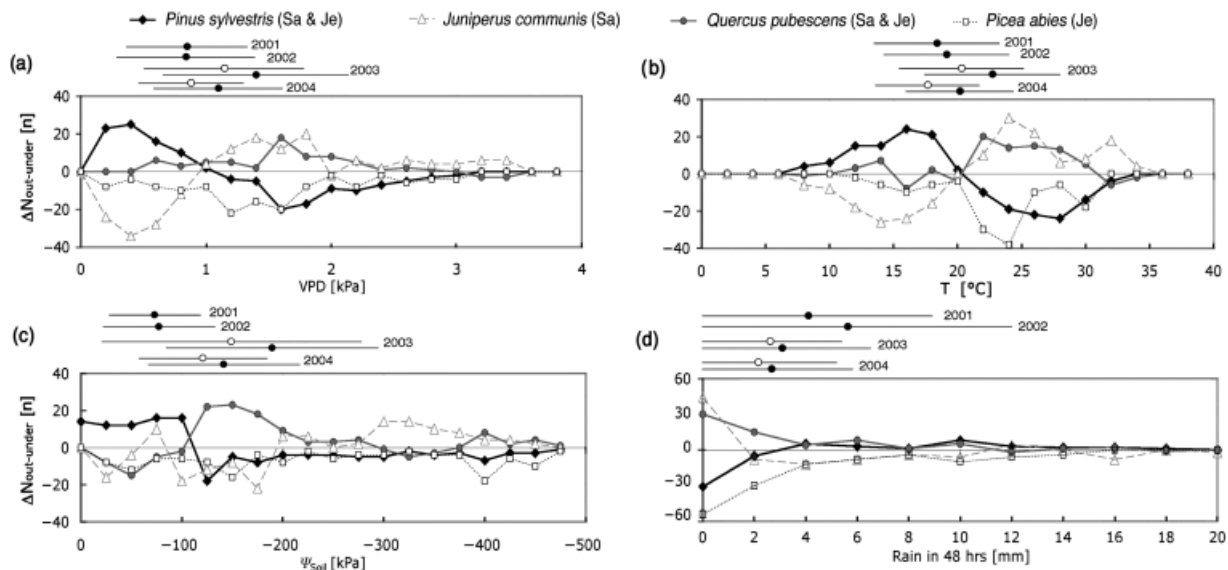
four species at both sites (Table 3). The combined results showed in which weather conditions a certain species had a greater  $\theta_E$  in comparison to the species associated with it (Fig. 5). In general, for  $VPD = 1$  kPa and  $T = 20^\circ\text{C}$ , transition points of  $\theta_E$  occurred where all four tree species performed more-or-less equally well.

*Pinus* had more open stomata than the associated species on relatively cool and humid days, and more closed stomata when the air and soil were dry, when there had been only a little rain within the past 48 h, when temperatures were above  $20^\circ\text{C}$  or when light intensity was high. *Quercus* had a higher  $\theta_E$  than the associated species when the air and soil were dry, but no extremes in  $VPD$  or  $\Psi_{Soil}$  were reached. Smaller  $\theta_E$  were observed during periods when soil conditions were wet or extremely dry. *Juniperus* had more open stomata than the associated species under the driest, hottest

and sunniest conditions, but opened its stomata less than its neighbours as soon as humidity in any form was present. *Picea* hardly ever competed with the associated species in terms of  $\theta_E$ . The few days when it had more open stomata than the associated species occurred under wet soil conditions after rain.

#### Inter-annual comparison

Comparison of annual differences between species-specific  $\Delta N_{out-unders}$  over 4 years (Fig. 6) showed that the wet year 2001 had the lowest value for *Juniperus*. The wet year 2002, with a drought in June, was similar for all species. The exceptionally hot and dry year 2003 led to a distinctly higher  $\Delta N_{out-unders}$  for *Juniperus*. And, again, the very dry year 2004 resulted in a distinctly lower value for *Pinus* in comparison with the more drought stress-tolerant



