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Growth response of Scots pine with different crown transparency status to drought release

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Abstract
· **Context** One short-term adjustment of trees to drought is the reduction of photosynthetic tissues via leaf shedding. But in conifers, it usually takes several years to fully restore needle mass and assimilation capacity.
· **Aims** This study aims to evaluate whether leaf shedding sustainably damages conifers or if these trees still have the ability to recover from drought with respect to their foliage and wood formation.
· **Methods** An irrigation experiment was established in a mature dry forest to test the growth reactions of Scots pine (*Pinus sylvestris* L.) differing in crown transparency (low, medium, high) to a drought release by irrigation in comparison with equivalent control trees growing under naturally dry conditions on the same site.
· **Results** Drought and high crown transparency had a combined negative effect on radial tree growth: Control trees with medium to high crown transparencies showed a substantially shorter growth period and a long-lasting growth depression in response to the severe summer drought in 2003. However, all trees benefited from irrigation, irrespective of their crown status, and immediately increased growth in response to irrigation.
· **Conclusion** The progressed drought-induced defoliation seemed to be a weakening factor for trees suffering from drought, but this can be reversed if the water supply is improved.

Key words *Pinus sylvestris* · Adjustment strategy · Intra-annual tree growth · Irrigation · Crown transparency · Recovery

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1 Introduction

With climate change trees in many parts of the world will have to cope with and to adjust to water shortages during the vegetation period (IPCC 2007). Under drought conditions, trees generally decrease their photosynthetic activity (Ciais et al. 2005; Granier et al. 2007; Reichstein et al. 2007), with negative consequences for tree performance. Chronic drought might lead to a continuous depletion of stored carbohydrates as a result of a persistent carbon imbalance since the tree's photosynthetic capacity might be reduced, while its demand for carbohydrates remains constantly high to maintain its metabolism (Eilmann et al. 2010; McDowell et al. 2008; Schwalm et al. 2010). Storage depletion is expected to result in a lower resilience of the trees to additional stressors, such as insects (Dobbertin et al. 2007; Rouault et al. 2006; Wermelinger et al. 2008). Consequentially, drought has demonstrated to be an important trigger of tree mortality, forest decline and rapid decline-induced vegetation shifts (Allen et al. 2010; Breshears et al. 2005; Gitlin et al. 2006; Martinez-Vilalta and Pinol 2002).

Trees exposed to drought show several mechanisms of adjustment to water shortage. One such mechanism is the downward shift of the zone of maximal water uptake in the roots via a higher carbon investment in root growth (Ericsson et al. 1996; Puhe 2003). As a result, trees have access to deeper water pools when the top soil dries out. This change in carbon allocation for the benefit of root growth leads to a

reduction in the shoot/root ratio under drought conditions (Linder and Axelsson 1982; Waring 1987).

The aboveground parts of the trees are also modified, as drought leads to crown decline via the reduction of needle length, needle area, and needle fresh and dry weight (Cinnirella et al. 2002; Dobbertin et al. 2010; Grill et al. 2004). Furthermore, the crown transparency of conifers often increases in the year following a drought event (Solberg 2004). These negative effects on needle mass may further be enforced by mistletoe infection (e.g. *Viscum album* ssp. *austriacum*) (Rigling et al. 2010; Zweifel et al. 2012) which particularly affects Scots pine at their southern distribution edge. But whether an increase in crown transparency under drought is just an adjustment to reduced water supply or rather a form of damage is still unclear (Sánchez-Salguero et al. 2012b; Metzger and Oren 2001; Dobbertin et al. 2010; Dobbertin et al. 2005). However irrespective of that, the assessed crown transparency can be used as a proxy for the impact of previous stresses especially of previous drought events on the tree in a water limited environment (Carnicera et al. 2011; Sánchez-Salguero et al. 2012a).

