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Morphological and physiological responses of Scots pine fine roots to water supply in a dry climatic region in Switzerland

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Summary In recent decades, Scots pine (*Pinus sylvestris* L.) forests in inner-Alpine dry valleys of Switzerland have suffered from drought and elevated temperatures, resulting in a higher mortality rate of trees than the mean mortality rate in Switzerland. We investigated the responses of fine roots (standing crop, morphological and physiological features) to water supply in a Scots pine forest in the Rhone valley. Before irrigation started in 2003, low- and high-productivity Scots pine trees were selected based on their crown transparency. The fine root standing crop measured in spring from 2003 to 2005 was unaffected by the irrigation treatment. However, irrigation significantly enhanced the fine root standing crop during the vegetation period when values from spring were compared with values from fall in 2005. Irrigation slightly increased specific root length but decreased root tissue density. Fine root O_2-consumption capacity decreased slightly in response to the irrigation treatment. Using ingrowth cores to observe the responses of newly produced fine roots, irrigation had a significantly positive effect on the length of fine roots, but there were no differences between the low- and high-productivity trees. In contrast to the weak response of fine roots to irrigation, the aboveground parts responded positively to irrigation with more dense crowns. The lack of a marked response of the fine root biomass to irrigation in the low- and high-productivity trees suggests that fine roots have a high priority for within-tree carbon allocation.

Keywords: drought, fine root growth, fine root physiological and morphological properties, fine root standing crop, high- and low-productivity pines, ingrowth cores, irrigation, Pinus sylvestris.

Introduction

Scots pine (*Pinus sylvestris* L.) forests along the southern borders of their distribution commonly cover the lower slopes of dry central valleys in the European Alps. Such valleys are characterized by high summer temperatures and low precipitation throughout the year, and occur in the transition zone between continental and Mediterranean climates in Austria (Inntal), Switzerland (Valais) and Italy (Valle d'Aosta, Vintschgau) (Bigler et al. 2006). Extraordinarily high tree mortality of Scots pine has recently been observed in several of these inner-Alpine valleys (Cech and Perny 2000, Rigling and Cherubini 1999, Rebetez and Dobbertin 2004). The mortality rate of Scots pines below 1100 m a.s.l. (> 1%) has been substantially higher than the mean rate in managed forests in Switzerland (0.4%) (Dobbertin et al. 2005). This might be the consequence of a more frequent occurrence of severe droughts and high temperatures (Rebetez and Dobbertin 2004, Bigler et al. 2006). The number of hot days in the Canton Valais with mean temperatures above 20 °C has doubled within the last 23 years, from 20 days in 1980 to 40 days in 2002, increasing the potential mean monthly evapotranspiration from about 50 to 70 mm (Rebetez and Dobbertin 2004), which potentially leads to a higher water demand. Other factors causing the death of Scots pine are pine mistletoe, bark beetles and pine wood nematodes (Dobbertin and Rigling 2006, Polomski et al. 2006, Dobbertin et al. 2007, Wermelinger et al. 2008).

Before trees die they usually experience a disease spiral with three categories of factors influencing their decline: predisposing factors (e.g., poor fertility and soil compaction), inciting factors (e.g., drought and frost) and contributing factors (e.g., bark- and wood-boring insects, root rot fungi and nematodes) (Manion 1981). According to Wermelinger et al. (2008), only Scots pines with a crown transparency > 65% were heavily colonized by bark- and wood-boring insects, which are considered contributing factors that eventually cause death. In pines with a crown transparency < 65%, these insects and hence the contributing factors were not abundant, raising the possibility that these trees might eventually recover. A crown transparency of 100% refers to a

crown that lacks needles (= dead tree), whereas a crown transparency of 0% refers to a fully foliated crown.

The main aim of this study was to investigate whether an additional supply of water would mitigate the consequences of climatic change on Scots pine trees growing in a dry region by improving their productivity and, subsequently, reducing their mortality. In particular, we investigated whether low-productivity pines would recover if they received additional water. In this context, little research has been done to investigate how the fine roots of coniferous trees behave if additional water is supplied. Meta-analyses have revealed that irrigation slightly, but not significantly, increases specific root length (SRL), whereas drought slightly reduces fine root biomass and SRL (Cudlin et al. 2007, Ostonen et al. 2007). The majority of studies applying water to forest ecosystems, however, have not observed any significant changes in either the biomass or morphology of fine roots (e.g., Pronk et al. 2002, Genenger et al. 2003, Coleman 2007); however, these studies were not performed in regions where water is a limiting factor.

Our objectives were to investigate the effects of irrigation on the morphological and physiological responses of Scots pine fine root standing crop and newly produced fine roots grown into ingrowth cores. We also compared fine root responses to irrigation between high- and low-productivity Scots pine trees.

