Fine roots of Scot pines with sparsely foliated crowns are not necessarily less vital, and irrigation influences its fine roots only marginal

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ABSTRACT

Scots pine (*Pinus sylvestris*) forests in inner-Alpine dry valleys of Switzerland have suffered in recent decades from drought and elevated temperatures, resulting in a higher tree mortality rate than in average. In the present study, we investigated the fine roots of two types of pines, high-productive Scots pines having a densely foliated crown, and low-productive Scots pines having a sparsely and scantily foliated crown. The analyses of the biomass and of the physiological and morphological properties of the fine roots revealed, that the two types of pines did not differed significantly from each other. In order to observe whether and how trees would react to an additional water supply, water from a nearby river was irrigated during three vegetation periods. This additional supply of water, although it improved the density of the pine crowns, did not influence the biomass of the fine roots or its physiological and morphological properties, except the root tissue density, which was significantly reduced. Using in-growth cores to observe the responses of newly produced fine roots, no differences between the fine roots of high- and low-productive pines were observed, except the length of the fine roots, which was significantly improved. The lack of a difference between the fine-root biomass of high- and low-productive pines and the lack of a strong response of the fine-roots physiology and morphology to irrigation suggests that fine roots of Scots pines have a high priority for within-tree carbon allocation in order to maintain an optimal water and nutrient uptake from the soils, also under unfavourable conditions.

KEYWORDS: Fine root physiological and morphological properties, fine root standing crop, high- and low-productive pines, in-growth cores, irrigation, *Pinus sylvestris*

1. 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 characterised 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). Extraordinarily high tree mortality of Scots pine has recently been observed in several of these inner-Alpine valleys. The mortality rate of Scots pines has been substantially higher than the mean rate in managed forests in Switzerland. This might be the consequence of a more frequent occurrence of severe droughts and high temperatures (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 to 40 days, which potentially leads to a higher water demand (Rebetez & Dobbertin 2005). Other factors causing the death of Scots pine are pine mistletoe, bark beetles, and pine wood nematodes (Dobbertin *et al.* 2007).

The aim of our 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-productive pines with sparsely and scantily foliated crowns would recover if they received additional water. The main interest was on the physiological and morphological responses of the fine roots to irrigation. Meta-analyses have revealed that irrigation slightly, but not significantly, increases specific root length (SRL), whereas drought slightly reduces fine root biomass and SRL (Ostonen *et al.* 2007).

2. MATERIALS AND METHODS

The stand selected for the study is located in the Rhone valley, an inner-Alpine dry valley in the southwest of Switzerland, in a Scots pine forest (Pfynwald) with the mean annual temperature of 9.2°C and the mean annual precipitation of 657 mm. The study area was set along the channel of the Rhone River to facilitate irrigation with the river water. The study area was divided into eight plots of 25 x 40 m (1000 m^2) each with 5 m buffer areas between and around the plots. In spring 2003, before the treatment started, the crown transparencies were visually rated from 0 to 100% in 5% steps based on reference photographs. A crown transparency of 0% refers to a fully foliated crown and a crown transparency of 100% refers to a crown without any needles.

Irrigation was started in spring 2003. Water was pumped from the nearby river channel and distributed by 80 sprinklers in the four treatment plots. 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 $night^{-1}$.

For the root sampling, six trees per plot were selected, three of which had a dense foliage with a crown transparency of 5-10% (high-productive trees), and three had a sparse foliage with a crown transparency of 55-60% (low-productive trees). The low-productive trees had significantly narrower tree ring widths than the high-productive trees. In total, the fine roots of 48 Scots pine trees were sampled. To determine the standing crop (dry biomass) of fine roots, two topsoil monolith samples with the fine roots included were taken per tree and year with a soil corer (4.5 cm in diameter) about 0.5-1 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 into plastic bags and transported to the laboratory and stored at low temperature until analysed. Then the soils were sieved and the roots rinsed with tap water. Fine roots (≤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 and year were analysed and averaged.

Samples for studying the physiological and morphological properties of Scots pine fine roots were collected by taking two soil monoliths per sample tree in September 2005 with a soil corer (4.5 cm in diameter). The fine roots 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 then the morphology. To measure O_2-consumption capacities, about 0.5 g of the fresh fine roots were washed in tap water and the attached soil particles removed. The consumption of O_2 was measured for 20 min with a Clark-type O_2-electrode (Hansatech, King’s Lynn, U.K.) 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). 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 analysed with WhinRhizo software, then they were dried at 60°C, and their dry mass determined (see also Brunner *et al.* 2009 for a more detailed description).

To study the development of new fine roots, four in-growth 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. They were refilled with sieved topsoil from outside the plots. The first two in-growth 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; see also Brunner *et al.* 2009 for a more detailed description).

3. RESULTS AND DISCUSSION

Analyses of the fine root standing crop revealed, although it varied between 123 and 205 $g\cdot m^{-2}$ before the start of the treatment, that it was not affected significantly by either irrigation or tree productivity status (Table 1). After one period of irrigation, the fine root standing crop of the low-productive trees was significantly lower than that of the high-productive trees. In 2005, the fine root standing crop was overall markedly lower, with values between 73 and 100 $g\cdot m^{-2}$, than during the two previous years (Table 1). Overall, the irrigation as well as the tree productivity status had no effects on the fine root standing crop (Table 1).