In this study, we aimed to find out more about the effect of increasing crown transparency on the performance of trees suffering from drought. To this end, an irrigation experiment was established in a mature Scots pine forest in Valais, a dry inner-Alpine valley. In Valais, as in other dry inner-Alpine valleys, Scots pine is the dominant species in forests at low elevations, but recently it has been affected by high mortality rates associated with drought events (Bigler et al. 2006; Dobbertin et al. 2005; Eilmann et al. 2009; Rigling et al. 2013). For all trees on the experimental site, we analysed basal area increment of trees growing under different water supply (naturally dry vs. irrigated) in relation to crown transparency to understand the role of the crown status in the pine decline process. To disentangle the interaction between the water status, the degree of crown transparency and tree growth, we selected 12 trees of three crown transparency classes (low, medium, and high) for a detailed analysis of tree-ring formation under contrasting water availability. Tree-ring formation acts as a proxy for tree performance, as it reflects growth limitation very well since tree rings are built with a lower priority than that, e.g., organs like roots or buds (Waring 1987). Tree-ring formation was analysed on the annual and intra-annual scale by detecting the amount of wood formed on a certain date during the growth period.

The main aim of this study was to ascertain whether an increase in crown transparency under chronic drought is an advantageous adjustment or rather a weakening factor for tree performance. In particular, we wanted to answer the following questions using radial growth as a proxy for tree performance.

- Are trees with high crown transparencies more limited in radial growth by drought?
- Are trees with high crown transparencies still able to benefit from improved water supply?

2 Material and methods

2.1 Experimental site and sample trees

We established an irrigation experiment in the driest central part of Valais, close to the village Susten (46°18′ N, 7°36′ E). The experimental site is situated on the valley floor (elevation 615 m) in an *Erico-Pinetum sylvestris* forest. The climate is continental-dry, with a mean annual temperature of 9.2 °C and a mean annual precipitation sum of 653 mm (norm period 1961–1990, MeteoSwiss, temperature taken from the climate station Sion, 20 km distance from the experimental site, and precipitation from the station Sierre, 3 km away). The parent material is an alluvial fan originated from debris flows. The soil is a very stony initial calceric regosol (FAO classification) with high permeability and low soil water storage capacity.

The whole experimental site of about 1 ha was split into eight plots each 1,000 m^2 in area. These plots were separated by a 5 m buffering strip. On four randomly selected plots, trees were growing under naturally dry conditions, on the other four plots trees have been irrigated since June 2003 continuing until today. Irrigation was applied at night during the growth period from April to October. Irrigation earlier than April or later than October was not possible due to the risk of frost damaging the equipment. Irrigation water was taken from an adjacent water channel, fed by the river Rhone, and was applied to the plots using sprinklers about 1 m above the ground. Irrigation more than doubled the annual precipitation (plus 700 mm per year). As the 2 years studied were drier compared to the long-term mean precipitation (2004, 477 mm; 2005, 500 mm), a distinct difference in water availability between the control and the irrigated plots was found (mean soil moisture measured at 10, 40, 60 cm depth 2004: irrigated=33 vol.%, control=22 vol.%; 2005: irrigated=37 vol.%, control=22 vol.%). On irrigated plots, soil moisture still increased after precipitation events, indicating that the soil had not been saturated through irrigation (for details about the soil moisture on the experimental plot, see Dobbertin et al. 2010, Eilmann et al. 2010, 2011).

Before the irrigation started crown transparency of 899 trees on the experimental site was estimated in March 2003 before the new shoots emerged. Crown transparency was visually estimated in 5 % steps, ranging from 0 %, i.e. fully foliated tree, to 100 %, i.e. dead tree (for details, see Dobbertin et al. 2004). We found the whole spectrum of crown transparencies on the site. Fully foliated trees were found to be growing close to trees with high crown transparencies. All trees on the experimental site were ranked into three crown transparency classes (low: ≤25 %; medium: 30 to 50 %; high: >55 %, cf. Fig. 1 and Table 1) based on the crown transparency estimation in 2003. On the experimental site, we found 333 pines representing the low crown transparency class, 384 pines were assigned to the mid
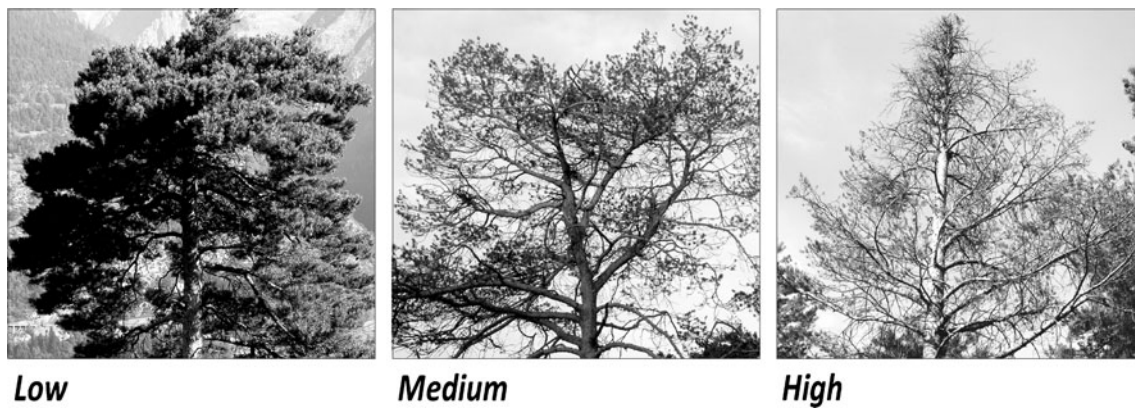
Fig. 1 The three classes of crown transparency

