

Competition for water in a xeric forest ecosystem – Effects of understory removal on soil micro-climate, growth and physiology of dominant Scots pine trees



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ARTICLE INFO

Keywords:

Competition
Drought stress
Forest management
Land-use change
Predawn water potential
Sap flow
Stem growth
Tree physiology

ABSTRACT

In many Central European areas, forests have been altered by century-long management practices, including grazing with domestic ungulates and litter harvesting. During the last century, most of these agro-forestry practices have been abandoned in many regions of Switzerland. As a consequence, stand density has increased, leading to higher competition for resources among trees, and particularly between overstory trees and understory vegetation. Only few studies investigated the effects of understory on the growth and physiology of overstory trees.

We conducted an understory removal experiment at a xeric Scots pine (*Pinus sylvestris* L.) forest in an inner-Alpine valley of Switzerland over a period of 5 years and compared data of soil temperature and water content, needle and shoot length, and radial growth and sap flow.

The removal of the understory increased soil temperature as well as soil water content at 5 to 60 cm soil depth, and led to a 4.6-fold higher mean annual radial growth and significantly longer needles and shoots. The removal of the understory further decreased tree water deficit and increased sap flow.

We conclude that reduced competition for soil water after removal of the understory vegetation was the primary cause of the increased performance of the overstory trees since light was not a limiting factor already before the understory removal. Thus, increases in understory density due to altered forest management may have exacerbated observed drought-induced decline processes. Therefore, our study demonstrates the need for a careful disentangling of climate and land-use change processes as they may evolve in parallel and potentially intensify their impact on the ecosystems. In contrast, the findings suggest decreasing understory density as a suitable management practice to increase overstory tree growth and vigour, and hence reduce mortality risk for a species like Scots pine in a drought-prone environment.

1. Introduction

Global change is typically associated with the reported increase in CO₂ emissions, leading to higher temperatures and an increase in the frequency of extreme events in recent decades (IPCC, 2013). Forest ecosystems have been shown to be particularly sensitive to these changes (Reichstein et al., 2013), and forest dieback as well as shifts in species distributions have been reported (Allen et al., 2010). However, simultaneously to climate, changes in land use may play an equally important role on forest dynamics and composition, particularly in regions having a long history of human activities (Caspersen et al., 2000; Hansen et al., 2001; Gimmi et al., 2010; García-Valdés et al., 2015). To

understand the effects of global change on forest dynamics, it is thus important to include both climate and land-use changes.

In the Alpine region, many forests have been shaped by century-long management practices, including logging, extensive grazing with domestic ungulates and litter harvesting (Tasser et al., 2007; Bürgi et al., 2013). In Switzerland, the progressive cessation of these traditional agro-forestry practices during the last century (Gimmi et al., 2010) has led to the development of a dense and bushy understory vegetation. An increase in stand density and enhanced inter- and intraspecific competition is known to lower the availability of water, nutrients and/or light of single trees, and therefore reduce stomatal conductance (Zweifel et al., 2009) and photosynthetic rates for single

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trees (Bréda et al., 1995; McDowell et al., 2003) in a species-specific manner. Moreover, an increased stand density can contribute to a lower stand resistance to drought, particularly at xeric sites (Giuggiola et al., 2013). In the context of climate change, competition may therefore act as a further predisposing factor that enhances the risk of drought-induced tree mortality (Bigler and Bugmann, 2003). As climate is predicted to get warmer and drier (IPCC, 2013), it is of particular interest to gain further knowledge on how alterations in stand dynamics through forest management may reduce the risks associated with changing water availability.

Thinning of overstory trees is a well-established forest management practice to increase light availability and potentially also increase soil water availability, decrease stand-level transpiration, and thus improve the drought resistance and recovery of forest stands after exceptionally dry periods (Giuggiola et al., 2013, 2015; Kerhoulas et al., 2013; Sohn et al., 2013, 2016; Gebhardt et al., 2014; Bottero et al., 2017). But disentangling the effects of altered light and soil water availability on tree performance is particularly complex (e.g., Giuggiola et al., 2015). The magnitude and duration of the response of trees to thinning is known to be related to thinning intensity, tree age and social status (Bottero et al., 2017).