**Fig. 5.** Relative stomatal performance of the four tree species investigated over microclimate gradients. The difference between the number of days that were selected as *out* and *under* ( $\Delta N_{out- under}$ ) is shown in relation to: (a) vapour pressure deficit (*VPD*), (b) air temperature (*T*), (c) soil water potential ( $\Psi_{Soil}$ ) and (d) rain within 48 h. A value  $>0$  means relatively more open stomata, and a value  $<0$  means relatively more closed stomata in comparison with the co-occurring species. Above each profile (a-d), the mean values (Salgesch (Sa): filled circles, Jeizinen (Je): open circles) and standard deviations of the seasons 2001-2004 (May-September) characterize the years investigated.

species *Quercus* and *Juniperus*. The absolute  $\theta_E$  values showed fewer distinct species-specific responses within a year, and more year-specific differences over time. In other words, a small absolute difference in  $\theta_E$  induced a big difference in  $\Delta N_{out- under}$ . These findings are further supported by the average seasonal microclimatic conditions (mean daytime values from 06:00 to 20:00 h from May 1 to September 30) of *VPD* and  $\Psi_{Soil}$  in comparison with the optimal climate niches (in terms of a high  $\theta_E$ ) of the three co-occurring tree species at Salgesch (Fig. 7). The range of climate conditions during 2001 and 2002 provided optimal niches for all the species, whereas the conditions in 2003 and 2004 were clearly suboptimal for *Pinus*.

## Discussion

### *Species-specific stomatal response to climate*

The co-occurring tree species showed distinctly different stomatal regulation patterns (Figs 3 and 4), which could be consistently assigned to specific microclimatic conditions (Fig. 5). Therefore, each species has its own climate niche in which it is able to keep its stomata relatively more open than its neighbours (Figs 6 and 7). This species-specific stomatal regulation occurred despite the fact that

the tree species had similar exposures to microclimate conditions in the air and soil. In the Introduction, we argued that species- and climate-specific stomatal responses must be identified in order to systemically link climate change to vegetation dynamics. The following sections discuss the physiological background of the findings and compare the species-specific stomatal responses to gradients of drought. We further analyse how far the stomatal response patterns over the last 4 years are in accordance with the changes in species abundances in Valais, Switzerland over the past 30 years (Dobbertin et al. 2005b; Bigler et al. 2006).

### *Link between tree water relations and carbon balance*

The gas exchange of a tree is largely determined by stomatal regulation. This means that this regulation physiologically links tree water relations to the carbon balance by permanently trading a maximized  $\text{CO}_2$  uptake for assimilation against a non-damaging loss of water through transpiration (Hetherington & Woodward 2003). Thus, the carbon balance of a tree is largely determined by the tree water relations through stomatal regulation (Rambal et al. 2003), particularly at dry sites such as those investigated in Valais (Zweifel et al. 2006). More open stomata mean more carbon uptake and



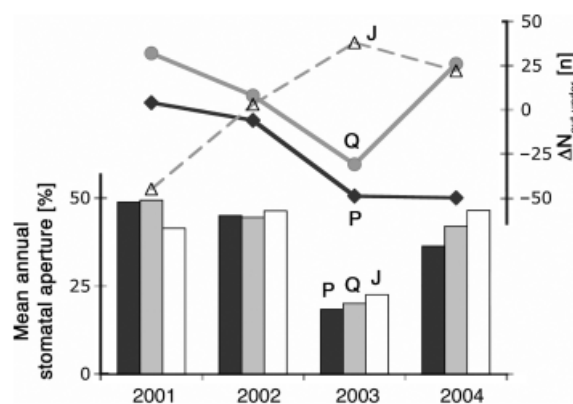
**Table 3.** Mean daytime values (06:00-20:00 h) of microclimatic conditions at Salgesch (4 years) and Jeizinen (2 years), Switzerland, when one of the tree species had more open (*out*) or more closed stomata (*under*) than its neighbours (Eqs. A1-A4). The significance of the differences between *out* and *under* (frequency distributions) over the respective climate gradient was tested with a double-sided t-test, \* $\alpha < 5\%$ , \*\* $\alpha < 2\%$ , \*\*\* $\alpha < 1\%$ , \*\*\*\* $\alpha < 0.2\%$ . *VPD* = vapour pressure deficit,  $\Psi_{Soil}$  = soil water potential, *Rad* = solar radiation, *T* = temperature, *Rain* = rain within the past 48 h, *n* = number of data points,  $x_{out}$  = mean value of the selection *out* of the respective climatic parameter,  $x_{under}$  = mean value of the selection *under* of the respective climatic parameter. + The data set for  $\Psi_{Soil}$  was found to be bimodal and subdivided into two groups. Each of these two groups was tested against *out*.