Materials and methods

Scots pine stand

The stand selected for study is located in the Rhone valley, an inner-Alpine dry valley, in the southwest of Switzerland in a *P. sylvestris* forest (Pfynwald, 46°18′ N, 7°37′ E, 610 m a.s.l., *Erico-Pinetum caricetosum albae* Br.-Bl., Werner 1985) on an alluvial fan and debris cone of the Ill river (Illgraben). The overstory of the stand is even aged (90–100 years) and mainly consists of *P. sylvestris* with the occasional *Quercus pubescens* Willd. individual. Mean height of the *P. sylvestris* trees is 11 m and stand density is 730 stems ha^{-1}, with a diameter at breast height of $\geq$ 12 cm and a stem basal area of 27.3 m^2 ha^{-1}. The understory comprises shrubs and young *Q. pubescens* with a cover of 60%. The ground cover is dominated by grasses, mosses and few dwarf shrubs with a total cover of 70%. The soil is a calcaric Regosol (FAO classification). Mean annual temperature recorded at the nearby weather station in Sion is 9.2 °C (1961–1990), and mean annual precipitation measured at the nearby weather station in Sierre is 657 mm (1961–1990).

Investigation area

The study area (1.23 ha) in the Scots pine stand was set along a channel of the Rhone river to facilitate irrigation with the river water. The study area was divided into eight plots of 25 × 40 m (1000 m^2) each with 5 m buffer areas between and around the plots. The plots were aligned side by side along the channel, from where water was taken to irrigate four randomly selected plots (irrigation). Four untreated plots served as controls. The Scots pine trees in the study area were numbered consecutively from 1 to 1123 before the treatment started. In spring 2003, before the treatment started, the stem diameters were recorded at breast height and their crown transparencies visually rated from 0% to 100% in 5% steps based on reference photographs (Müller and Stierlin 1990). A crown transparency of 0% refers to a fully foliated crown and a crown transparency of 100% refers to a crown without any needles. In the following years, 2004–2006, the crown transparency of all the Scot pine trees was rated on every March before the vegetation period by the same observers without reference to the previous ratings.

Eight soil profiles were opened to a depth of 70 cm in the study area and morphologically described according to Walthert et al. (2004). Soil samples were taken from each horizon, taken to the laboratory, dried at 60 °C, and passed through a 2-mm sieve. The pH values were measured in a soil suspension containing 0.01 M $CaCl_2$, and the exchangeable cations were extracted with unbuffered 1 M NH_4Cl (Brunner et al. 2002). The effective cation-exchange capacity (CEC_{eff}) was calculated by summing the charge equivalents of the exchangeable cations, and the base saturation (BS) was expressed as the fraction of the base cations Na, K, Ca and Mg of CEC_{eff}.

For the root sampling, six trees per plot were selected, three of which had a dense foliage with a crown transparency of 5–10% (hereafter high-productivity trees) and three had sparse foliage with a crown transparency of 55–60% (hereafter low-productivity trees). The low-productivity trees had significantly narrower tree ring widths than the high-productivity trees (Eilmann 2008). We sampled the fine roots of 48 Scots pine trees and rated their crown transparencies.

Irrigation treatment

Irrigation was started for the first time in spring 2003. Water was pumped from the nearby river channel and distributed by 80 sprinklers set at a height of 110 cm in the four treatment plots. The sprinklers were placed along four parallel tubes per plot with five sprinklers per tube and a sprinkling radius of 7 m per sprinkler. The treatment plots were irrigated during the vegetation period on nights when there was no precipitation. The amount of irrigated water applied corresponded to about 700 mm $year^{-1}$ or 5 mm $night^{-1}$. Periods of irrigation were from June 19 to October 21, 2003, May 5 to October 26, 2004 and April 23 to October 4, 2005 (see Figure 2).

Meteorological and soil climate data

Air temperature was measured continuously with a capacitive sensor (Hygromer MP 400A, Rotronic AG,

Bassersdorf, Switzerland) at a height of 1.50 m in the buffer area of the study site. Precipitation data were recorded at a nearby meteorological station in Sierre (MeteoSwiss data). Soil water content was monitored hourly in one control and in one irrigated plot by time domain reflectometry (Tektronix 1502B cable tester, Beaverton, OR) at four locations per plot and at soil depths of 10, 40 and 60 cm. In the same plots, soil temperatures were recorded in 2003 and 2004 at a depth of 5 cm with UTL-1 data loggers (Geotest AG, Zollikofen, Switzerland). All data per plot and soil depth were averaged. Soil temperature in 2005 and snow cover between 2002 and 2005 were modeled with CoupModel, a coupled heat and mass transfer model for soil-plant-atmosphere systems (Jansson and Karlberg 2004). Meteorological data such as relative humidity, wind and global radiation were obtained from the nearby weather station in Sion (MeteoSwiss data), because they were not measured at the study site or at the nearby weather station in Sierre.

Fine root sampling

To determine the standing crop (dry biomass) of fine roots, samples were taken clockwise around the stem of each sample tree, with only two samples per year and tree. Two topsoil monolith samples with the fine roots included were taken per tree per year with a soil corer (4.5 cm in diameter) about 0.5–1.0 m away from the stems down to the rocks of the subsoil at an approximate depth of 8–12 cm. Samples were taken in April 2003 (before irrigation started), May 2004 and May 2005. After sampling, the soil monoliths were packed in plastic bags and transported to the laboratory and stored at low temperature until they were analyzed. Then the soils were sieved and the roots rinsed with tap water. Fine roots ($\leq$ 2 mm in diameter) were sorted out and dried at 60 °C for dry biomass analyses. To calculate fine root biomass, the two samples per tree per year were analyzed and averaged.