crown transparency class and 182 pines showed a crown transparency higher than 50 % and thus were classified in the high transparency class. To analyse the effect of irrigation on the crown transparency, crown assessments were repeated every year until 2010.

In addition, the basal area (BA) of each tree in the experimental plot was calculated based on circumference measurements at breast height in 2003 and 2010. The BA in 2003 and 2010 was then used to calculate the basal area increment for this period (BAI_{03-10}). The relative basal area increment ($rBAI_{03-10}$) was then calculated by relating the BAI_{03-10} to the basal area in the year 2003 (BA_{03}).

$$rBAI_{03-10} = BAI_{03-10} \times 100 \Big/ BA_{03}$$

$rBAI_{03-10}$ was then related to the mean crown transparency calculated for the period from 2003 to 2010.

In addition, we selected two trees per crown transparency class and treatment in 2003 randomly, i.e., in total 12 sample trees for the detailed analysis of wood formation.

2.2 Sampling and sample preparation

To analyse the intra-annual increment, we used the pinning method. This involved injuring the cambium regularly with a thin needle (diameter 0.6 mm) and using the resulting wound reaction for the exact dating of the wood formation (Nobuchi et al. 1993; Wolter 1968; Yoshimura et al. 1981). Trees were injured at breast height on a weekly or biweekly basis during the growth period 2004 (April 14th to October 27th) and 2005 (April 13th to October 13th). Following the instructions of Schmitt et al. (2004), each sample tree was wounded three times on each pinning date.

The 12 trees were harvested in spring 2006 and the trunk section, including the pinning wounds, and an additional stem disk from above the pinning section were sampled. Material was stored at minus 20 °C to avoid fungal infestation. Annual increment (tree-ring width) was measured along two radii on the sanded stem disks, using a combination of a Lintab digital positioning table and the software TSAP (both Rinntech, Germany). The two measurements per tree were averaged to obtain a single tree chronology.

To compare the tree-ring parameters with climatic conditions, the climatic water balance (CWB) was calculated as estimate for water availability. CWB was computed as

Table 1 Tree characteristics within three crown transparency classes (each value is the mean of two trees) separated for the irrigated and the control trees. Tree-ring width was calculated for the 10 years before irrigation was started (1993–2002). Crown transparency values show the estimates of March 2003 (=Before) before the start of irrigation, and March 2006 (=After) after 2.5 years of irrigation. Tree height, steam diameter, crown length and crown diameter were measured during sampling (spring 2006)

		Crown transparency [%]		Age [years]	Tree-ring width [mm]	Tree height [m]	Stem diameter [cm]	Crown length [m]	Crown diameter [mm]
		Before	After						
Irrigated	Low	8	8	90	1.45	11.3	26.0	4.7	5.6
	Medium	30	28	99	0.59	11.3	26.0	3.9	4.5
	High	65	60	103	0.32	11.3	25.8	3.6	4.0
Control	Low	10	30	94	0.80	10.3	22.0	3.7	3.9
	Medium	30	50	100	0.76	10.7	22.8	4.3	4.3
	High	70	73	98	0.46	10.7	24.5	3.2	4.0

CWB=P−PET using monthly data of precipitation sums (P) and potential evapotranspiration (PET) according to Thornthwaite (1948). The climate data originate from the weather stations in Sion and Sierre (at 20 km or 3 km distance from the experimental site). The monthly CWB was averaged for the period from January to September including the months of the pre-vegetation period due to their importance for the start of tree growth as well as for the development new shoots and needles (Dobbertin et al. 2010).