	<i>Quercus pubescens</i>			<i>Pinus sylvestris</i>			<i>Juniperus communis</i>		
	$x_{out}$ ( <i>n</i> = 134)	$x_{under}$ ( <i>n</i> = 58)	$\alpha$	$x_{out}$ ( <i>n</i> = 50)	$x_{under}$ ( <i>n</i> = 137)	$\alpha$	$x_{out}$ ( <i>n</i> = 85)	$x_{under}$ ( <i>n</i> = 106)	$\alpha$
<b>Salgesch</b>									
<i>VPD</i> (kPa)	1.2	1.5		0.4	1.5	****	1.5	0.6	****
$\Psi_{Soil}$ (kPa)	-162	-46/-330 <sup>+</sup>	****	-71	-132	****	-198	-103	****
<i>Rad</i> (W)	390	435		217	451	****	402	271	***
<i>T</i> (°C)	21.5	23.6		14.5	24.2	****	23.6	15.7	***
<i>Rain</i> (mm)	1.9	4.1		8.0	1.4	****	2.0	4.3	****
	<i>Quercus pubescens</i>			<i>Pinus sylvestris</i>			<i>Picea abies</i>		
	$x_{out}$ ( <i>n</i> = 76)	$x_{under}$ ( <i>n</i> = 27)	$\alpha$	$x_{out}$ ( <i>n</i> = 59)	$x_{under}$ ( <i>n</i> = 46)	$\alpha$	$x_{out}$ ( <i>n</i> = 6)	$x_{under}$ ( <i>n</i> = 99)	$\alpha$
<b>Jeizinen</b>									
<i>VPD</i> [kPa]	1.5	0.7	****	0.6	1.6	****	1.0	1.3	
$\Psi_{Soil}$ (kPa)	-246	-71	****	-97	-248	****	-68	-208	****
<i>Rad</i> (W)	432	382		343	455	*	487	408	
<i>T</i> (°C)	23.0	14.6	***	14.8	24.0	****	18.2	21.7	
<i>Rain</i> (mm)	1.7	1.6		2.7	1.7		0.5	2.6	****

thus allow payment of the necessary carbon costs for maintenance, growth and adaptations to changing environmental conditions (Sterck et al. 2008). Further, an increased carbon uptake increases the accumulation of carbon resources to endure non-productive (drought) periods or infestations by pathogens (Bale et al. 2003). Closed stomata, in contrast, may avoid sudden death by drought-induced hydraulic failure in the short term (McDowell et al. 2008), but they need to re-open not only for carbon uptake but also to avoid overheating of the leaves (Haldimann et al. 2008). This means the complex physiological processes can be simplified: as a rule of thumb, more open stomata indicate lower drought stress and more carbon uptake, and thus a better chance of survival of a tree species in the long term.