To study the development of new fine roots, four ingrowth cores (glass-fiber-netting cylinders 11 cm in height, 5 cm in diameter, with a 5 mm mesh size) per tree were inserted in 2003 into holes where the topsoil monoliths had been taken previously with the soil corer (two of four topsoil monoliths were used for the fine root standing crop study). They were refilled with sieved topsoil from outside the plots. The first two ingrowth cores were harvested after one year in May 2004, and the last two were harvested in May 2005 with a large soil corer (8.5 cm in diameter). After harvest, the ingrowth cores were packed undisturbed in plastic bags, transported to the laboratory and stored at a low temperature until they were analyzed. The ingrowth cores were then cut out with a knife, the length of the samples recorded, the netting removed with scissors, the soils sieved and the fine roots rinsed with tap water. The Scots pine fine roots were sorted out and stored in tap water at 1 °C until fine root morphology was analyzed.

Samples for studying the physiological and morphological properties of Scots pine fine roots were collected by digging out one sample per tree in May 2004 from the topsoil with a hand shovel at a distance of 0.5–1.0 m from the tree stems for starch analyses, or by taking two soil monoliths per tree in September 2005 with a soil corer (4.5 cm in diameter) for analyses of fine root biomass, O_2-consumption capacity and morphology. The fine roots for starch analyses were washed with tap water and immediately frozen in liquid nitrogen in the field, and then lyophilized in the laboratory for 2–3 days. The fine roots sampled for O_2-consumption analysis were kept in the soil monoliths, packed into plastic bags, and transported under cool conditions to the laboratory. The soils were then sieved, the roots rinsed with tap water, and the Scots pine fine roots sorted out. Whole samples or aliquots of the fine roots were used to measure O_2-consumption capacity and morphology as described below. The remaining fine roots were dried at 60 °C and weighed.

The turnover of fine roots was calculated as annual fine root production divided by maximum fine root standing crop (Gill and Jackson 2000). Annual fine root production data were obtained as the difference between the dry mass of the ingrowth cores in May 2004 and 2005 and maximum fine root standing crop data were obtained from the soil monoliths in September 2005.

Fine root O_2-consumption capacity and starch concentration

To measure O_2-consumption capacities, about 0.5 g of the fresh fine roots were washed with tap water and the attached soil particles removed (cf. Richter et al. 2007). The consumption of O_2 was measured for 20 min with a Clark-type O_2-electrode (Hansatech, King's Lynn, UK) while the roots were submersed in 2.5 ml of stirred 1 mmol $CaSO_4$ in 5 mmol MES buffer (adjusted with KOH to pH 5.5; Comas and Eissenstat 2004, Richter et al. 2007). The whole system was kept at a constant temperature of 25 °C. After the O_2-consumption measurements, the fine roots were weighed, scanned, and their morphology analyzed with WhinRhizo software (see below), then they were dried at 60 °C, and their dry mass determined. Consumption of O_2 was expressed per gram fresh mass (fw) per unit time. For the calculations, the two samples per tree were analyzed and averaged.

Fine root starch concentration was determined by a modified enzymatic assay with amyloglucosidase and hexokinase, as described by Brunner et al. (2002). Briefly, 20 mg of lyophilized fine root material was ground for 3 min in 2-ml Eppendorf tubes with a swing mill (Retsch, Germany) and 0.5 ml of 0.5 M perchloric acid was then added and the mixture incubated for 1.5 h at 60 °C. Afterward, 1.5 ml of Na acetate, adjusted to pH 4.8 with 0.17 M NaOH, was added and the mixture was incubated for 10 min at 100 °C. After centrifugation for 5 min at 10,000*g*, 20 µl