The tissues containing the pinning wounds were extracted from the trunk with a keyhole saw (19 mm) and stored at minus 20 °C in Strasburger solution (one third ethanol (95 %), one third glycerol (99 %), and one third distilled water) to keep the samples moist and avoid crack building due to a drying of the samples. We cut thin sections (10 μm thick) from the extracted tissue using a sliding microtome (Reichert, Germany). The sections were stained with safranin (1 % solution) and astrablue (2 % solution) to improve the contrast between the cell wall and the cell lumen. To permanently store the thin sections, we dehydrated them along an alcohol concentration gradient (70 %, 95 % and absolute ethanol) and xylol (>98 %) and embedded them in Canada balsam. Finally, thin sections were photographed for image analysis (100 times magnification, microscope: Olympus BX41, Japan; camera: ColorView III, Soft Imaging system, Germany).

2.3 Measurement on the intra-annual scale

We determined the period of wood formation according to Seo et al. (2007). We considered wood formation to have begun if we found mature cells with a secondary cell wall below the wound, and tree-ring formation to be complete if the wound tissue was separated from the current tree ring by a continuous band of flattened latewood cells. Due to the very low increment in one control tree with a very transparent crown, we were not able to detect the amount and timing of the increment of this tree in 2004 and 2005.

We applied an analysis of covariance for the response variables: beginning of radial growth, end of radial growth, growing duration and ring width. We analysed them separately in 2004 and 2005, using the irrigation as the treatment and the crown transparency assessment in 2003 as the covariate. Treatment and covariate were tested for interaction. p values of significance were used as indicators of factor importance without applying a procedure to correct for multiple testing.

We measured the intra-annual increment as the distance between the previous tree-ring border and the last matured cell at the time of pinning (=last cells with a secondary wall below the wound, method according to Seo et al. (2007)). This last cell was determined with polarised light. The intra-annual increment was measured on both sides of the needle entry (image analysis software IMAGE PRO PLUS, Media Cybernetics USA) and averaged to a mean. According to Grotta et al. (2005) we calculated the relative increment as the percentage of the tree ring

formed by the pinning date by relating it to the total ring width measured outside the tissue of wound reaction (increment$_{relative}$= increment$_{intra-annual}$/tree-ring width).

3 Results

3.1 Tree growth and crown transparency

Basal area increment decreased clearly with increasing crown transparency (Fig. 2). Over the course of 8 years (2003–2010) irrigated trees were able to produce more wood than control trees with the same development in crown transparency. In addition irrigated trees developed denser crowns as crown transparency clearly decreased within the experiment. In contrast, control trees showed rather an increase in crown transparency over the course of the experiment. Meanwhile irrigated trees tend to have more individuals with high basal area increment. Hence, irrigation had a positive effect on basal area increment and on needle growth indicating the water status as important driver of crown transparency but also for tree productivity.

3.2 The timing of wood formation

The timing of wood formation was strongly affected by crown transparency and irrigation (Fig. 3 and Table 2). Across treatments, pines with very transparent crowns started wood formation about 4 weeks later than pines with denser crowns. Irrigation prolonged the growth period, and irrigated trees stopped wood formation up to 5 weeks later than control trees.
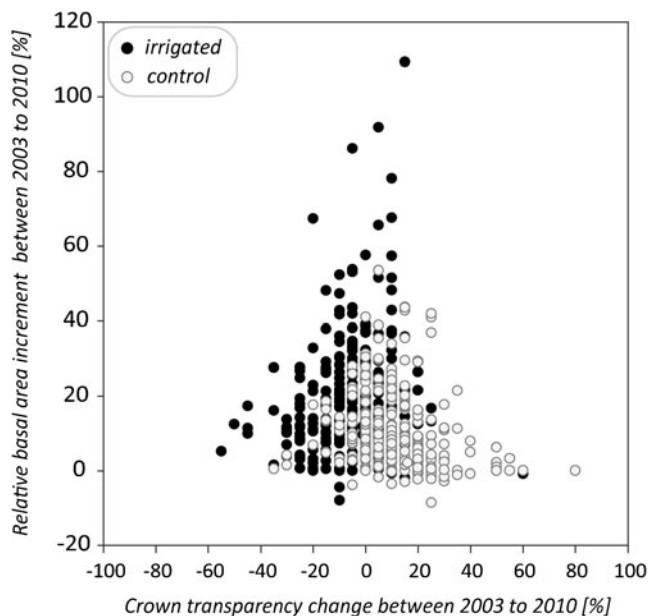

