Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest

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Summary   In Valais, Switzerland, Scots pines (*Pinus sylvestris* L.) are declining, mainly following drought. To assess the impact of drought on tree growth and survival, an irrigation experiment was initiated in 2003 in a mature pine forest, approximately doubling the annual precipitation. Tree crown transparency (lack of foliage) and leaf area index (LAI) were annually assessed. Seven irrigated and six control trees were felled in 2006, and needles, stem discs and branches were taken for growth analysis. Irrigation in 2004 and 2005, both with below-average precipitation, increased needle size, area and mass, stem growth and, with a 1-year delay, shoot length. This led to a relative decrease in tree crown transparency (−14%) and to an increase in stand LAI (+20%). Irrigation increased needle length by 70%, shoot length by 100% and ring width by 120%, regardless of crown transparency. Crown transparency correlated positively with mean needle size, shoot length and ring width and negatively with specific leaf area. Trees with high crown transparency (low growth, short needles) experienced similar increases in needle mass and growth with irrigation than trees with low transparency (high growth, long needles), indicating that seemingly declining trees were able to 'recover' when water supply became sufficient. A simple drought index before and during the irrigation explained most of the variation found in the parameters for both irrigated and control trees.

Keywords: leaf area index, needle size, ring width, Scots pine, shoot length.

Introduction

During the 20th century, several waves of high mortality rates of Scots pine *(Pinus sylvestris* L.) have been observed with increasing tendency since the 1990s in central Valais, the dry inneralpine Rhone valley in south-western Switzerland (Dobbertin et al. 2005, Dobbertin and Rigling 2006, Rigling et al. 2006). While in the late 1970s this decline could partly be attributed to fluorine air pollution (Flühler 1981), pollution has now been largely ruled out as a dominant cause (Dobbertin et al. 2007). Observations of similar pine decline were made in other parts of the European Alps, such as the Aosta valley, Italy (Vertui and Tagliaferro 1998), the Inn valley, Austria (Oberhuber 2001), the Vienna bassin, Austria (Cech and Wiesinger 1995) and the Vinschgau, Italy (Minerbi 1998).

Mortality rates of Scots pines in Valais at low altitudes, where the climate is drier and warmer, were found to be substantially higher (>1%) than the average rate in managed forests in Switzerland (0.4%, Dobbertin et al. 2005). This might already be the consequence of the observed increase in temperatures coupled with re-occurring droughts (Rebetez and Dobbertin 2004). Temperature in Switzerland has risen by 1.6 °C over the last 100 years. While this increase occurred mainly during winter months (Begert et al. 2005), summer temperature has risen at a fast rate over the last three decades (Rebetez and Reinhard 2008). Summer drought and heat waves as in 2003 are predicted to become more frequent with global warming (Schär et al. 2004). Increasing summer temperature, on the other hand, increased evaporative demands in Valais (Rebetez and Dobbertin 2004). Scots pine reacts to increased summer temperature and drought with decreasing stomata openness in comparison to more drought-adapted species, such as pubescent oak (*Quercus pubescens* Willd., Zweifel et al. 2009). Drought is, therefore, considered both an inciting and a predisposing factor for the observed decline (Dobbertin et al. 2005, Bigler et al. 2006).

Growth of trees, as expressed by needle/leaf elongation or shoot and stem growth, is influenced by climate, in particular temperature and water availability (Kozlowski et al. 1991, Raison et al. 1992, Whitehead et al. 1994, Dobbertin 2005). Therefore, growth may serve as an indicator of the effects of changes in temperature and precipitation.

As a result of the ongoing research, an irrigation experiment was established to test if re-occurring drought is predisposing or triggering Scots pine decline in the Rhone valley

Table 1. Annual precipitation and added irrigation amount from 2002 to 2007.

Year	Precipitation (mm)	Irrigation amount (mm)	Prec. + irrigation (mm)
2002	881	0	881
2003	414	280	694
2004	566	750	1316
2005	565	790	1355
2006	665	780	1445
2007	846	610	1456

(Brunner et al. 2009). Instead of inducing even higher drought in a drought experiment, it was hypothesized that reducing drought stress in this forest via irrigation would affect tree vitality and eventually reverse the observed trends of tree mortality. For this purpose, a naturally regenerated, mature Scots pine stand was selected for an irrigation experiment.

The following hypotheses were tested in this study: (i) Irrigation increases tree growth, including foliage production, i.e., needle length, mass and area, tree stem growth and shoot elongation. (ii) Irrigation reduces the transparency of tree crowns, as transparency should be inversely related to needle size and shoot length. As a consequence, it increases leaf area index (LAI), which should be positively correlated with needle size and shoot length. (iii) Trees with high crown transparency, believed to be less vital, show less reaction to the irrigation.

To test whether the effects were really caused by the added water and not by other changed environmental conditions as a side effect of irrigation, we computed a simple drought stress before and during irrigation and correlated it with the response variables.

Materials and methods

Study region

The Pfynwald ('Pfyn' forest) is the largest closed Scots pine forest in Switzerland. It is located on an alluvial fan and debris cone of the Ill river ('Illgraben') at 610 m altitude. The forest is dominated by Scots pines in mostly single-storey stands. The irrigation site is situated within the main forest along a water channel used for hydro-energy. The soil has a pH of 7.9 and a base saturation (BS) of 99.4% (at 40 cm depth), with a high content of skeletal materials (Brunner et al. 2009).

The mean stand age is 95 years. The top tree height is 10.8 m. The stand density is 730 stems per hectare (ha) with a breast height diameter (DBH) $\geq$12 cm or a basal area of 27.3 m^2 ha^{-1}. The mean annual temperature at the nearest climate station of the Federal Office of Meteorology and Climatology (MeteoSwiss, station Sion, 492 m a.s.l., 20 km distance from the study area) was 9.2 °C for the period 1961–90 but 10.4 °C for the period 1991–2007. The mean annual precipitation at the nearby MeteoSwiss rainfall station Sierre (565 m a.s.l., 4 km distance from the study area) is 657 mm. The annual rainfall during the irrigation time considered in this study is given in Table 1. Annual precipitation was below average during 2003–05, average in 2006 and above average in 2002 and 2007.

Irrigation experiment

In winter 2002–03, an approximately 1-ha study site was delineated next to the water channel (Figure 1). All trees with a minimum diameter of 8 cm at breast height were numbered and geo-referenced, and their diameter, species and dead or alive status were recorded.

Within the study site, eight plots of 25 × 40 m were delineated, leaving a 5-m buffer strip between the plots and towards the study site boundary (Figure 1). The eight plots were aligned from south to north along the water channel from where water was pumped to irrigate four randomly selected plots.