In contrast, much less is known about the effects of reduced understory vegetation on water availability for the remaining trees and therefore the driving factors of changed physiological responses to the understory removal (e.g., Riegel et al., 1992). The understory can contribute considerably to stand-level transpiration and thus stand water loss, and particularly after heavy thinning of a dense stand, the understory develops quickly and needs to be taken into account when considering mitigating effects of thinning (Simonin et al., 2007; Gebhardt et al., 2014). On the one hand, the removal of the understory vegetation is expected to decrease belowground competition and thus to enhance the soil water availability for the overstory trees (Zahner, 1958). On the other hand, removing the understory vegetation may influence microclimatic conditions and lead to increased soil temperature, and thus enhanced evaporation (Matsushima and Chang, 2007), lower relative air humidity, and increased air temperature (Aussenac, 2000). Only few studies have investigated the effects of an understory removal on the growth and physiology of overstory trees in xeric environments, although forest grazing is a traditional management practice applied worldwide (Riegel et al., 1992; Miller et al., 1998; Li et al., 2012).

To shed light on these relationships, we conducted an understory removal experiment in a xeric Scots pine (*Pinus sylvestris* L.) forest at low elevation in the inner-Alpine valley Valais in Switzerland. This experiment allowed to solely analyse the effects of stand density reduction on soil water availability, tree growth and physiology without the parallel and confounding effects of the altered light regime, which is a fundamental difficulty in most thinning studies (Giuggiola et al., 2015). The Valais is of particular interest for investigating the effects of changing management practices on xeric forests since the Scots pine forests in this region grow at their physiological limit in terms of drought tolerance (Zweifel, 2006; Zweifel et al., 2009). Moreover, high rates of drought-induced Scots pine mortality have been observed in recent decades in Valais (Rigling et al., 2013), particularly within south-facing stands at low elevations and on shallow soils. Further, traditional agro-forestry practiced for centuries in these forests has been largely abandoned after 1950 (Gimmi et al., 2010).

The main objective of this study was to investigate the effects of experimental understory removal on the growth and physiology of the overstory Scots pine trees. The following research questions were addressed: (1) How does understory removal affect soil temperature and soil water content? (2) Does the growth of the overstory Scots pine trees increase with understory removal? (3) Can we quantify changes in tree water relations (diurnal stem shrinkage and sap flow) in response to the understory removal and pinpoint them as drivers for the changed tree performance?

2. Materials and methods

2.1. Study site

The experimental site is located in the driest part of the Swiss Rhône valley (Valais), on a south-facing slope above the village of Salgesch (46°17'N, 7°33'E), between 800 and 940 m a.s.l. During the 2005–2014 period, the yearly amount of precipitation and mean annual temperature \pm SE in this region amounted to 620 ± 43.7 mm and 11.5 ± 0.16 °C (Agrometeo station of Salgesch, 627 m a.s.l., at 1 km distance from the experimental site; <http://www.agrometeo.ch/fr>). The plots were nearly flat to moderately steep (slope of 1–25%), with 40–100 cm deep stony soils derived from calcareous colluvial material (calcaric cambisol; WRB, 2014) - occasionally covering older loess deposits (calcaric colluvic cambisol over calcaric cambisol) - and featuring a low water-holding capacity (Rigling et al., 2002; Ancy and Collaud, 2015). As indicated by the forest structure and herbaceous layer, the natural vegetation is a low-stature, open, basophilous, xero-thermophilous and mixed Scots pine – downy oak (*Quercus pubescens* Willd.) forest, with a diverse and thick understory of thermophilous shrubs and sclerophyll herbs (*Odontito-Pinetum caricetosum humilis*), as typically observed in central Valais (Plumettaz, 1988; Ancy and Collaud, 2015). Forest structure and species composition have been deeply affected for centuries of human activities as well as recent changes in agro-forestry practices (Gimmi et al., 2010). The actual forest consists of scattered mature Scots pine ranging from 6 to 15 m in height and a thick understory consisting of young trees and shrubs up to 6 m tall, strongly shading an often scarce herbaceous vegetation. Less than a century ago, the forest was certainly more open, with a lush herbaceous layer (Weber et al., 2008).