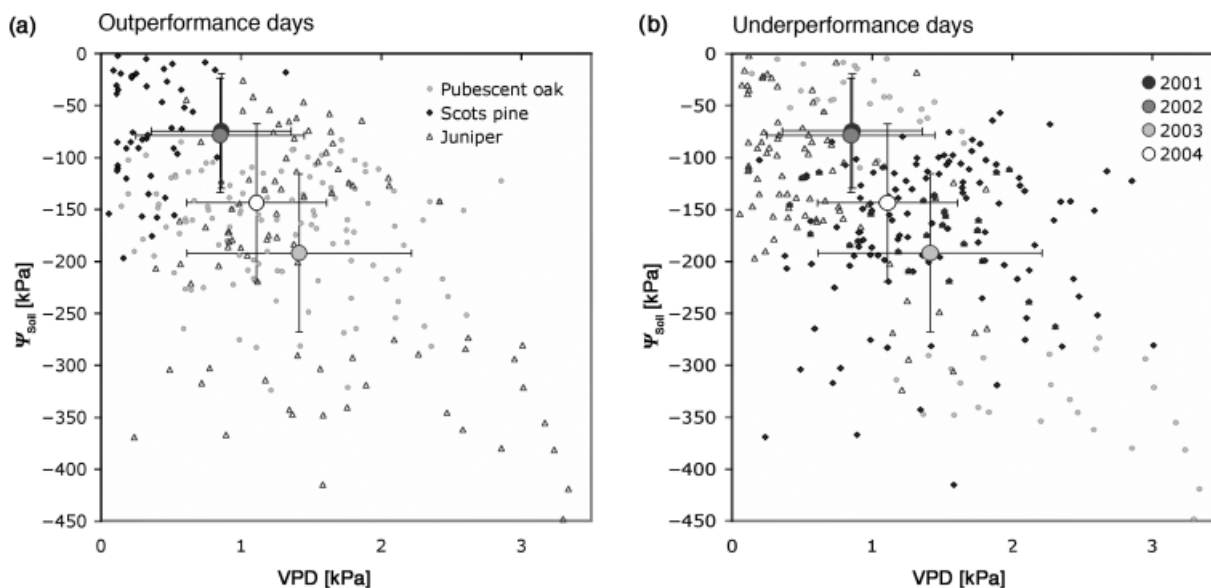
#### Drought stress strategies

The species-specific responses of  $\theta_E$  to varying microclimate conditions revealed that the four tree species had distinctly different drought stress strategies. Drought stress was differently induced by dry conditions in the soil and/or the air (Fig. 5). Overall, *Juniperus* was found to be the most drought-tolerant species, followed by *Quercus*, *Pinus* and *Picea*.



**Fig. 6.** Mean annual stomatal aperture (daytime values from 06:00 to 20:00 h, May 15-September 30, bars, left axis) and the relative stomatal performance of the three species at Salgesch ( $\Delta N_{out-under}$ , line graph, right axis). A value of 0 means the number of days selected as out-performance days (*out*) equals the number of days selected as underperformance days (*under*) in a particular year. A value  $> 0$  means there were more *out* days than *under* days, and a value  $< 0$  means there were fewer *out* days than *under* days. P = *Pinus sylvestris*, Q = *Quercus pubescens*, and J = *Juniperus communis*.

*Juniperus* needs higher temperatures and drier air (Fig. 7) than its neighbours to fully open its stomata and thus, to reach maximum net carbon assimilation. Humid and cool air seems to



**Fig. 7.** Seasonal (May-September) mean daytime conditions (06:00-20:00 h) of vapour pressure deficit ( $VPD$ ) and soil water potentials ( $\Psi_{soil}$ ) in the years 2001-2004 (large circles with standard deviations) in comparison to the conditions of (a) out-performance days (according to Eqs. A1-A4) and (b) underperformance days of the three co-occurring tree species at Salgesch (small symbols). Clusters of points of one species indicate a species-specific climate niche in terms of stomatal response to  $\Psi_{soil}$  and  $VPD$ .

slow-down the effect on re-opening of *Juniperus* stomata. The high drought tolerance of juniper species has been reported by many other authors (Linton et al. 1998; McDowell et al. 2008) and can be partly explained by their ability to sustain extraordinarily low-water potentials, down to  $-6$  MPa.

*Quercus* appeared to be second best in terms of drought stress tolerance. Its climatic niche is on the dry side of the conditions investigated, but not at the extreme end, which is covered by *Juniperus*. The course of  $\theta_E$  for *Quercus* shows, in general, less variation than those of *Juniperus* and *Pinus* (Fig. 4). Under conditions with wet air and  $T < 20^\circ\text{C}$ , this species out-competes *Juniperus* but is less competitive than *Pinus* (always in terms of  $\theta_E$ ). *Quercus*, as a sub-Mediterranean species, is adapted to be most productive under dry and hot conditions (Mediavilla & Escudero 2004) without extremes. Accordingly, extreme droughts, such as that in the summer of 2003, move *Quercus* towards its physiological limit at Salgesch, when it had already dropped its leaves by the end of July (Zweifel et al. 2007).