In each treatment plot, trees were irrigated throughout the vegetation period during rainless nights using 20 sprinklers,
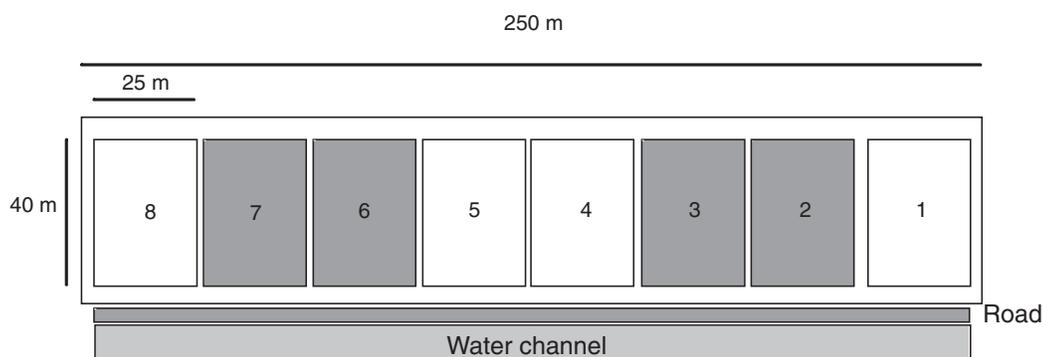
Figure 1. Schema of the irrigation experiment with irrigated (grey) and control (white) plots and the water channel.
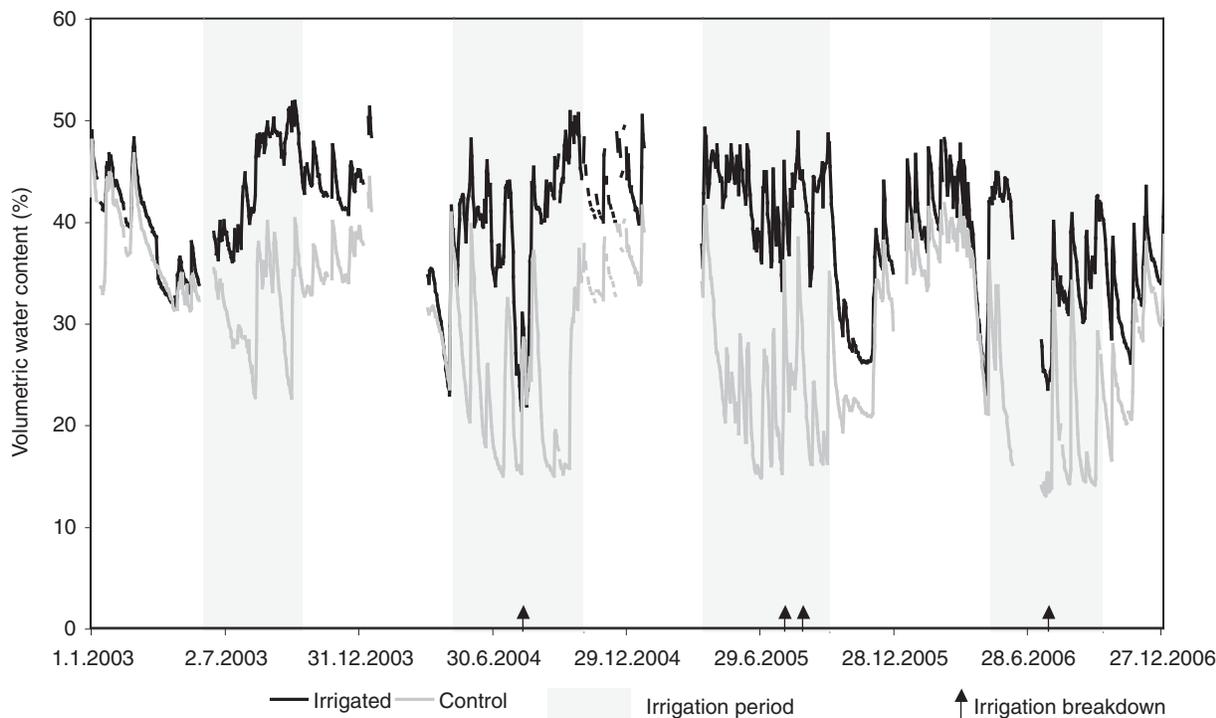
Figure 2. Mean measured water content in control and irrigated plots at 10-cm soil depth for the irrigation years 2003, 2004, 2005 and 2006.

watering at a height of 110 cm and with an action diameter of 7 m per sprinkler. With the exception of 2003, irrigation began in April and stopped in October due to the risk of early or late frost. In 2003, however, irrigation started later than planned due to technical reasons and did not reach its optimum until July 2003. With the exception of 2003, irrigation doubled the long-term annual precipitation at the site (Table 1).

Soil water content was monitored hourly in one control and in one irrigated plot using Time Domain Reflectometry (Tektronix 1502B cable tester, Beaverton, OR, USA) at four different sites per plot and at the three soil depths 10, 40 and 60 cm (Brunner et al. 2009). All data per plot for the same soil depth were averaged. Figure 2 shows the mean volumetric water content at a soil depth of 10 cm in the control and irrigated plots between 2003 and 2006. The water content in the irrigated plot was higher than the water content measured in the control plot during the irrigation periods from 2003 to 2006, except at the beginning of the experiment in July 2003 and during short periods in summer 2004, 2005 and 2006 due to failure of the irrigation system (Figure 2). The mean volumetric water content at a depth of 10 cm over the four irrigation periods was significantly higher (38.3 ± 0.4 vol.%, $\pm 2 \times$ standard error) than the water content in the control plot (28.7 ± 0.4 vol.%). Irrigation also increased significantly the soil moisture at depths of 40 and 60 cm (data not shown).

Nutrient content of the irrigation water was analysed at the beginning of the experiment in 2003 and compared to rainfall chemistry at the nearby level II monitoring site Visp (20 km distance, 650–700 m a.s.l.) using bulk deposition from open-field samplers. Mean concentration of nitrate at Visp during the

period 2003–07 was 0.35 mg l^{-1} N and of ammonium 0.4 mg l^{-1} N. Irrigation water contained 1.1 mg l^{-1} nitrate-N and 0.3 mg l^{-1} ammonium-N. Bulk deposition for an annual precipitation of 600 mm at Visp was estimated at 4.2 kg ha^{-1} total N. However, estimated total deposition including dry deposition was almost 10 kg ha^{-1}. Total N addition due to the irrigation from 2003 to 2005 (mean 610 mm) was estimated at 8.7 kg ha^{-1} $year^{-1}$. We conclude that N addition due to the irrigation is higher (+4.5 kg $ha^{-1}year^{-1}$) than it would be if rainfall water had been added. But since the total amount of N is relatively low, no strong fertilization effect should be expected.

The water in the channel had high pH values. As the soil type is calcareous with high pH values, this only influenced the upper soil layer which is more acidic. pH in the upper 0–5 cm was significantly increased by the year 2008 (5.5 in the control, 6.0 in the irrigated plots), but at 5–10 cm soil depth, differences were not significant (6.1 in control plots, 6.3 in the irrigated plots). This should not have affected the tree nutrient supply.

Concentrations of Ca and Mg in irrigation water were more than a magnitude higher than found in rainwater. K was also higher, while P was almost below the detection limit. Nutrient concentrations in needles of control and irrigated trees were measured several times since irrigation started. Nutrient concentrations in needles of both control and irrigated trees were found to be mostly in the optimum range of nutrient concentrations when compared to values from the literature. K was found to be at the higher end of the range, while P concentrations were found to be at the lower end. Content of N, K, Ca and Mg in current year needles of both control and irrigated

Table 2. Statistics of the 13 felled trees and their mean age, size, assessed crown transparency and viewing path-adjusted crown transparency by treatment at the time of felling in April 2006 (if not indicated otherwise).