Table 1. Fine root standing crop [$g\cdot m^{-2}$] of high- and low-productive Scots pines before (April 2003) and during the irrigation treatment (May 2004, May 2005). Two-way ANOVA and repeated measures ANOVA: *** P<0.001; * P<0.05; ns = not significant.

Sampling year	High-productive		Low-productive		*P*	
	Control	Irrigation	Control	Irrigation	Productivity	Irrigation
2003	167.4	171.4	204.6	123.5	ns	ns
2004	199.0	219.4	127.3	165.1	*	ns
2005	73.7	100.4	81.7	83.8	ns	ns
P (rep. measures): Productivity		ns				
P (rep. measures): Irrigation		ns				
P (rep. measures): Time		***				

Fine root O_2-consumption capacities were slightly but not significantly altered by the irrigation treatment (Table 2). Among the fine root morphological properties analysed, irrigation slightly increased specific root length (SRL) and significantly decreased root tissue density (RTD) (Table 2), likely reflecting an increase in fine root length but not in biomass. Other morphological parameters, such as mean diameter and tip and fork frequencies, were unaffected by irrigation. The productivity status of the trees had no effects at all on the fine root parameters (Table 2).

Table 2. Fine root physiological and morphological properties of high- and low-productive Scots pines in the third year of irrigation. Two-way ANOVA: * P<0.05; (*) P<0.1; ns = not significant.

Fine root properties	High-productive		Low-productive		*P*	
	Control	Irrigation	Control	Irrigation	Productivity	Irrigation
O_2 consumption [nmol $O_2\cdot g^{-1}{}_{fw}\cdot s^{-1}$]	0.96	0.76	0.84	0.70	ns	(*)
Specific root length SRL [$cm\cdot mg^{-1}$]	0.80	0.99	0.79	0.95	ns	(*)
Root tissue density RTD [$mg\cdot cm^{-3}$]	153.3	135.1	167.3	135.3	ns	*
Average diameter [mm]	1.10	1.02	1.03	1.05	ns	ns
Tips [$n\cdot cm^{-1}$]	1.10	1.07	1.18	1.14	ns	ns
Forks [$n\cdot cm^{-1}$]	1.32	1.26	1.14	1.03	ns	ns

From the in-growth cores, it appeared that the biomass of newly produced fine roots nearly doubled from the first to the second year of observation (Figure 1). In addition, mean diameters of the newly produced fine roots increased significantly from 0.8 mm after the first to 1.2 mm after the second year, whereas the frequencies of the tips and forks significantly decreased (data not shown). Irrigation significantly increased the lengths of the newly produced fine roots, but only slightly increased their biomass (Figure 1). However, the irrigation had no effects at all on mean diameters, SRL, RTD, or tip or fork frequencies (data not shown).

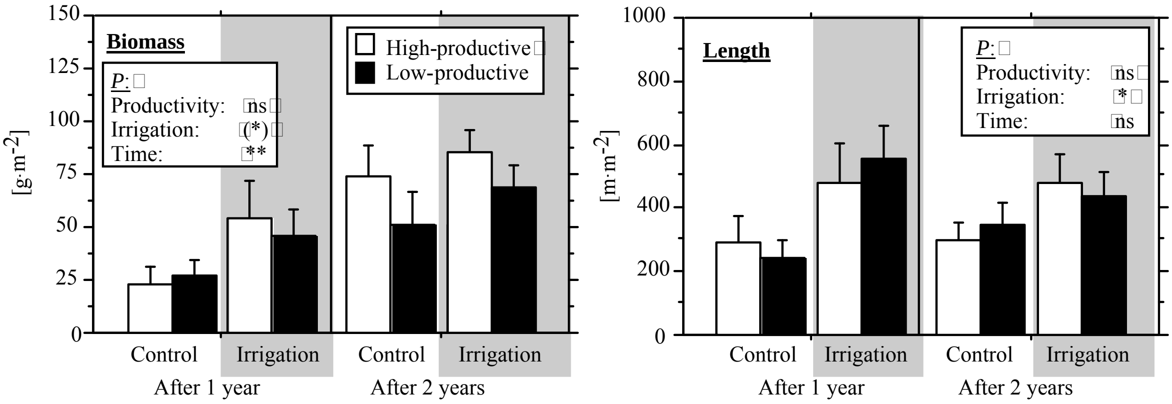

Figure 1. Biomass and length of newly produced fine roots (from in-growth cores) of high- and low-productive Scots pines after one and two years of irrigation. Repeated measures ANOVA: ** *P*<0.01; * *P*<0.05; (*) *P*<0.1; ns = not significant. Bars = SE.

In our study, a strong positive reaction of the fine roots to the additional water supply was not obvious: only the fine root tissue densities and the lengths of the newly produced fine roots were significantly affected. Because the irrigation treatment did not influence the fine root biomass, the results support 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 in order to maintain an optimal water and nutrient uptake from the soils, also under unfavourable conditions. However, we incorrectly predicted that the fine roots of low-productive Scots pine trees growing in a climatic region where water is a limiting factor would respond to irrigation by increasing their fine root biomass. Thus, our results also support the observations made by 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.'

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