*Pinus* is well known as a drought-tolerant species (Weber et al. 2007). However, in comparison with *Quercus* and *Juniperus*, it is more a specialist for wet and cool conditions in this dry environment. Valais is on the southwestern border of the occurrence of *Pinus* and on the northern border of

*Quercus*. We hypothesize that *Pinus* has a strategy that is optimized for a sub-boreal climate (Kullman 2007), in which it is more important for a tree to be able to have high assimilation during moderate conditions, but also to be able to withstand brief periods with high temperatures and drought. Accordingly, *Pinus* needs rain at regular intervals (once every 1-3 weeks) to keep its stomata open (Fig. 5d) and to remain productive (Berninger 1997). *Pinus* has a lower hydraulic flow resistance than *Quercus* and is not able to withdraw comparable amounts of stored water from its stem and crown, as simulations of  $\theta_E$  with a hydraulic plant model revealed (Zweifel et al. 2007). Zweifel et al. (2007) further showed that *Pinus* maintains minimum water potentials at a significantly higher level than *Quercus* (*Pinus*: leaves/roots:  $-2.5$  MPa/ $-1.6$  MPa; *Quercus*:  $-4$  MPa/ $-3.6$  MPa). It is very likely that this minimum water potential disfavours *Pinus* in relation to *Juniperus* and *Quercus* with respect to withdrawing water from dry soils.

*Picea* was rarely competitive under any of the climate conditions measured throughout the two seasons in 2003 and 2004 (Figs 4 and 5), which were among the hottest and driest ever recorded in Switzerland (Beniston 2004). *Picea* might have benefited from the warmer periods in spring, autumn and winter, but these periods were not included in this analysis. Under the conditions analyzed

(May-September), however, this species was not competitive since gas exchange in the trees almost ceased for >2 months in both summers (Fig. 4).

#### *Responses to the years 2001-2004*

The years 2001-2004 offered a wide range of relative (dis-)advantages in terms of  $\theta_E$  for the four tree species according to their microclimatic preferences (Figs 5-7). After the relatively humid seasons in 2001 and 2002, there followed an extremely hot summer in 2003 and a very dry year in 2004 (Fig. 1). In 2001, total rainfall was slightly lower than in 2002 but rain was more evenly distributed over the season. This means that conditions were favourable for both *Pinus* and *Quercus* (Fig. 6). In contrast to 2001, there was a remarkable drought for 3 weeks in June 2002 (Fig. 4). This may have improved conditions for *Juniperus* and thus led to equal average stomatal performances of the three tree species investigated at Salgesch (Fig. 6).

*Juniperus* was the only species that could cope with the extreme drought conditions in 2003. Accordingly, its stomata were distinctly more open than those of its neighbours (Fig. 6). Just how unfavourable was the climate for *Pinus* in 2003 is shown in Fig. 7b:  $VPD$  and  $\Psi_{Soil}$  were almost exactly in the centre of the range for stomatal underperformance of this species. According to findings in Figs 6 and 7, *Quercus* seemed close to being successful in 2003, but some physiological thresholds were crossed in the prevailing climate conditions, which led to early defoliation in July (Zweifel et al. 2007).

The recovery potential of *Quercus* was evident again in 2004, which was also a very dry but less hot year. The average  $\theta_E$  almost returned to the value in 2002, whereas that of *Pinus* remained low (Fig. 6). Radial growth data for *Pinus* and *Quercus* from the same study sites (Zweifel et al. 2006) support the finding that *Quercus* had a much less marked decrease in annual growth than *Pinus* in both 2003 (*Quercus*: -26%, *Pinus*: -42%) and 2004 (*Quercus*: -19%, *Pinus*: -38%). In general, the inter-annual variation in radial growth was much larger for *Pinus* than for *Quercus*. This indicates that, although the average growth of *Pinus* is higher (1.1 mm) than that of *Quercus* (0.45 mm) at both Salgesch and Jeizinen, *Pinus* responded much more sensitively to stresses, particularly to dry and hot conditions, at our sites as well as at other sites in the region (Rigling et al. 2002; Eilmann et al. 2006; Dobbertin et al. 2007; Weber et al. 2007).