Trees	Age	DBH	Tree height	Crown length	Crown width	Viewing path	Crown transparency				Viewing path-adjusted crown transparency			
	Years	cm	m	m	m	m	2003 (%)	2004 (%)	2005 (%)	2006 (%)	2003 (%)	2004 (%)	2005 (%)	2006 (%)
Irrigated														
A 816	118	26	11.8	4.3	5.3	4.2	5	35	15	10	7	41	21	16
B 440	61	18	10.8	5.0	4.4	3.9	10	10	5	5	9	10	6	8
C 1123	71	22	12.9	3.6	3.5	3.2	25	30	15	30	21	26	13	29
D 388	127	24	9.7	4.2	5.5	4.1	35	45	35	25	39	51	42	33
E 745	117	25	11.8	2.7	4.6	2.8	55	50	55	60	44	40	47	55
F 170	88	22	10.8	4.4	3.3	2.7	70	50	55	45	63	42	47	38
G 871	124	21	10.9	3.1	3.6	3.0	75	65	70	60	72	61	67	57
Total mean	101	22.6	11.2	3.9	4.3	3.4	39	41	36	34	37	39	35	34
Control														
A 486	115	20	9.0	2.9	4.3	2.9	5	15	5	10	1	9	3	7
B 123	74	18	11.6	4.5	3.5	2.9	15	20	20	50	8	14	15	46
C 581	66	20	11.4	3.9	4.3	3.7	25	30	45	60	27	33	49	64
D 178	74	18	10.0	4.6	4.2	3.8	35	35	35	40	38	39	39	45
E 1084	125	24	10.5	4.5	5.0	4.3	60	35	55	60	67	44	63	68
F 915	70	18	10.8	1.9	3.0	1.9	80	80	80	85	67	67	68	76
Total mean	87	19.7	10.6	3.7	4.1	3.3	37	36	40	51	35	34	39	51

trees were also within the range of values found at the two nearby level II sites Visp and Lens (15 km distance, 1050 m a.s.l.) for the years 1997–2007, while P was slightly lower. In a preliminary analysis of the effect of irrigation, no significant effects of irrigation were found on P, N and Ca (P. Schleppi et al., in preparation). Of the main nutrients, only K increased, but it was within the optimum range, as in control trees.

Tree condition assessment

All co-dominant and dominant pines with a minimum of 12 cm in diameter were annually assessed for crown condition. Assessment took place in March before the new shoots emerged. Assessment included a visual rating of the crown transparency (also termed defoliation) in 5% steps using reference photographs ranging from 0% (= a fully foliated tree) to 100% (= a dead tree; for more detail, see Dobbertin et al. 2004). This assessment is not a strict crown transparency assessment as tree crown foliage is judged relative to the optimum foliage a tree of the same species can achieve. It is, however, also not a defoliation assessment where only missing needles due to some known cause are reported.

All transparency assessments were made independently of the prior assessments, i.e., observers did not know the values of the previous assessment. Every 100 trees, the prior values of five trees in the buffer zone were made known to the observer, to avoid a drift in the assessment (Dobbertin et al. 2004). Transparency of Scots pine had been shown in previous studies to highly correlate with subsequent tree mortality (Dobbertin and Brang 2001), mistletoe infection rates (Dobbertin and Rigling 2006) and bark beetle infestations (Wermelinger et al. 2008) and tree growth (Dobbertin

2005). Thus, it was considered a good proxy for the vitality status of the tree. For the analysis of changes in crown transparency, only trees that were alive before the start of the irrigation were considered.

LAI estimation

Hemispherical pictures were taken from three points along the main axis of each plot at the end of each vegetation period (2004 to 2008). These points were marked by stakes and used year after year. A digital camera (Coolpix 4500, Nikon, Tokyo) with a fish-eye lens (Nikon FC-E8) was fitted to self-levelling gimbals (SLM2, Delta-T, Cambridge, UK) mounted on a tripod at 1 m above ground. The compass of the gimbals was used to set the north direction of the pictures. All pictures were taken with delayed release to prevent camera shake. They were saved in high-quality JPEG files with a resolution of 2272 × 1704, yielding a horizon circle with a diameter of 1520 pixels. The exposure was set manually according to the light measured with a spot-meter (Asahi Pentax V, Asahi, Tokyo) on sky patches near the zenith. The pictures were overexposed between one and two exposure stops compared to these readings, i.e., by a factor between 2 and 4. This procedure (Schleppi et al. 2007) makes the exposure independent of the portion of visible sky. It is meant to optimize the use of the sensor range of the camera without producing a blooming of the sky patches. Such a blooming would occur at least under dense canopies with an automatic exposure, making canopy gaps appear larger than they really are and causing a negative bias in the estimation of LAI. All photographs were analysed with the *Hemisfer* software, version 1.4 (http://www.wsl.ch/dienstleistungen/hemisfer). Five rings of 12.5° width were used, for a total angle

of 62.5° adapted to size of the plots and to the height of the trees. In order to improve the contrast between vegetation and sky, the analysis was done in the blue colour channel only. The threshold was automatically determined according to the method of Nobis and Hunziker (2005). The γ factor for this operation was set to 2.2 according to the light response curve of the camera. A correction factor Ω for canopy clumping was further calculated by the software according to the method of Chen and Cihlar (1995) adapted to hemispherical photographs.

Sampling and measuring

For a more detailed study, seven trees each were selected from the irrigation plots and the control plots. The seventh tree of the control was later found to be outside of the plot delineation and had been used in a mistletoe cutting experiment. Therefore, it had to be excluded. Selection of these trees, which had to be without visual stem damage, followed a stratified random sampling covering the range of transparency scores assessed before the irrigation began in March 2003.

In April 2006, the trees were felled, stem discs at 2 m tree height were cut and two large branches without mistletoe infection and visible injuries were removed from the upper 1.5 m of the crown of each tree and transported to the laboratory. Tree parameters like tree height, crown length and diameter were also measured on the felled trees during sampling (data in Table 2).

For the tree-ring analysis, the stem discs were sanded (35 µm particle diameter). The tree-ring width of the last 10 years (1996–2005) was measured along two radii using a Lintab digital positioning table and the software TSAP (both Rinntech, Germany). The two measurements per tree were averaged.

From the branches cut during sampling, the five main shoot leaders were selected and shoot length measured to the millimetre going back to the year 2000. Within each annual shoot, 20 needles were selected close to the centre of each annual shoot; the short shoot needle pairs were separated and one needle kept for needle length and area measurements. Altogether, up to 10 samples of 20 needles were measured for each tree. If less than 20 needles were found on a shoot and less than five shoots were found with at least 20 needles, the assessment was excluded from the analysis. The fresh mass of the 20 needles was determined to the milligram, and the needles were scanned and analysed with winSEEDLE software (winSEEDLE 2006 Régent Instruments Inc.) and their length, projected needle area and fresh mass obtained. Afterwards needles were oven-dried at 70 °C for 48 h and the dry mass of 20 needles, the specific needle area (SLA, projected needle area per needle mass) and the dry/fresh mass ratio per shoot determined.