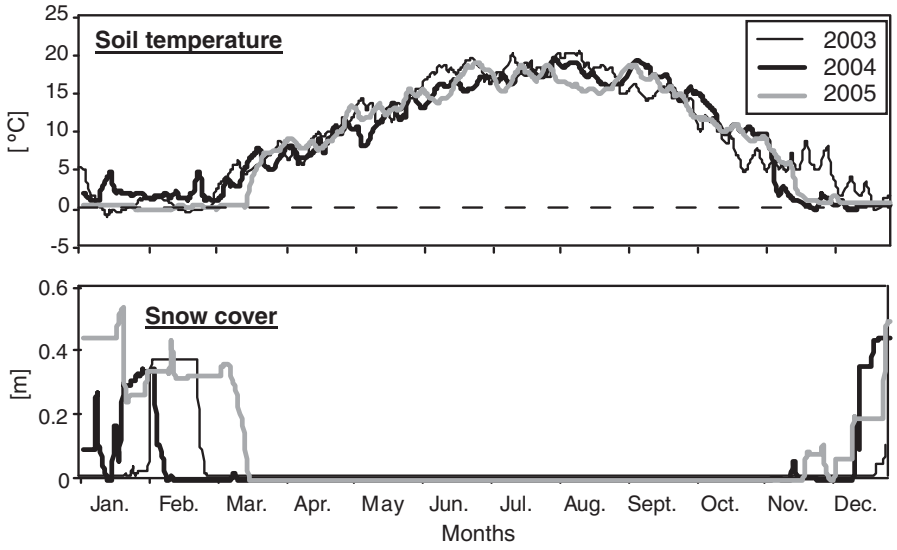

Figure 1. Soil temperature at a soil depth of 5 cm (measured data: 2003, 2004; modeled data: 2005) and snow cover (modeled data).

of the supernatant was put in each new 2-ml Eppendorf tube, 200 µl of amyloglucosidase solution was added to each tube, and the tubes were incubated for 15 min at 55–60 °C. One ml of tri-ethanol-amine-ATP-NADP-Mg buffer and 800 µl of water were then added, and the absorption at 340 nm in 300 µl of the solution was determined. Finally, 20 µl of hexokinase solution was added and after a 15-min incubation period, absorption at 340 nm was re-measured.

Fine root morphology

The fine roots from the ingrowth cores and from the O_2-consumption capacity measurements were scanned for morphological analyses. From the scanned pictures, the properties of the fine roots (total length, mean diameter, and numbers of tips and forks) were analyzed with WinRhizo Version 4.1c software (Regent Instruments, Quebec, Canada). The software counts the ending of a root as a tip and the branching of a root as a fork: root tips thus coincide with root apices. Specific root length (SRL; cm mg^{-1}), root tissue density (RTD; mg cm^{-3}), and numbers of tips and forks per root length (n cm^{-1}) were then calculated. After analyses, the fine roots were dried at 60 °C and dry biomass determined. For the fine root biomass and morphology analyses, the data per tree and sampling event were averaged.

Statistical analyses

Statistical analyses were performed with one- and two-way analyses of variance (ANOVA), and repeated-measures ANOVA using StatView Version 5.0 software (SAS Institute, Cary, NC). Repeated-measures ANOVA was applied when samples were taken consecutively from the same trees at different times. The significance of the differences between treatments was tested by Fisher's protected least significant difference.

Results

Site and soil characteristics

The study area in the Scots pine stand has a mean slope of 8% and a tree density of 900 trees ha^{-1}. The soil has an 8–12-cm-thick topsoil comprising a 3–6-cm-thick organic layer and a 2–6-cm-thick humic mineral soil layer. Below the topsoil, the subsoil has a high percentage of skeletal material (20–50% or above) with rocks originating from the bed load of the Ill river. The pH of the topsoil ranges from 4.1 to 6.7 with a mean of 5.4, and that of the subsoil ranges from 6.6 to 7.8 with a mean of 7.5. The CEC_{eff} of the topsoil varies from 120 to 542 $mmol_c$ kg^{-1} with a mean of 354 $mmol_c$ kg^{-1}, and that of the subsoil ranges from 117 to 202 $mmol_c$ kg^{-1} with a mean of 157 $mmol_c$ kg^{-1}. Both topsoil and subsoil have a high BS with a low mean variation of 99.0% for the topsoil and 99.9% for the subsoil.

Meteorological conditions

The weather during the study period was marked by the hot summer in 2003. Mean air temperature from June to August was 21.6 °C in 2003, whereas it was only 18.7 °C in 2004 and 18.4 °C in 2005 (data not shown). The heat wave in summer 2003 resulted in a higher soil temperature (Figure 1). During the study period, 2003–2005, annual precipitation at the nearby meteorological station in Sierre was always lower than the long-term mean (657 mm, 1961–1990; MeteoSwiss data). The year 2003 was particularly dry with only 414 mm, whereas the years 2004 and 2005 were slightly wetter with 566 and 565 mm, respectively (MeteoSwiss data). Based on CoupModel simulations, snow covered the soil surface much longer in 2005 than in 2004 (36 days longer) and 2003 (16 days longer), because temperatures in the first half of March 2005 were particularly low (Figure 1). Mean soil temperature between March

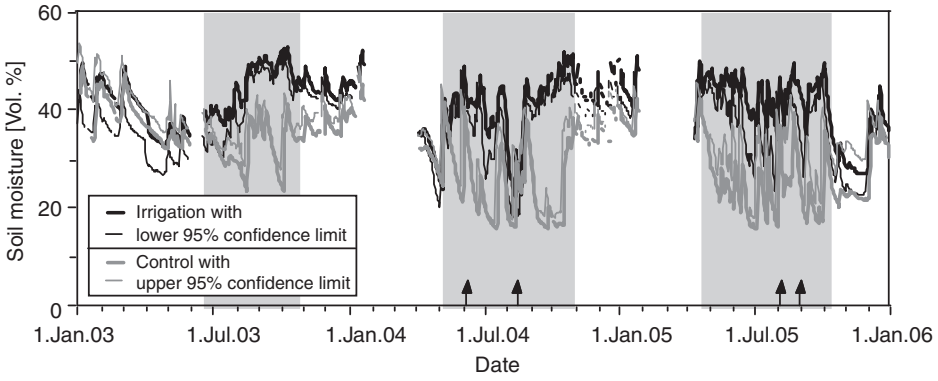

Figure 2. Soil water at a soil depth of 10 cm in the irrigated and control plots. Shaded areas represent the irrigation periods and the arrows indicate irrigation breakdowns. The 95% confidence limits are calculated as the mean ± 2 SE.