2.2. Experimental design

The understory removal experiment was set up in April 2010. From our experimental site, solitary overstory Scots pine trees were selected which had a similar understory density and were accessible for our field measurements. From these trees, we randomly picked six pairs of overstory Scots pine trees. These pairs were chosen on the basis of similar diameter at breast height (DBH), tree height, and woody understory (Table 1) as well as similar crown transparency and mistletoe occurrence (data not shown). From six of those trees (one of each pair) the understory was mechanically removed within a plot of 5 m in radius. In three cases, the understory composition was dominated by broadleaved species, in the other three cases the understory was dominated by young Scots pine trees (Table 1). The remaining six trees were taken as control trees where no treatment was executed. The treated plots were subsequently weeded in 2011 and 2013, eliminating regrowth, new woody seedlings, and the herbaceous layer. The minimum distance between a pair of trees (control/treated) was 17.2 m, and between the different pairs the minimum distance was 18.4 m.

2.3. Characteristics of the solitary trees and understory

To characterize the overstory trees, the DBH and tree height were measured. In order to calculate the pre-experimental basal area of the understory, the DBH, and the height of each individual shrub or tree (DBH stems > 1 cm) were recorded within a radius of 5 m around the investigated overstory trees before the entire understory was first removed in April 2010 (Table 1). The mean understory leaf area index \pm standard error was estimated as 2.9 ± 0.2 m² m⁻² for the treated and 2.6 ± 0.3 m² m⁻² for the control plots (data not shown).

2.4. Soil temperature and soil water content

Soil temperature and volumetric water content (VWC) were measured around three control trees and three treated trees (Table 2). Each

Table 1

Characteristics of the 12 overstory Scots pine trees and their understory characteristics measured before the understory removal in 2010.

Tree number	Treatment	Tree age at breast height (year)	DBH (cm)	Tree height (m)	BA conifer (m ² ha ⁻¹)	BA broadleaves (m ² ha ⁻¹)	BA total (m ² ha ⁻¹)
1	UR	144	29	12.4	5.0	4.0	9.1
2	C	146	29	12.1	2.2	6.0	8.2
3	UR	125	22	7.9	4.8	4.3	9.0
4	C	134	21	7.2	8.1	4.2	12.3
5	UR	141	23	12.3	18.4	0.8	19.2
6	C	118	20	11.8	15.2	3.3	18.5
7	UR	131	30	10.1	3.9	4.1	8.0
8	C	140	30	11.5	5.4	3.7	9.0
9	UR	129	23	13.8	17.2	1.0	18.1
10	C	168	26	13.4	16.1	0.3	16.4
11	UR	139	28	13.9	17.0	1.5	18.5
12	C	135	33	14.2	11.5	3.6	15.1

Table 2

Summary of the measured traits of the Scots pine overstory trees. The grey shaded area represents the years in which the corresponding trait was measured. N = number of trees per treatment (removal/control).

	N	Year of measurement						
		2008	2009	2010	2011	2012	2013	2014
Soil water content and	6							
Soil temperature	6							
Sapflow	6							
Daily stem fluctuation	6							
Predawn leaf water potential	8							
Needle and shoot length	12							
Tree-ring width	12							

tree rhizosphere was sampled by installing three and four decagon sensors (EC-TM; Decagon Devices, WA, USA) at 5 cm and 30 cm soil depth in four directions and at different distances to the target trees (0.8 m north, 1.6 m east, 2.4 m south, and 3.2 m west) in 2010. Three additional EC-TM sensors were installed at 60 cm soil depth at similar distances to the target tree in 2011. Measurements from all 60 sensors were logged (Em50R, Decagon Devices, WA, USA) hourly. Small data gaps (< 3 h) were filled linearly, and larger gaps by data from a sensor of the same replication, provided linear regression between the sensors yielded $R^2 > 0.95$. For a better visualization of possible treatment effects, mean differences (Δ) in soil temperature and VWC between the treated and control trees were calculated.