Crown transparency adjustment

Crown transparency assessment can be influenced by the length of the viewing path the observer has through the tree crown. For this purpose, observers should always observe trees from the same position for repeated assessments. In addition,

the distance to the tree should be approximately one tree length. To test the influence of different viewing path length for trees with different crown dimensions, we applied a method described in Metzger and Oren (2001) to adjust the assessed transparency rating. We calculated the viewing path in 2006 for each felled tree through the centre of the tree crown assuming a 45° viewing angle and conical tree crowns. We adjusted the viewing path for the past years by assuming that the mean shoot length measured from the sampled branches occurred in all directions of the crown and reduced the viewing path accordingly. We used the following formula for crown transparency as a function of viewing path length (Metzger and Oren 2001):

$$CT = 100e^{-\alpha d} \tag{1}$$

where CT is the assessed crown transparency, d is the viewing path length and α is a parameter that combines mean needle density (square metre of needle area per cubic metre of crown volume) and the spatial organization of the foliage. While the spatial organization of the foliage should be fairly invariant in time, mean needle density might be the best indicator for tree health status. For two trees with the same health status or α, a longer viewing path d would result in lower transparency assessments. With the calculated d and the assessed crown transparency, we estimated α. Using the mean viewing path length of all sampled trees and annual α, we adjusted the crown transparency values for each annual crown transparency assessment for each year (Table 2).

Drought index

For the comparison between growth and climate, a simple drought index (DRI) was used. DRI was calculated based on monthly data of precipitation (P) and potential evapotranspiration (PET) according to Thornthwaite (1948) based on temperature data from the climate station Sion and for precipitation from the station Sierre:

$$DRI_t = P_t - PET_t \tag{2}$$

with P_t equal to the monthly precipitation sum of the time period t during which the evaluated tree growth took place; or in case of shoot growth the primordia were formed. PET equals the sum of estimated potential evapotranspiration for the same period as a function of monthly mean temperatures and geographical latitude. We used the period from April until June to compute the drought index for needle length, the period from June to September of the previous year for the new shoot formation and the period from April to September for stem growth. To calculate the drought index for irrigated plots, the irrigation amount for those selected periods was added ($P_t + I_t$).

Statistical analysis

The change in crown transparency between annual assessments and between the 2003 and 2006 transparency scores

Table 3. Mean crown transparency by plot and treatments and changes between 2003 and 2006. Wilcoxon rank sum test was used to test for between-treatment differences in the same blocks and for all blocks combined (P-values in table, bold for $P < 0.05$).

Blocks	Plots	Treatments	No. trees	Crown transparency (%)		Change in crown transparency (%)			
				2003	2006	2004−03	2005−04	2006−05	2006−03
1	1	Control	98	33.1	43.5	4.0	0.8	5.6	10.4
	2	Irrigation	96	33.9	26.7	−0.5	−0.3	−6.5	−7.2
Wilcoxon rank sum test						**0.016**	0.158	**< 0.001**	**< 0.001**
2	4	Control	67	22.5	31.9	1.5	1.5	6.4	9.4
	3	Irrigation	54	27.7	26.6	−1	−0.7	0.6	−1.1
Wilcoxon rank sum test						0.257	0.312	**< 0.001**	**< 0.001**
3	5	Control	62	30.6	36.9	−0.6	3.9	3.0	6.3
	6	Irrigation	76	36.4	28.6	−1	−0.1	−6.8	−8.0
Wilcoxon rank sum test						0.84	**0.014**	**< 0.001**	**< 0.001**
4	8	Control	69	31.2	36.9	−3.7	8.0	1.4	5.7
	7	Irrigation	60	32.0	28.0	0.1	2.2	−6.3	−4.0
Wilcoxon rank sum test						0.058	**0.007**	**< 0.001**	**< 0.001**
Total	Total	Control	286	29.7	38	0.68	3.3	4.3	8.2
		Irrigation	296	33	27.4	−0.6	0.2	−5.2	−5.6
Wilcoxon rank sum test						0.386	**< 0.001**	**< 0.001**	**< 0.001**

was compared between adjacent plot pairs (blocks) using Wilcoxon rank sum test using a one-sided test statistic (expectation was that irrigation reduced transparency relative to the control). No correction factor for multiple testing was applied as the obtained P-values for the treatment effect was in most cases much lower than 0.001. Mean crown transparency per plot and mean LAI were analysed using a one-way analysis of variance (ANOVA) for treatment effects separately for each year.

For the 13 felled trees, we first analysed the relation between assessed crown transparency and viewing path-adjusted transparency with measured growth parameters. We also correlated mean measured needle length and mean measured shoot length with adjusted crown transparency before tree felling. Because neither needle nor shoot length was changed by the late irrigation start in 2003, the adjusted crown transparency scores from March 2003 and March 2004 could be averaged for the 13 trees to reduce observer error (see Table 2).

For the multivariate analysis, mean values per tree for a given year were used for all the measured variables of tree needle size, shoot length and stem growth. Analysis of covariance (ANCOVA) was applied for each year separately using the irrigation treatment versus control and the covariate adjusted crown transparency prior to irrigation (i.e., the mean values for 2003 and 2004) and their interaction (test for separate slopes, JMP® 7.02, 2007 SAS Institute Inc.) according to the following model:

$$y_j = \mu_j + \alpha_{ij} + \beta_j x_j + \gamma_{ij} x + \varepsilon_{ij} \qquad (3)$$

where y_j stands for the response variables j, μ_j is the mean effect, α_{ij} is the treatment effect for treatment i, β_j is the parameter estimate for the covariate x (adjusted crown trans-

parency), γ_{ij} is the parameter for the interaction between treatment i and the covariate x and ε_{ij} is the error term.

Finally, Pearson's correlation between calculated drought index and needle length, shoot length and ring width for irrigated and control trees was calculated.

Results

Crown transparency and LAI

Crown transparency values before irrigation were fairly similar between plots with insignificantly higher values in plots selected for irrigation (Table 3). We used all trees per treatment for the effect of irrigation on tree transparency. The crown transparency observation in March 2004, after half a year of irrigation, showed no significant change in transparency (Table 3). In March 2005 after the second year of irrigation, a significant overall decrease of transparency was found in irrigated plots, but no consistent effect between treatments was yet observed. After the third year of irrigation, all irrigated treatments had reduced transparency in comparison to the control treatment in the adjacent plot. The 3-year difference in treatments was also highly significant. Although the absolute changes in crown transparency have to be interpreted with care due to a possible between-year assessment bias, the trees on all control plots had significantly increased in crown transparency (mean: +8.2%), while in three out of four irrigated plots, trees showed significantly reduced transparency (mean: −5.6%).

LAI was first calculated at the end of the 2004 growing season and ranged from 1.8 to 2.6, with a mean of 2.2 and no significant difference between treatments. LAI was not uniform across plots due to different initial stand density
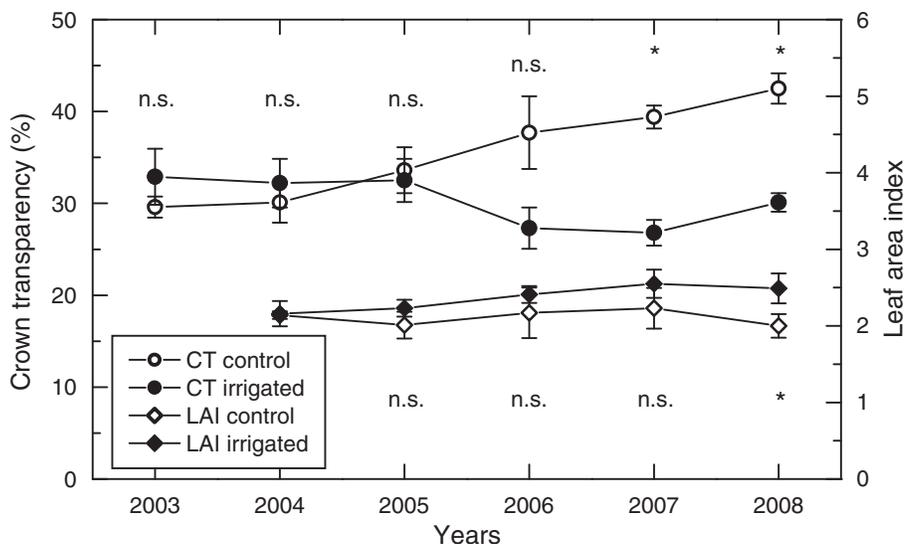
Figure 3. Development of the mean leaf area index (LAI) and crown transparency (CT) for irrigated and control plots with standard error bar. Indicated are the results for the one-way ANOVA model for LAI differences to the year 2004 and crown transparency to the year 2003 for each year (n.s., not significant, *, significant at $P = 0.05$).