Fig. 2 Relative basal area increment, showing the basal area increment between 2003 and 2010 in relation to the basal area in the year 2003, is shown relative to the change in crown transparency in the experimental period 2003 to 2010

Fig. 3 Timing of wood formation for irrigated and control trees with different crown transparencies (*low*, *medium*, and *high*); p1 to p18 mark the 15 (2004) or 18 (2005) pinning dates per year, respectively; *arrows* mark the time period where irrigation takes place
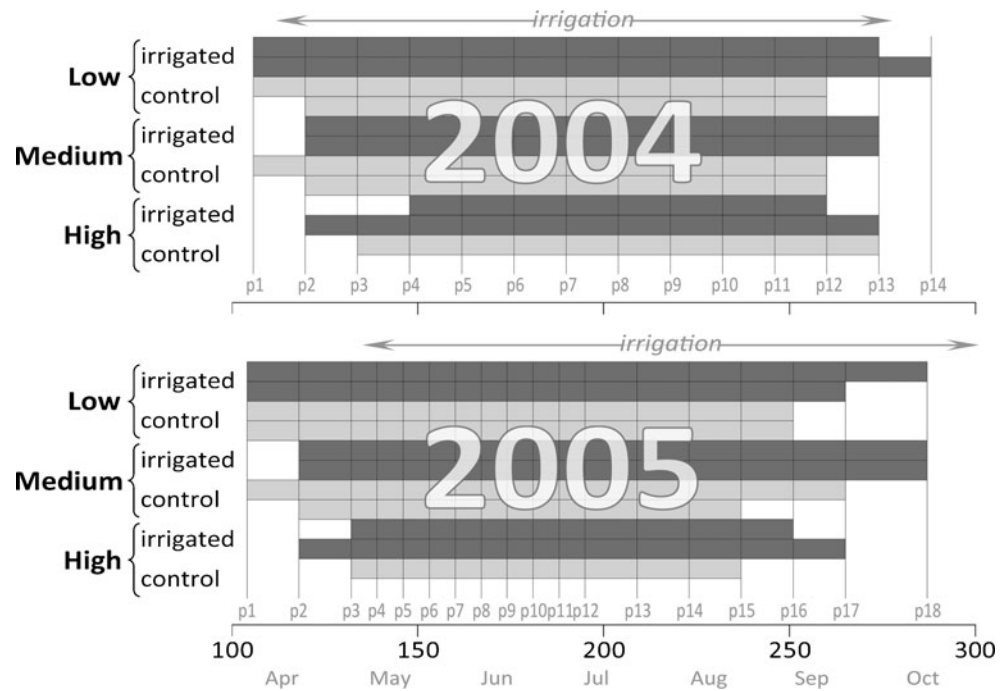
The growth period was thus shortest for control trees with very transparent crowns, e.g., 15 weeks in 2005, while irrigated trees with dense crowns had the longest growth period, e.g., 26 weeks in 2005.

These results were confirmed by the analysis of covariance applied for the days of the year when cambial growth started or ended and for the total growing period and ring width (Table 2). As no significant interactions between crown transparency and treatment were found for any response variable, models were used without the interaction term. Ring width in both years was significantly positively influenced by irrigation ($p_{04} < 0.05$, $p_{05} < 0.01$) and negatively by crown transparency ($p_{04, \, 05} < 0.01$). Irrigation was not significant for the beginning of growth, while crown transparency was ($p_{05} < 0.01$). For the end of growth, no significant effects were detected in 2004, but in 2005 irrigation was significantly associated with growing ending later ($p_{05} < 0.01$). Growing length was significantly increased, at least in 2005, for both, reduced crown transparency ($p < 0.01$) and irrigation ($p < 0.01$).