2.5. Shoot and needle length, needle nitrogen content

To analyse changes in morphological characteristics in the shoot and needle length of Scots pine, two branches per tree (six control and six treated trees) were cut from the upper part of the crown in November 2011 (Table 2). The shoot length of each year (2008 to 2011) was manually measured with an electronic gauge (± 0.1 mm) and averaged per tree. To obtain the curved length of each needle, 20 fresh needles per current and previous needle generations (2008 to 2011) of each branch were randomly selected and subsequently scanned using the image analysis software WinSEEDLE (Regent Instruments, Inc. Quebec, Canada). Further details on this method are given in Dobbertin et al. (2010). To measure the needle nitrogen concentration, 20 additional fresh needles per tree were randomly selected of the needle cohort 2011. These needles were subsequently dried for 48 h at 80 °C (Pérez-Harguindeguy et al., 2013), ground and 20 mg were weighted into tin capsules. Nitrogen concentration ([N]; mg g⁻¹) was measured with a CN analyzer NC2500 (CE instruments, Italy).

2.6. Predawn water potential

Predawn needle water potential (Ψ_{wp}) was measured between 3 and 4 am on average every 10 days from April to October for the years 2010 and 2011. Two branches from four control and treated trees each were sampled from the upper third part of the crown using a 9 m pole pruner (Table 2). Ψ_{wp} in current-year twigs was measured upon harvesting using a Scholander pressure bomb (M 600, Mosler Tech Support, Berlin, Germany) and a hand lens.

2.7. Sap flow

Stem sap flow was measured with the heat dissipation method (Granier, 1985), using the same plots as for soil temperature and water content assessments (sap flow SF-G, Ecomatik, Germany; Table 2). The sensors were located 1.8 m above the ground on the uphill side (i.e., north-facing). Each sensor was protected against direct radiation and rain using reflective bubble insulation foil. Measurements were logged every 30 s and averaged over 5 min (DecentControl, DecentLab, Switzerland). The output (temperature difference between the two measurement needles, °C) was converted into sap flow (SF, kg h⁻¹) according to the approach of Granier (1985) and taking the sapwood area of each tree into account. Sapwood area was estimated from tree cores for each tree with a sap flow sensor.

2.8. Tree-ring width

Two cores for six control and six treated trees were taken at breast height and at opposite radii perpendicular to the field slope after the growing season in November 2011 (Table 2). The cores were measured using a Lintab digital positioning table and the software TSAP-Win (RINNTech, Heidelberg, Germany). The six trees per treatment were averaged yearly, encompassing two pre-treatment years (2008 and 2009) and two post-treatment years (2010 and 2011).

2.9. Radial stem growth and tree water deficit

Stem radius (SR) fluctuations were measured on three control and three treated trees from 2011 to 2014 using point dendrometers (ZB06, natkon.ch, Oetwil am See, Switzerland; Table 2). Sensors were mounted at a stem height of 1.5 m above ground on the same tree side as the sap flow sensors (north). Displacement readings (in μ m) were logged every 30 s and averaged over 5 min (DecentControl, DecentLab, Switzerland). The temperature sensitivity of the ZB06 including the power source and logging devices used was found to be < 0.3 μ m per degree Celsius and was not further corrected. SR was separated into irreversible growth-induced expansion of new cells (cell division and cell expansion) (GRO), and reversible water-related shrinkage of the stem (tree water deficit, TWD) according to Zweifel (2016) and Zweifel et al. (2016). We further used the point dendrometers to determine the timing of tree