Table 4. Minimum and maximum Pearson's correlation coefficient of assessed crown transparency and crown transparency adjusted for viewing length bias (Metzger and Oren 2001) for the four assessments made in March 2003, 2004, 2005 and 2006 with corresponding needle length, area, mass, dry/fresh needle mass, specific needle area (SLA), shoot length and ring width (irrigated and control trees combined).

	Needle length	Needle area	Needle mass	Dry/fresh mass	SLA	Shoot length	Ring width
Assessed crown transparency	−0.59, −0.80	−0.65, −0.91	−0.63, −0.89	0.26, 0.78	0.65, 0.76	−0.77, −0.88	−0.50, −0.81
Adjusted crown transparency	−0.57, −0.76	−0.59, −0.92	−0.58, −0.90	0.20, 0.60	0.57, 0.70	−0.80, −0.91	−0.44. −0.76

varying between 54 and 98 trees per plot. Individual ANOVA analysis of the LAI change was not significant for the years 2005 to 2007 but significant in 2008 (Figure 3). In 2008, the LAI of irrigated plots was 0.47 or roughly 20% higher than the LAI of the controls. Development of plot LAI was parallel to the mean changes in individual tree crown transparency, though with opposite signs (Figure 3). Mean plot transparency differences to the 2003 value were not significant between treatments in a one-way ANOVA in 2004, 2005 and 2006 but significant in 2007 and 2008 (Figure 3).

Individual tree condition and growth comparison

Tree age, tree height, crown length and crown transparency of the 13 felled trees were not different between treatment groups before the beginning of the experiment (Table 2). Tree age at roughly 2 m stem height varied between 61 and 127 with mean 87 for the control trees and 101 for the irrigated trees. The mean viewing path for the crown assessment was almost identical in the seven irrigated and six control trees. Therefore, the mean values of the adjusted crown transparency scores and their difference between years did not change much as compared to the original value, but individual assessment values changed between −13 and +9%. Although

viewing path correlated negatively with assessed transparency ($r = −0.4$ to $−0.5$), adjusted crown transparency and assessed crown transparency showed very similar correlation with needle shoot and stem growth variables (Table 4). For the needle length, area and mass measurements correlation coefficients ranged between −0.57 and −0.91, for shoot length between −0.77 and −0.91 and for ring width between −0.44 and −0.81. Crown transparency correlated positively with dry to fresh mass ratio and SLA with, in general, higher correlations achieved for the SLA. Mean needle length and mean shoot length per tree over the years 2002 to 2005 correlated highly with the adjusted crown transparency in March 2006 ($r = −0.71$ and $−0.78$, respectively). This was not related to the irrigation treatment (Figure 4A and B).

In the ANCOVA analysis in almost all models, identical significances were found when using assessed or adjusted crown transparency (though with slightly different P-values). In the following, only the results for the adjusted crown transparency will be presented. In the ANCOVA, no interaction (different slopes) between treatment and crown transparency was found significant. Therefore, the models were recalculated for equal slope assumption (Tables 5 and 6). For almost all needle and growth variables, the covariate adjusted crown transparency was found to be significant at the 5% significance level. The
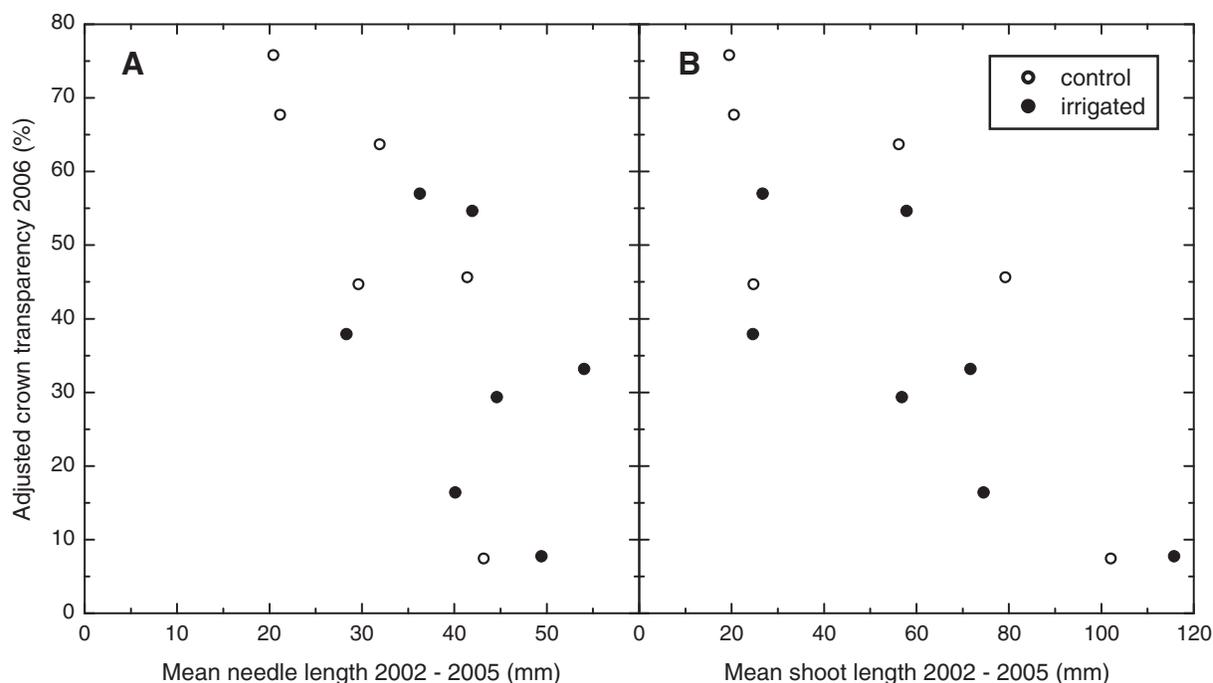
Figure 4. Mean needle length (A) and mean shoot length (B) per tree for the years 2002–05 and viewer-path-adjusted crown transparency in March 2006 for irrigated and control trees.

exceptions were dry/fresh needle mass ratio in year 2002 and 2005, SLA in 2002 and the changes in individual crown transparency in all years. Irrigation treatment was significant for needle length, area and mass in 2004 and 2005, for shoot growth only in 2005, for ring width in 2004 and 2005, for SLA in 2004 and for change in transparency between 2006 and 2003 (Tables 5 and 6, Figure 5).