Table 1. Crown transparency (%) of high- and low-productivity *P. sylvestris* trees in March 2003 (before the irrigation treatment started), 2004, 2005 and 2006. One-way ANOVA (*P*) and repeated-measures ANOVA (P^1): $^{**}P < 0.01$; $^{*}P < 0.05$; ns, not significant ($n = 12$).

Rating year	High-productivity			Low-productivity		
	Control	Irrigation	*P* value	Control	Irrigation	*P* value
2003	8.33	7.50	ns	58.33	56.25	*
2004	7.92	10.42	ns	58.33	52.92	ns
2005	11.25	10.83	ns	65.42	50.00	*
2006	14.58	8.75	ns	67.92	42.08	**
P^1 irrigation	ns			*		
P^1 time	*			ns		

1 and 15 was 0.3 °C in 2005, whereas it was 3.8 °C in 2003 and 3.0 °C in 2004 (Figure 1).

Irrigation treatments

The amount of water applied in 2003 was 279 mm, less than planned because of difficulties in optimizing the irrigation system. In 2004 and 2005, the amount of water applied was 749 and 790 mm, respectively. When summed with the natural precipitation, the total amount of water applied to the irrigated plots in 2003 was only about 700 mm, compared with about 1300 mm in 2004 and 2005. The irrigation treatment did not significantly influence soil temperature at a depth of 5 cm (data not shown), but irrigation had a pronounced effect on soil water content. The soil water content at a depth of 10 cm was significantly higher in the irrigated plots than in the control plots during the irrigation periods (Figure 2). Mean volumetric water content during the three irrigation periods was 42 ± 6% in the irrigated plot and 26 ± 7% in the control plot. Similar results were found at depths of 40 and 60 cm (data not shown). Exceptions were at the beginning of the experiment in July 2003, when the irrigation system was being optimized and during short periods in summer 2004 and 2005 when the irrigation system became blocked (Figure 2).

Crown transparency

Before the irrigation treatment started, mean stem diameters at breast height were between 19.7 and 23.4 cm, and they did not differ significantly in response to irrigation or to the productivity status of the trees (data not shown). Before the start of the irrigation treatment, the high-productivity trees had a mean crown transparency of about 8% and the value for the low-productivity trees was about 57%. Crown transparency did not differ significantly between the control and the irrigated trees (Table 1). After 3 years of irrigation, the high-productivity trees had more or less maintained their crown transparency at about 8–9%, whereas crown transparency in the low-productivity trees had decreased markedly from 56% to 42%. In contrast, the crowns of the low-productivity and high-productivity control trees became more transparent during the 3-year study changing their transparency from 58% to 68% and from 8% to 15%, respectively (Table 1).

Fine root standing crop

Analyses of the fine root standing crop revealed that, although it varied between 123 and 205 g m^{-2} before the start of the treatments, it was not affected significantly by either irrigation or tree productivity status or its interaction (Table 2). In spring 2004 after one period of irrigation, the fine root standing crop of the low-productivity trees was significantly lower than that of the high-productivity trees. In spring 2005, the fine root standing crop was overall markedly lower, with values between 73 and 100 g m^{-2}, than during the two previous years, independently of both irrigation and tree productivity status (Table 2). After the irrigation period in 2005, however, the fine root standing crop was significantly greater (almost twice) in the irrigated

Table 2. Fine root standing crop (g m^{-2}) of high- and low-productivity *P. sylvestris* trees in April 2003 (before treatment started), May 2004 and May 2005. Two-way ANOVA (P) and repeated-measures ANOVA (P^1): ***$P < 0.001$; *$P < 0.05$; ns, not significant (2003, 2005, $n = 12$ and 2004, $n = 11$). The interaction between productivity status × irrigation was not significant in any sampling year.