#### *Climate change and vegetation shift*

The clear species-specific stomatal responses to climate raise the question of whether this physiological response has any explanatory power for the vegetation shift observed in Valais and other regions. Representative vegetation data for south-exposed slopes at the investigated altitudes are available for *Pinus* and *Quercus*, but not for *Picea* and *Juniperus* (Fig. 1). *Picea* is very rare on these slopes and altitudes and *Juniperus* seems never to have been quantified. However, the reported pine decline and vegetation shift towards *Quercus* is in accordance with physiological characteristics of the tree species found in this study. Our results suggest that, despite the large potential influence of factors other than climate on vegetation dynamics, stomatal regulation patterns indicate the potential of a species to be more successful in a specific region under a particular climate. The ongoing climate change towards warmer conditions means that Valais is becoming more and more unfavourable for *Pinus*, and that these conditions favour, at least up to a certain threshold, the more drought-tolerant *Quercus* and *Juniperus* (Figs 5-7). However, up to now, the extreme drought years have not led to extinction of any of the tree species in Valais, unlike in some other regions (Allen & Breshears 1998; Breshears et al. 2005).

#### **Conclusions**

Each of the four tree species at the two forest sites appeared to have their specific climatic niche in which they are more successful in terms of  $\theta_E$  than their neighbours. We found that the characteristics of these physiological responses to climate are in accordance with the observed shift from *Pinus* to *Quercus* in Valais over recent decades. We conclude that the stomatal response pattern of a tree species to climate may potentially be a reasonable indicator of its growth and likely survival among its neighbouring trees at a specific site.

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## App. 1

### *Mathematical selection of the underperformance and outperformance days*

Days where  $\theta_E$  of one species was higher than the average were selected as outperformance days (*out*) according to Eq. (A1), and those where it was

**Table A1.** Calculated weighting factors ( $\beta$ ) to fulfill Eqs. (A3) and (A4).

	Salgesch		Jeizinen	
	$\beta_{out}$	$\beta_{under}$	$\beta_{out}$	$\beta_{under}$
<i>Quercus pubescent</i>	0.27	0.27	1.39	0.1
<i>Pinus sylvestris</i>	0.32	0.32	0.42	0.42
<i>Juniperus communis</i>	0.3	0.3	n.a.	n.a.
<i>Picea abies</i>	n.a.	n.a.	0.001	1.24

lower than the average were selected as under-performance days (*under*) according to Eq. (A2):

$$out_a = \frac{\theta_{Ea} - \frac{\theta_{Eb} + \theta_{Ec}}{2}}{\frac{\theta_{Ea} + \theta_{Eb} + \theta_{Ec}}{3}} \times \beta_a \quad (A1)$$

$$under_a = \frac{\frac{\theta_{Eb} + \theta_{Ec}}{2} - \theta_{Ea}}{\frac{\theta_{Ea} + \theta_{Eb} + \theta_{Ec}}{3}} \times \beta_a \quad (A2)$$

where  $a$ ,  $b$ , and  $c$  indicate the different species and  $\beta$  is a weighting factor to keep the number of selected da-

ys equal for all species (Table A1).  $\beta$  ( $\geq 0$ ) was chosen to solve Eq. (A3):

$$N_{out} + N_{under} = 0.2N_{Total} \quad (A3)$$

where  $N_{out}$  is the number of *out*,  $N_{under}$  is the number of *under*, and  $N_{Total}$  is the total number of measured days. This procedure led to selection of days on which the deviation between  $\theta_E$  of a certain species and the average of all associated species was largest, regardless of whether this deviation was negative or positive. A restriction for  $\beta$  applied when the ratio between  $N_{out}$  and  $N_{Total}$  was smaller than 25% or larger than 75%.

$$0.25 \leq \frac{N_{out}}{N_{Total}} \leq 0.75 \quad (A4)$$

In this case  $\beta$  was separated into  $\beta_{out}$  and  $\beta_{under}$ , and set to values that met the conditions of Eqs. (A3) and (A4).

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