Adjusted crown transparency before irrigation started correlated highly with most tree growth and needle parameters following the irrigation: examples for needle length in 2004, shoot length in 2005, stem growth in 2004 and specific leaf area in 2004 are presented in Figure 6. Irrigation resulted in an additive effect in most of the measured growth and needle parameters, which is also indicated in the non-significant interaction term in the ANCOVA. In other words, irrigation increased needle, shoot and stem growth and reduced SLA almost by identical amounts regardless of initial crown transparency.

Relation between drought index and needle and tree growth parameters

Finally, needle length and shoot and stem growth in control and irrigated plots were compared against computed drought stress, once including and once not including irrigation amount (Table 7). The drought index using only precipitation and potential evapotranspiration correlated highly with needle length, shoot length and ring width of the control trees, but correlation was low or not existent for the irrigated trees. On the other hand, the drought index with irrigation amount

gave almost no correlation with tree growth of the control trees but correlated highly with growth of the irrigated trees.

Discussion

Crown transparency, LAI, needle properties

The LAI calculated in our study (around 2 in the control plots) ranges at the lower end of studies on LAI in closed Scots pine forests (Bernhofer et al. 1996, Cermak et al. 1998, Xiao et al. 2006, Montes et al. 2007). Given the fact that mean crown width in our study was less than 4 m, tree height only 11 m and stand density 730 trees per hectare, the low LAI in our study is not surprising. Mean needle size found in the light crown of our trees (length between 20 and 40 mm in control trees) was smaller than found in most other studies on Scots pine except on extremely infertile sites (Niinemets and Lukjanova 2003) or at high latitude (Junttila and Heide 1981). SLA (3.8–5.4 in control trees), on the other hand, was comparable to other studies (van Hees and Bartelink 1993, Pensa and Sellin 2002, Xiao and Ceulemans 2004, Xiao et al. 2006, Montes et al. 2007). Many studies have observed a high variability of needle size and SLA usually related to the relative position of needle within the crown (van Hees and Bartelink 1993, Xiao and Ceulemans 2004, Xiao et al. 2006), tree age and altitude (Li et al. 2006). SLA for even-aged needles, for example, has been shown to increase with the whorl position or distance to the top of the tree (Oren et al. 1986, van Hees and Bartelink 1993, Xiao and Ceulemans

Table 5. Analysis of covariance models for all needle size variables as response variable and irrigation treatment as variate and mean crown transparency 2003–04 as covariate (*P*-values are given for the parameters and adjusted R^2 for the overall model performance).

Effects	NL02	NL03	NL04	NL05	NA02	NA03	NA04	NA05	NW02	NW03	NW04	NW05	SLA02	SLA03	SLA04	SLA05	DFW02	DFW03	DFW04	DFW05
Intercept	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Irrigation	0.2312	0.2529	0.0001	0.0110	0.7381	0.3648	0.0004	0.0274	0.6665	0.3436	0.0007	0.0521	0.4230	0.4455	0.0016	0.1697	0.8106	0.5144	0.0584	0.2637
Adjusted crown transparency	0.0145	0.0083	0.0032	0.0067	0.0081	0.0074	0.0045	0.0144	0.0101	0.0103	0.0071	0.0269	0.0893	0.0121	0.0012	0.0286	0.7112	0.0313	0.0373	0.1130
Adjusted R^2	0.46	0.45	0.80	0.60	0.73	0.45	0.75	0.51	0.67	0.41	0.72	0.42	0.32*	0.39	0.76	0.34	0.00*	0.27*	0.39	0.15*

NLx, needle length in year x; NAx, needle area in year x; NWx, ofen dried needle mass in year x; SLAx, specific needle area (NA/NW) in year x; DFWx, dry mass/fresh mass in year x. *Overall model not significant at the 0.05% level.

Table 6. Analysis of covariance models for shoot and stem growth and change in transparency as response variable and irrigation treatment as variate and mean viewer-path-adjusted crown transparency 2003–04 as covariate (*P*-values are given for the parameters and adjusted R^2 for the overall model performance).

Effects	SL02	SL03	SL04	SL05	RW02	RW03	RW04	RW05	adCT43	adCT53	adCT63
Intercept	0.0001	0.0001	0.0001	0.0001	0.0010	0.0004	0.0001	0.0001	0.0841	0.2648	0.0280
Irrigation	0.8790	0.9605	0.1291	0.0020	0.7478	0.6958	0.0363	0.0070	0.6174	0.2720	0.0393
Adjusted crown transparency	0.0001	0.0009	0.0005	0.0004	0.0357	0.0312	0.0027	0.0035	0.0674	0.3303	0.0797
Adjusted R^2	0.80	0.71	0.67	0.77	0.26*	0.26*	0.60	0.65	0.16*	0.05*	0.41