Sampling year	High-productivity		Low-productivity		P value	
	Control	Irrigation	Control	Irrigation	Productivity	Irrigation
2003	167.41	171.35	204.62	123.54	ns	ns
2004	199.03	219.39	127.30	165.11	*	ns
2005	73.71	100.44	81.68	83.75	ns	ns
P^1 productivity	ns					
P^1 irrigation	ns					
P^1 time	***					

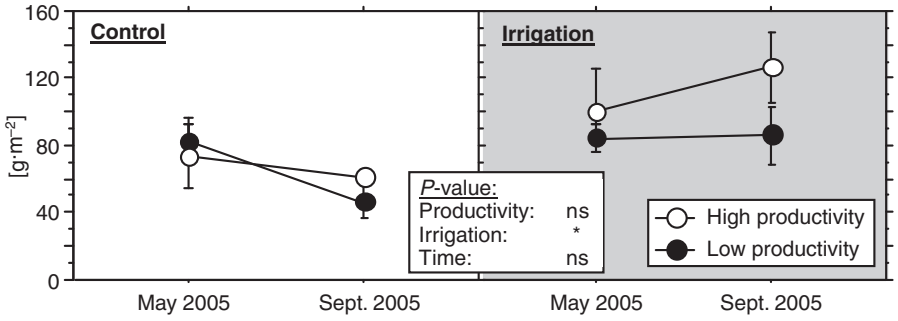

Figure 3. Seasonal changes in the fine root standing crop of high- and low-productivity *P. sylvestris* trees in the third year of irrigation (2005). Repeated-measures ANOVA: *$P < 0.05$; ns, not significant; error bars = SE; and $n = 12$.

Table 3. Fine root physiological and morphological properties of high- and low-productivity *P. sylvestris* trees (root samples were taken in September 2005, except for starch in May 2004). Abbreviations: SRL, specific root length; RTD, root tissue density. Two-way ANOVA: *$P < 0.05$ and ns, not significant ($n = 12$). There were no significant effects of either productivity status or the interaction between productivity status and irrigation on any of the fine root properties.

Fine root properties	High-productivity		Low-productivity		P value
	Control	Irrigation	Control	Irrigation	Irrigation
O_2 consumption (nmol O_2 g_{fw}^{-1} s^{-1})	0.96	0.76	0.84	0.70	ns
SRL (cm mg^{-1})	0.80	0.99	0.79	0.95	ns
RTD (mg cm^{-3})	153.3	135.1	167.3	135.3	*
Average diameter (mm)	1.10	1.02	1.03	1.05	ns
Tips (n cm^{-1})	1.10	1.07	1.18	1.14	ns
Forks (n cm^{-1})	1.32	1.26	1.14	1.03	ns
Starch (mg g^{-1})	63.1	64.5	63.2	63.6	ns

plots than in the control plots (Figure 3). Tree productivity status had no effect on the fine root standing crop in 2005 (Figure 3).

Fine root physiological and morphological properties

Fine root O_2-consumption capacities were slightly, but not significantly, altered by the irrigation treatments (Table 3). Neither tree productivity status nor the interaction between irrigation and productivity status influenced fine root O_2-consumption capacities (Table 3). Among the fine root morphological properties analyzed, irrigation slightly increased SRL (from about 0.8 to 1.0 cm mg^{-1}), and significantly decreased RTD (from about 160 to 135 mg cm^{-3}) (Table 3), likely reflecting the increases in fine root lengths but not in biomass. Other morphological parameters, such as mean diameter and tip and fork frequencies, were unaffected by irrigation. We did not detect significant effects of tree productivity status or an interaction between irrigation treatment and tree productivity status on any of the fine root physiological and morphological parameters analyzed. Starch concentrations varied between 63.1 and 64.5 mg g^{-1}, and did not differ between treatments or with tree productivity status or its interactions (Table 3).

Biomass and morphology of newly produced fine roots in ingrowth cores

From the ingrowth cores, it appeared that the biomass of newly produced fine roots nearly doubled from the first