3.3 The quantity of wood formation

The irrigation experiment started late in June of the drought year 2003, when the bulk of the tree ring was expected to have already formed. Hence, independent of the treatment and the crown status, the tree-ring widths of all trees were reduced in this first year of the experiment (Fig. 4). From 2004 on, differences between the treatments occurred as irrigated trees increased their increment irrespective of their crown transparency. Pines with low crown transparency on the control plot were also able to increase their increment in 2004 and 2005 due to increased precipitation (mean drought index, January to September, 2003, −44 mm, 2004, −22 mm, 2005, −21 mm). In contrast, pines with medium to high crown transparency on control plots had constantly low increments in 2004 and 2005.

Irrigation and crown transparency strongly affected the intra-annual increment of the pines (Fig. 5a). Trees with little crown transparency always had the highest increment followed by trees with more transparent crowns. This ranking

Table 2 p values obtained in the analysis of covariance for beginning of radial growth (BG), end of radial growth (EG), growing length (LG) and ring width (RW) for the years 2004 ($_{04}$) and 2005 ($_{05}$) with treatment effect (irrigation) and covariate (crown transparency assessed in March 2003; $n=11$)

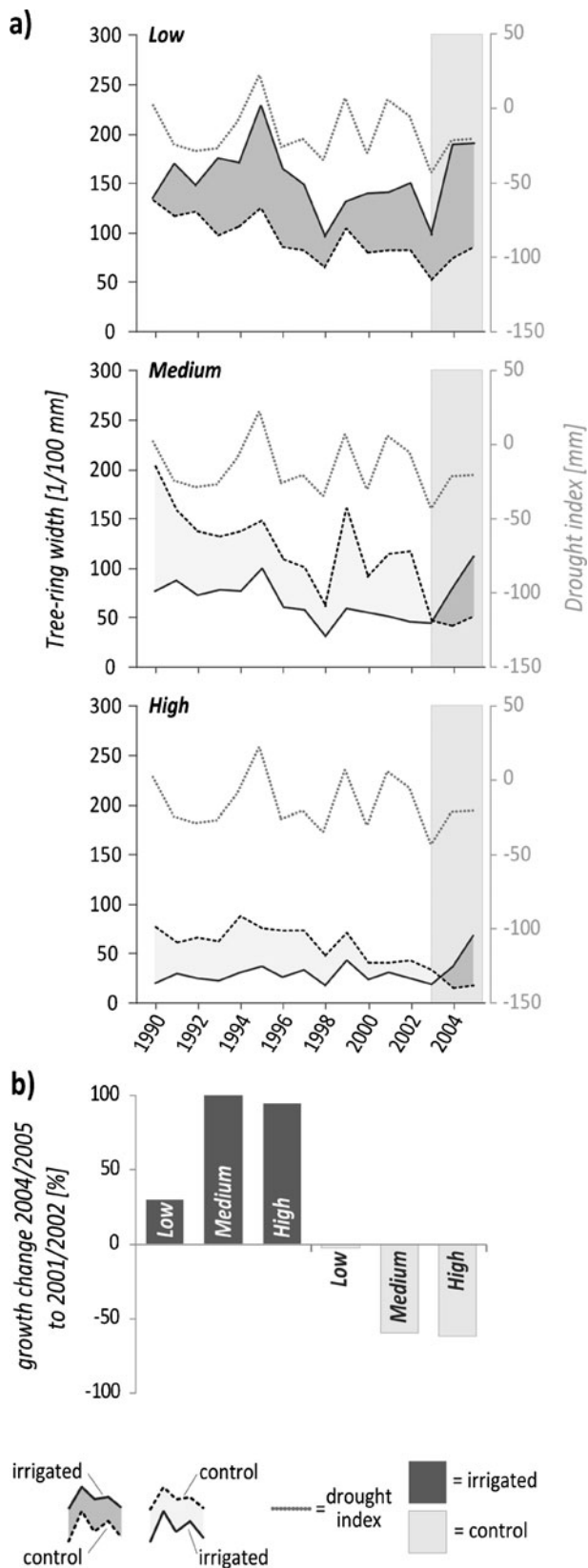| Variable	Model							
	BG_{04}	EG_{04}	LG_{04}	RW_{04}	BG_{05}	EG_{05}	LG_{05}	RW_{05}
Intercept	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Irrigation	0.934	0.248	0.422	0.031	0.755	0.008	0.003	0.002
Crown transparency	0.127	0.516	0.051	0.001	0.002	0.060	0.007	0.001
Total	0.046	0.438	0.120	0.002	0.007	0.014	0.003	0.001