SLx, shoot length in year x; RWx, ring width in year x; adCTxy, change in adjusted crown transparency between years x and y. *Overall model not significant at the 0.05% level.
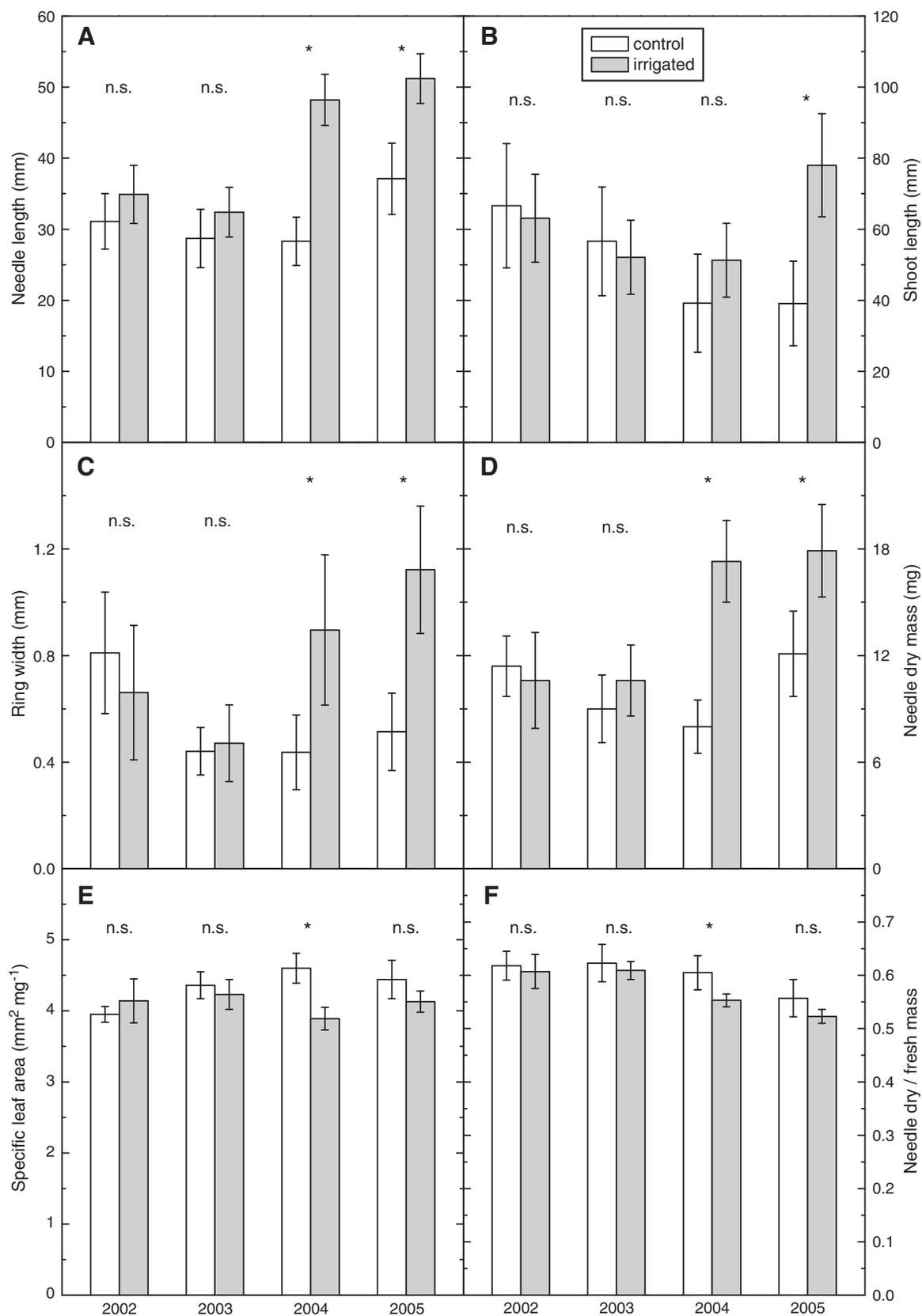
Figure 5. Mean annual changes in needle length (A), shoot length (B), ring width (C), needle mass (D), specific leaf area (E) and needle dry to fresh mass (F) for control and irrigated plots with standard error (n.s., treatment not significant in an analysis of covariance, *, significant at $P = 0.05$).
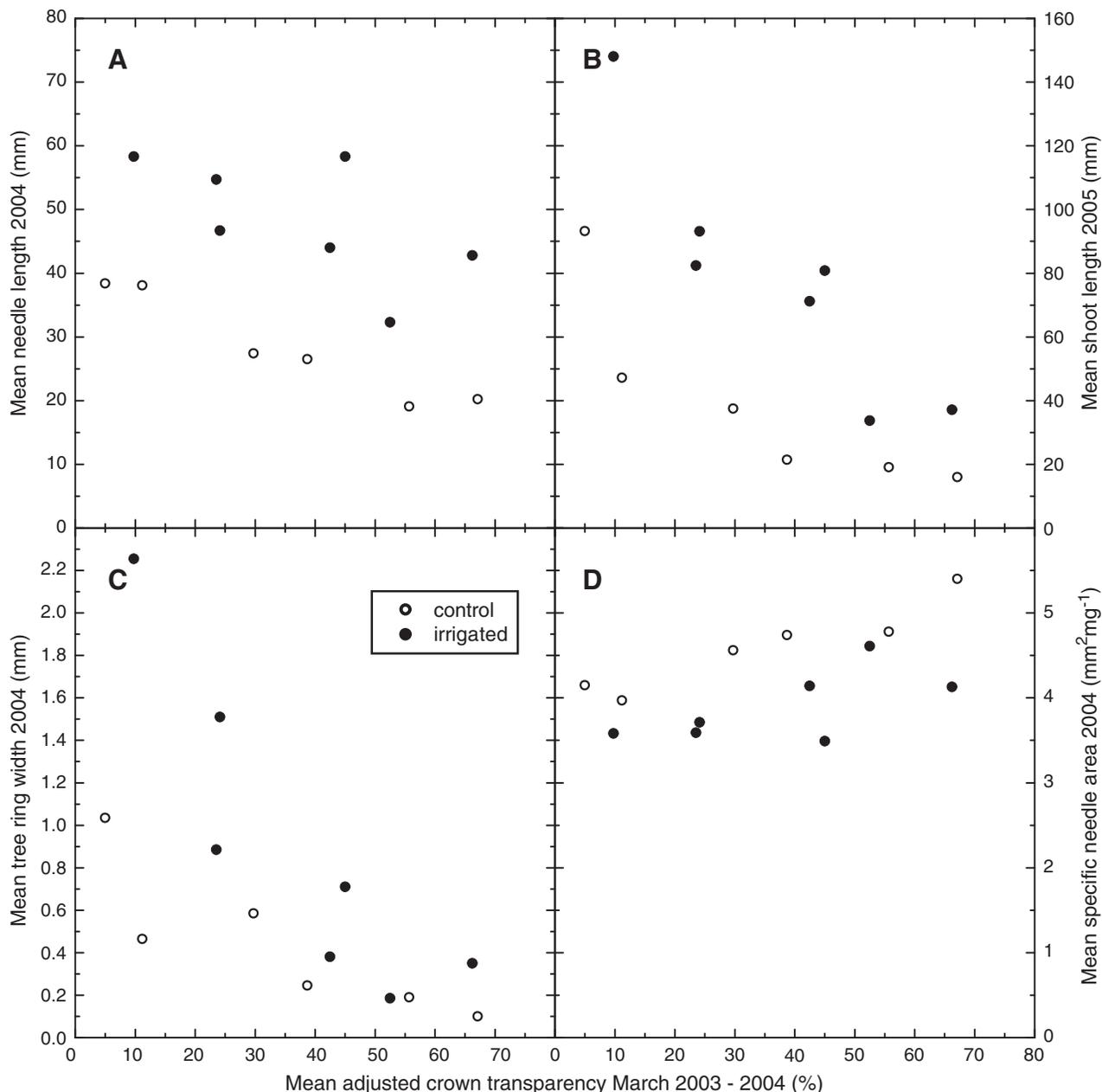
Figure 6. Mean viewer-path-adjusted crown transparency for the years 2003 and 2004 and (A) mean needle length in 2004, (B) mean shoot length in 2005, (C) mean ring width in 2004 and (D) mean specific needle area in 2004 for irrigated and control trees.

2004, Xiao et al. 2006) and to increase from the edge to the interior of the crown (Xiao et al. 2006), thus being highly dependent on the actual light conditions. In addition, SLA decreases with needle age (van Hees and Bartelink 1993, Xiao and Ceulemans 2004, Xiao et al. 2006). Usually, differences between mean SLA were smaller between trees of the same social position. In our study, we demonstrated that even when needles are sampled from the same crown position, large differences existed between trees. These differences were largely related to initial tree crown transparency. The finding that SLA of transparent trees was higher than that of trees with dense foliage cannot be explained by increased

radiation in these trees, as this should have reduced SLA (Oren et al. 1986).

Effect of irrigation

In our irrigation experiment, we found that the differences in LAI and crown transparency between the irrigated and the control plots evolved over time and became significantly different after 3 to 4 years of irrigation for crown transparency and after 5 years for LAI. Mean needle longevity in Pfynwald is around 4 years and usually changes little from year to year (Pouttu and Dobbertin 2000). As irrigation started to increase

Table 7. Pearson's correlation coefficient of a drought index computed as the difference between precipitation (P) with and without irrigation (I) amount and computed potential evapotranspiration (PET, Thornthwaite 1948) and mean annual needle growth, shoot length and ring width for control trees and irrigated trees (considered months for needle length, April–June; shoot length, June–September of the previous year; ring width, April–September; expected higher correlations are indicated in bold).