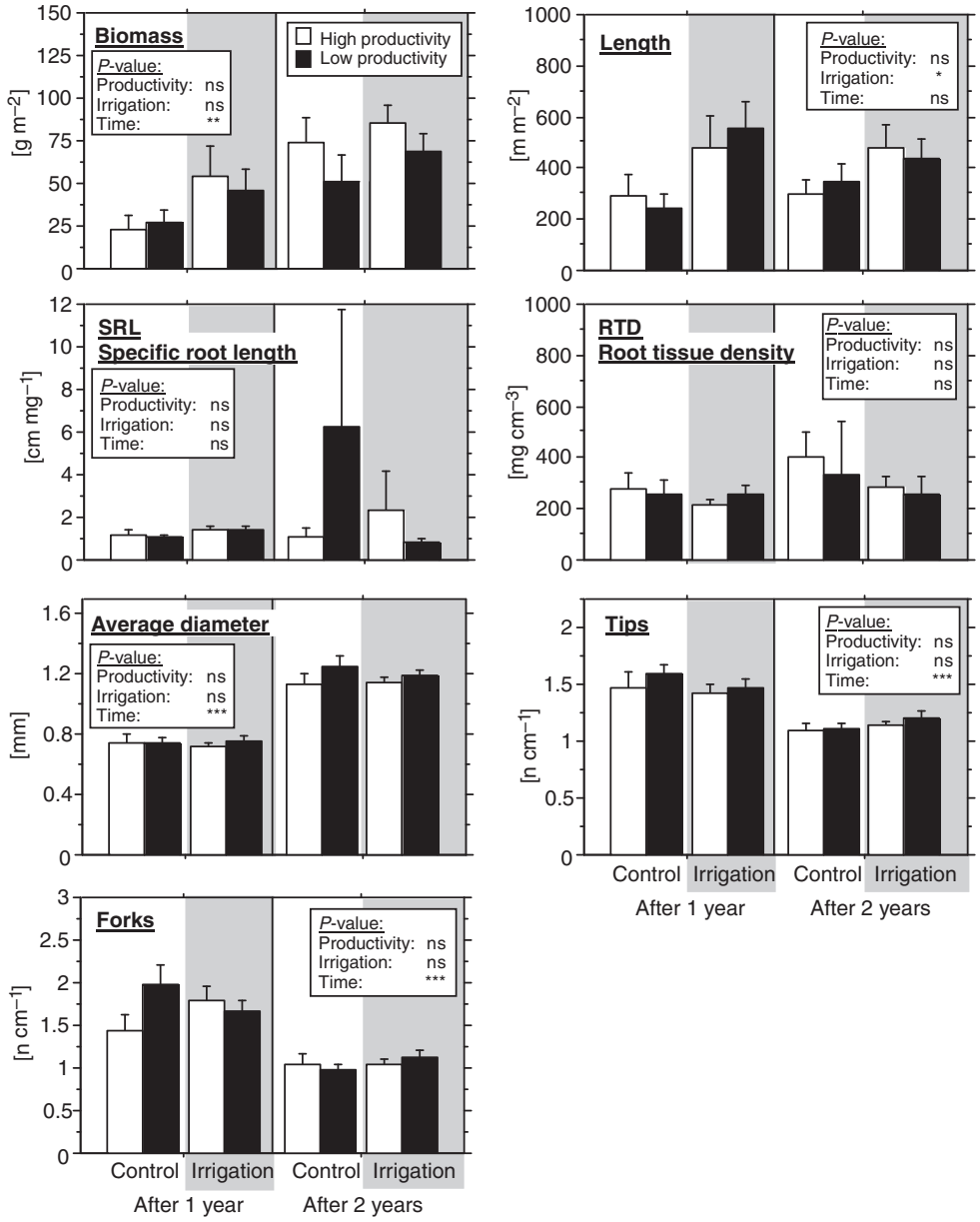

Figure 4. Ingrowth fine root properties of high- and low-productivity *P. sylvestris* trees after 1 and 2 years of irrigation (harvests in May 2004 and May 2005). Repeated-measures ANOVA: ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; ns, not significant; error bars = SE and $n = 12$.

to the second year of observation (Figure 4). In addition, mean diameter of the newly produced fine roots increased significantly from about 0.8 mm after the first year to 1.2 mm after the second year, whereas the frequencies of the tips and forks significantly decreased. Irrigation significantly increased the lengths of the newly produced fine roots, but only slightly increased their biomass, and had no effect on mean diameter, or tip or fork frequencies (Figure 4). Although SRL and RTD varied greatly they were not significantly affected by either the time or the irrigation treatment. Tree productivity status had no influence on any of the properties of the newly formed fine roots (Figure 4).

Calculations of fine root turnover for 2005 revealed that it was not significantly affected by irrigation or by tree productivity status (data not shown). Although turnover values varied greatly from 0.28 to 1.80 year^{-1}, we were unable to draw coherent conclusions from these calculations.

Discussion

Analyses of the responses of Scots pine fine roots to irrigation showed that the standing crop increased slightly in May 2004 compared with the values of April 2003, except

in the low-productivity control trees. Irrigation also significantly increased biomass values in the high-productivity trees at the end of September 2005 compared with the values of May 2005. However, a statistically significant positive reaction of the fine root standing crop to the additional water supply was not obvious when the yearly samples collected in spring were compared with each other. The interaction between irrigation treatment and tree productivity status did not result in any significant differences. Although we examined only the uppermost portion of the fine root systems (rooting depths > 1 m, Burnand 1976), other irrigation studies have also shown no major changes in fine root biomass in response to irrigation. De Visser et al. (1994), Bredemeier et al. (1998) and Genenger et al. (2003) applied irrigation treatments for 3 years to various forest sites supporting *Picea abies* (L.) Karst. or *Pseudotsuga menziesii* (Mirbel) Franco in Central Europe and did not observe any significant differences in the amounts of fine root biomass produced. Gower et al. (1992) studied a *P. menziesii* forest in North America and observed that net primary production of fine roots was significantly lower in the irrigation treatment than in the control treatment. Joslin et al. (2000) conducted a 5-year study of wet, ambient and dry treatments in a mature, mixed deciduous forest of *Quercus* spp. and *Acer rubrum* L. and observed slight, but not significant, changes in trees in the wet treatment, which had the highest production, mortality, and turnover rates of fine roots.