Fig. 4 **a** Development of tree-ring width in trees with different crown transparencies (low, medium, high) growing on irrigated or control plots. The *hatched grey line* shows the averaged drought index (DI averaged for January to September). If the irrigated trees show higher increment than the control trees the area between the two curves is tinted in *dark grey*. If the control trees showed higher increment than the irrigated trees the area between the two curves is tinted in *light grey*. The irrigation period (2003 to 2005) is marked by the shaded area. **b** Growth change in percentages in the years 2004/2005 (mean DI=0.5) referring to the growth in the years 2001/2002 (mean DI=−21.3) in irrigated and control trees with different crown transparencies

in increment according to crown transparency was consistent across the years and the treatments. The relative increment was also affected by both irrigation and crown transparency (Fig. 5b). While all irrigated trees showed constant intra-annual increment rates over the year with a late flattening of the increment curve, the increment rate of the control trees differed according to crown transparency. Control trees with medium to high levels of crown transparency completed most of the tree ring already in June, before the dry season in July and August. In contrast, the relative increment of control trees with denser crowns had patterns very similar to that of irrigated trees, with a constant intra-annual increment rate in summer despite increasingly drier conditions and a late flattening of the growth curve (not until September, Fig. 5b).

4 Discussion

Our data clearly support the hypothesis that the increase in crown transparency is a weakening factor for tree growth under drought. While decreasing increment with increasing crown transparency (Figs. 2 and 5a) might be seen as an advantageous adjustment as less tissue needs to be maintained (Metzger and Oren 2001), our data indicate that water shortage and increasing crown transparency have a negative cumulative impact on tree growth. Comparing trees with the same development in crown transparency control trees show lower levels of basal area increment than irrigated trees (Fig. 2). This coincides with the growth response after the extreme drought year 2003 where trees with medium and high crown transparencies showed lasting growth depressions until 2005, whereas the trees with only low crown transparency immediately recovered in 2004 and 2005 (Fig 4). Similar findings were made by Sánchez-Salguero et al. (2012a) who found in Spain that declining *P. silvestris* and *P. nigra*, as determined by crown transparency assessments, were more vulnerable to growth depression on drier sites. This might be due to the earlier reduction of intra-annual growth (Fig. 5b) as well as the general shortening of the growth period (Fig. 3) as shown in this study for control trees with increasing crown transparency.

The combined negative effects of drought and high crown transparency with no significant interaction between crown