	Needle length (2002–05)		Shoot length (2000–05)		Ring width (1996–2005)	
	Control trees	Irrigated trees	Control trees	Irrigated trees	Control trees	Irrigated trees
Drought index (P − PET)	**0.57**	0.21	**0.92**	0.26	**0.69**	0.34
Drought index ($P + I$ − PET)	0.46	**0.88**	−0.09	**0.79**	−0.26	**0.72**

needle length in the second year and shoot length in the third year of the experiment, it is obvious that it may take several years until all needle years are affected by irrigation and whole stand effects become visible. As stand density did not change during the time of treatment, changes in individual tree transparency and stand LAI should develop in parallel, which could be shown on felled trees in our study. Irrigation in our study increased needle length, mass and area (70% in year 2004), shoot length (100% in 2005) and ring width (120% in 2005). In correspondence with our results, several studies have shown a negative effect of drought on needle and shoot length: Raison et al. (1992) analysed the needle length in 10- to 14-year-old *Pinus radiata* D. Don plantation in Australia in a 4-year irrigation and nitrogen fertilization experiment. At this summer-drought-prone site, they found that irrigation and irrigation plus fertilizer increased needle length by up to 40% but not fertilizer alone. Needle length development was directly correlated with current season drought stress integral. For the same experiment, Benson et al. (1992) reported a 43% increase in basal area increment. Fertilizer treatment alone resulted only in a 24% increase, and combinations of irrigation and fertilizer doubled basal area growth. In a 9-year irrigation/fertilizer experiment in *Pinus taeda* L. stands, Albaugh et al. 2004 observed an increase of 23% in stem biomass due to irrigation alone but 119% by fertilization alone, while height growth was increased by 21 and 53%, respectively. Murthy and Dougherty (1997) found 37% increased first flush length in *P. taeda* due to irrigation.

In our experiment, shoot growth reacted with a 1-year delay as compared to needle and stem growth. This is in agreement with the fact that Scots pine shoot growth occurs in a single flush from buds formed the previous season (fixed growth, Lanner 1976). Thus the shoot growth of Scots pine is predetermined by the period of the bud formation. During bud formation, the shoot apical meristem initiates all the major structures that will appear in the elongated shoot, including bud scale primordia and spirally arranged leaf primordia (Lanner 1976). Consequently, the length of the new shoot is, to a large degree, determined by the number of stem units laid down during the bud formation (Burger 1926, James et al. 1994, Junttila and Heide 1981, Junttila 1986, Salminen and Jalkanen 2005).

Irrigation increased LAI by roughly 20% in 4–5 years. Joint fertilizer and irrigation experiments usually find increased LAI due to fertilization but no consistent effect of irrigation. Whether irrigation increased LAI depended on the natural climatic condition and the actual canopy closure. In areas not limited by drought during the irrigation period, LAI is either not or only slightly increased (Albaugh et al. 2004, Ewers et al. 2007, Trichet et al. 2008). Although we found increases in needle length between 40 and 70% and in shoot length between 30 and 100%, LAI did not increase that much. This is reasonable as the branches sampled for needle and shoot analysis came from the upper light crown, and the increased needle mass in the upper crown must not be reflected in the lower crown due to increased shading. In addition, we did not assess whether branching in the crown increased at a similar rate as needle size and shoot length and thus whether individual tree needle mass increased proportionally to needle and shoot size.

In 2004, a significant reduction in SLA and dry to fresh needle mass ratio was found for irrigated trees but not in 2005. Raison et al. (1992) found no effect of irrigation on SLA in irrigated *P. radiata* plantations, and also Murthy and Dougherty (1997) found no effect of irrigation on SLA of *P. taeda* trees. The significant effect of irrigation on SLA found in our study during the extremely dry spring of 2004 needs, therefore, to be tested in further studies.

Are there confounding effects of the irrigation treatment?

Any irrigation or water removal experiment has to consider that water addition or removal also adds or removes nutrients from the system. We therefore tested the potential effect of nutrient additions in the irrigation water. The water for the irrigation experiment was taken from a water channel used for hydro-electricity. The water comes from the Rhone River and is fed by water from glaciers and mountain streams. The watershed of the Rhone River before the start of the channel is sparsely settled with around 30 inhabitants per square kilometre. The upper Rhone River down to its delta into lake Geneva is considered a relatively clean river with low concentrations of nutrients, in particular nitrogen or phosphorus.

The chemical analysis of the irrigation water and needle samples demonstrated that the elements P and N that are slightly deficient or close to deficiency (and thus critical for the nutrition of the trees) were not affected by the irrigation in their needle concentrations. On the other hand, the elements for which we observed concentration changes were not critical because they remained perfectly within the optimum nutritional range. The irrigation thus did not really affect the

nutritional status of the trees. These findings and the fact that the drought index correlated highly with growth parameters of trees when irrigation amount was included suggest that the main cause of increased needle, shoot and stem growth was due to increased water supply and not to a confounding fertilizing effect.

High crown transparency—sign of low tree vigour?

We found highly significant negative relation between assessed tree crown transparency and most of the tree growth parameters. This relationship was also found when crown transparency was adjusted for viewing path length, as long viewing path length would cause lower transparency assessments of trees with large crowns. The relationship between adjusted transparency and mean needle and shoot length can be expected because tree crown transparency should be a function of needle size, shoot size and needle longevity (i.e., needle mass per volume). The consistent significant relation of crown transparency with subsequent needle, shoot and stem growth regardless of irrigation suggests that initial crown transparency is a valid indicator of tree vigour as has been found in previous studies (Solberg 1999, Dobbertin 2005). Långstöm et al. (2004) found that Scots pines that were heavily defoliated by the pine looper in Sweden had reduced needle length in the year of defoliation as compared to less defoliated trees but not the following year when insects were controlled. Shoot length, on the other hand, was significantly reduced the year following defoliation. As irrigation improved needle production and subsequently reduced crown transparency, it can be hypothesized that irrigation has also improved tree vigour. Interestingly, the increase in foliage production was independent of initial crown transparency. This means that trees with low transparency responded with similar absolute increase in needle production and growth and had therefore a higher relative response to irrigation than trees with low transparency. This was unexpected and shows that mature pines with seemingly low vigour can still react to increased water availability.

Carbon allocation under drought

The strong effect of the irrigation in above-ground tree growth found in this study stands in contrast to the effects of irrigation on root growth reported recently in the same experiment by Brunner et al. (2009). These authors found fine root standing crop measured each spring from 2003 to 2005 to be unaffected by the irrigation treatment. However, irrigation significantly enhanced the fine root standing crop between spring and autumn of 2005 and slightly increased specific root length. No significant difference was found between trees with high and low crown transparency. They concluded that, in accordance with the carbon allocation priorities formulated by Waring (1987), fine roots have higher priority for within-tree carbon allocation under drought stress. Waring had postulated that in general carbon allocation in trees is highest for roots and foliage as com-

pared to stem growth, storage and defence compounds. However, Waring also stated that under drought stress foliage growth is reduced in comparison to root growth resulting in lower shoot/root carbon allocation ratio (Linder and Axelsson 1982, Waring 1987). This was supported by the reduced above-ground growth in our study.

In summary, our experiment demonstrated that, for the investigated forest, water is the limiting factor for tree growth. Irrigation increased growth of stems, shoots and foliage. With the increase in needle mass, stand LAI increased, and mean crown transparency was reduced. Different than expected, trees with high crown transparency and apparently low vigour could recover when water was added and responded with needle, shoot and stem growth increase of the same magnitude as trees with low transparency.

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