Our finding that irrigation did not influence fine root biomass supports the hypothesis of Waring (1987), who stated that fine roots have, next to buds and foliage, a high priority for carbon allocation within a tree. However, we incorrectly predicted that the fine roots of low-productivity Scots pine trees growing in a climatic region where water is a limiting factor would respond to irrigation by increasing their fine root biomass. Moreover, in addition to fine root biomass, neither fine root O_2-consumption capacity nor starch concentration differed significantly between the low-productivity and high-productivity Scots pine trees. These results also support Waring's hypothesis (Waring 1987) that fine roots have a high priority for carbon allocation within a tree, and accord with the observation of Joslin et al. (2000) who reported on 'the apparent resilience of a forest ecosystem in ostensibly maintaining a relatively constant fine root mass over the long-term, despite seeming short-term declines during certain periods, particularly in the dry treatment'. Our May 2005 observation that, independently of irrigation treatment and tree productivity status, the fine root biomass of all sampled Scots pine trees was small compared with the previous years, also seems to support the hypothesis of Waring (1987). It is likely that the fine root biomass of our Scots pine trees decreased after the long winter period with low soil temperatures up until March, which probably reduced the time for root growth before sampling. However, we cannot exclude the possibility that other climatic events, such as the heat wave in 2003, also had an effect.

Only a few irrigation studies have considered the fine root morphological properties of coniferous trees, and they generally did not observe any significant changes in response to irrigation in fine root length, mean diameter, tip or fork frequency, SRL, RTD or turnover (Pronk et al. 2002, Genenger et al. 2003, Coleman 2007). We found that irrigation led to an increase in fine root length. In particular, the newly produced fine roots in ingrowth cores were longer in the irrigated plots than in the control plots. The fine root standing crop, when sampled at the end of the irrigation period in 2005, also showed an increased SRL and a reduced RTD. In addition, the O_2-consumption capacity was slightly reduced, perhaps because the fine root tissue became somewhat more spongy with irrigation. De Visser et al. (1994) also observed an increase in SRL at a depth of 20–40 cm in *P. menziesii* as a result of fine roots becoming longer and thinner; however, this finding was inconsistent with the observations made at other soil depths.

In contrast to irrigation, drought can significantly reduce root tip frequency and increase RTD (Trubat et al. 2006, Cudlin et al. 2007, Konopka et al. 2007). An increase in RTD is mainly a consequence of a nutrient deficiency, which often coincides with water deficiency (Trubat et al., 2006). Drought can also lead to shorter fine roots and, subsequently, a reduced SRL as found in *Fagus sylvatica* L. (Meier and Leuschner 2008). Konopka et al. (2007) observed that the mortality of fine roots with a diameter < 1 mm is higher than that of fine roots with a diameter of 1–2 mm when *Cryptomeria japonica* D. Don is subjected to water stress. Richter et al. (2007) reported that decreasing soil water content was significantly correlated with the decreases in O_2 consumption and tetrazolium reduction capacity in fine roots of *P. abies* seedlings.

Although the belowground parts of our Scots pine trees appeared to be only slightly affected by the supply of additional water, their aboveground parts responded positively to irrigation. In the third year of treatment, the crowns of the irrigated trees were more dense and, subsequently, significantly less transparent than the control trees; consequently, their crown transparency decreased from 15% to 9% in the high-productivity trees and from 68% to 42% in the low-productivity trees. Gower et al. (1992) observed, in a similar 2-year irrigation study, that total foliar mass increased by 31% and leaf area index increased by 12%. A study with *Pinus ponderosa* Dougl. ex Laws. showed that pine needles responded to increased water supply with enhanced stomatal conductance, resulting in a higher net photosynthetic rate and a higher carbon uptake (Panek and Goldstein 2001). Water stress, in contrast, results in stomatal closure, which leads to lower transpiration, lower respiration, and lower net carbon assimilation (Panek 2004, Sterck et al. 2008, Breda et al. 2006, Zweifel et al. 2005, 2007, Matyssek et al. 2006).

We assumed that low-productivity trees would not only have a reduced fine root biomass but also a decreased fine root physiological capacity, and that decreases in both of

these fine root properties would result in a reduced need for energy (i.e., photosynthetic products). Consequently, we predicted that the addition of water would improve the physiological capacity of fine roots. However, we did not observe a marked change in fine root O_2-consumption capacity or starch concentration in response to irrigation or tree productivity status. In an earlier study (Brunner et al. 2002), starch concentrations varied between 90 and 171 mg g^{-1} for *P. abies* and between 145 and 175 mg g^{-1} for *Pinus cembra* L. and *Pinus montana* Miller from subalpine regions. Our values (about 64 mg g^{-1}) were well below the values from that study, but neither tree productivity status nor irrigation treatment seemed to influence starch concentrations. Thus, it can be assumed that the physiological capacity of Scots pine fine roots is maintained at a high level, independently of the productivity status of the trees.

In conclusion, irrigation mainly resulted in increases in the lengths of the Scots pine fine roots and, thus, less dense fine root tissue. Low-productivity Scots pine trees did not have an altered fine root biomass or an altered fine root physiology or morphology compared with high-productivity trees. However, irrigation significantly decreased crown transparency, indicating that irrigation can be applied to Scots pine stands to mitigate the negative consequences of an increased frequency of hot days associated with climate change.

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