Fig. 5 **a** Absolute and **b** relative radial increment of irrigated (*closed black symbols*) and control trees (*open grey symbols*) at the pinning dates, in trees with different crown transparencies (=mean curves of two trees)
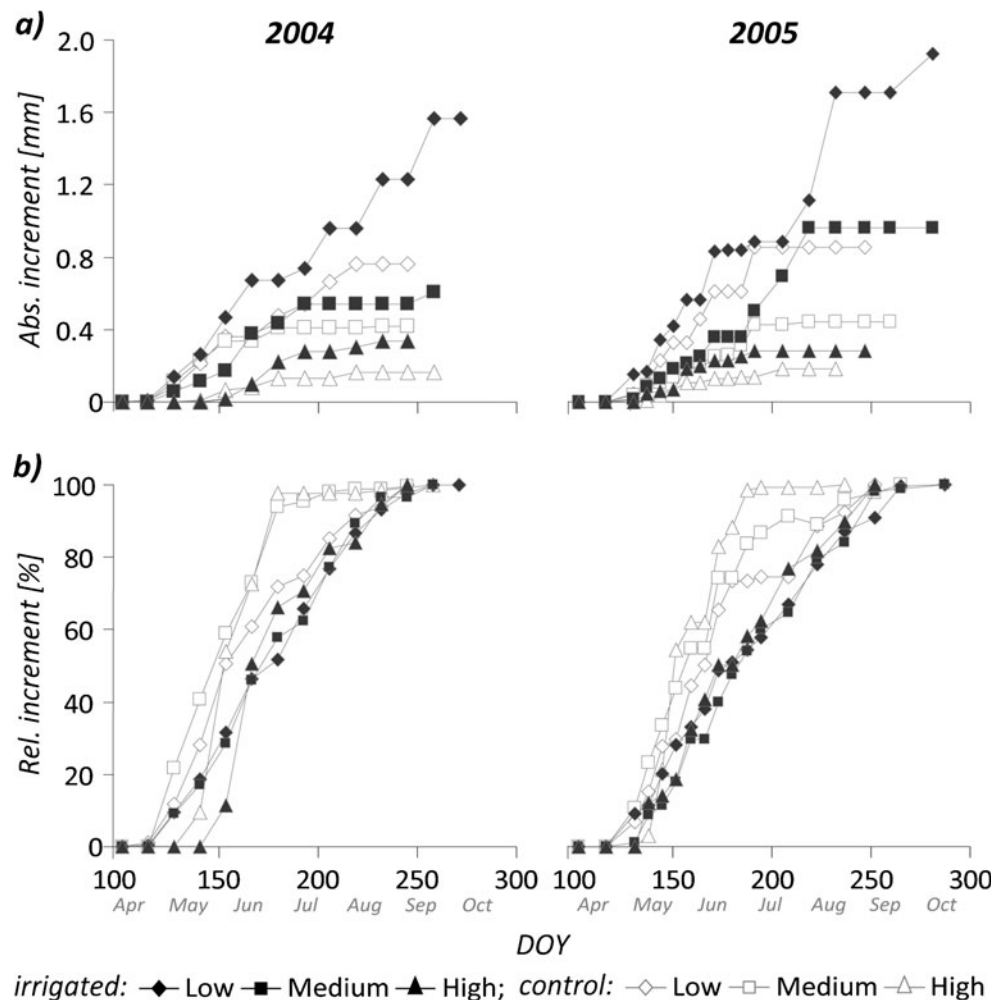
transparency and treatment might be due to the fact that both factors foster carbon storage depletion, which is a process recently suggested as relevant for the drought-induced decline in Scots pine (Eilmann et al. 2010). This is in accordance with Galiano et al. (2011), who found a close relationship between carbon storage depletion and drought-induced defoliation. However, there is still an on-going debate on the importance of storage depletion in the process of tree mortality arguing that tree growth under drought may rather be limited by the direct hampering of cambial activity by low water supply than by low availability of carbohydrates (Salla et al. 2012). Furthermore, storage depletion might be only relevant for species growing far beyond their ecological optimum that are repeatedly exposed to severe droughts, as Eilmann et al. (2010) suggest. This would explain why recent studies on comparatively less drought-exposed sites in the Austrian Alps were not able to find evidence for storage depletion in Scots pine (Gruber et al. 2011; Oberhuber et al. 2011). Tree mortality might thus be caused by other factors like hydraulic failure during extreme drought events (Bréda et al. 2006; McDowell

et al. 2008) or just by the inability to mobilise stored carbohydrates under water shortage. Thus further research is needed to understand the relevance of storage depletion for tree performance and survival under drought conditions

When irrigated, all trees at the study site had increased growth rates irrespective of their crown transparency (Figs. 4a and 5a), and experienced no further loss of photosynthetic tissue (constant crown transparency, see Table 1) which is in line with the results of Dobbertin et al. (2010) analysing the effect of irrigation on crown transparency for all trees within the experiment. The trees with the highest crown transparency showed the highest relative growth increase in regards to tree-ring width (Fig. 4b), which was accentuated because they had a lower growth rate prior to irrigation (Black and Abrams 2003). These results indicate that the process of drought-induced tree decline is reversible, regardless of the crown conditions, if water availability improves. Consequently, when modelling drought-induced tree decline, not only the exacer-bating effect of multiple drought years must be considered (Bigler et al. 2006), but also the easing effect of multiple moist years.

5 Conclusion

Our data showed, when frequent drought events have led to a crown transparency >25 %, the resulting negative effects of crown transparency under drought on the performance of the tree are greater than its benefits. Thus, our data support the view that high crown transparency under drought conditions poses a long-term risk for the future performance of the tree rather than an advantageous adjustment strategy. Accordingly, we can conclude with respect to our first research question that the trees with mid to high crown transparencies were more affected by drought than trees with denser crowns. However, our results also showed that all trees, even those with very transparent crowns, were able to recover if water availability improved. So, the process of decline is usually reversible as all trees have the availability to recover from periods of drought.

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