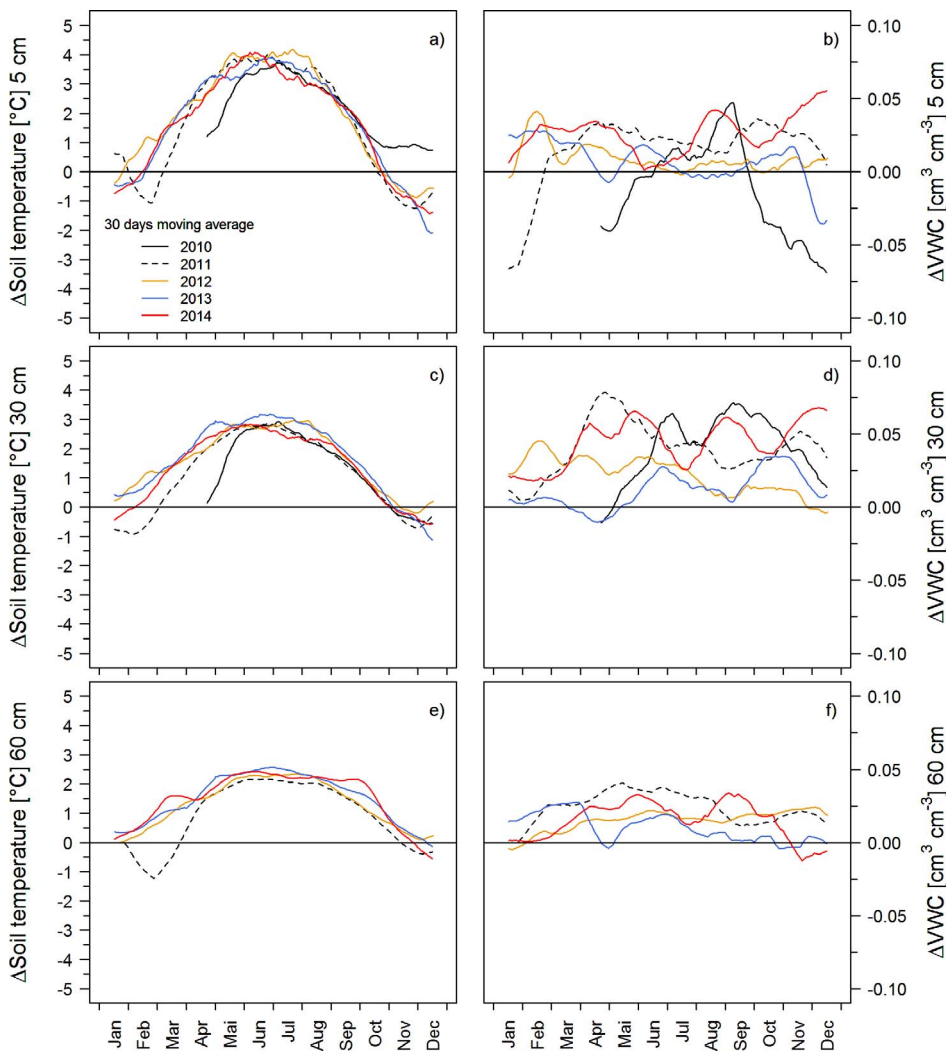


Fig. 1. Mean differences (Δ) in soil temperature and volumetric soil water content (VWC) between the treated (understory removal) and the control plots ($N = 3$) for the soil depth at 5 (a, b), 30 (c, d), and 60 cm (e, f). Values represent 30 days moving averages. No data are available for the 60 cm soil depth in 2010. The understory was removed in April 2010, and subsequently weeded in 2011 and 2013. Positive values indicate higher temperatures and VWC in the treated plots.

growth according to Zweifel et al. (2016), where the maximum stem radius of the previous year was used as zero-line for determining the onset of growth in the current year.

2.10. Modelling stomatal aperture

Stomatal aperture was estimated from sap flow and microclimate data by calculating the ratio between measured sap flow (SF) and potential transpiration (ET; Zweifel et al., 2002). The ET calculation is based on the single leaf evaporation approach of Penman (1948) and Monteith (1965). Since this ratio depends mainly on stomatal conductance (Hsiao and Acevedo, 1974), SF/ET can be used as a good approximation for the degree of the average stomatal aperture ranging from 0 (completely closed stomata) to 100 (fully open stomata) according to the approach of Zweifel et al. (2009).

2.11. Statistical analyses

To test for significance ($P < .05$) between treatment (understory removal and control) and years (fixed variables) of radial growth, shoot and needle length, linear mixed models were developed, with the individual tree as the random factor, nested in the treatment. If the model was significant, we used the same linear mixed models, but with the fixed effect being a merged variable (treatment-year) in order to calculate the orthogonal contrasts between the treatments for each year (control2008 vs. understory removal2008, control2009 vs. understory

removal2009, control2010 vs. understory removal2010, control2011 vs. understory removal2011). To distinguish differences in pre-dawn leaf water potential between the control and the treated trees at each measured date, a repeated analysis of variance (ANOVA) was applied to the data. For the analysis of changes in stem radius and annual VWC and soil temperature, one-sided t -test were used to assess differences between treated and control trees and plots. The linear models and calculations of orthogonal contrasts were performed with the software R (R core team, 2014), while the other analysis were carried out with SPSS 2.0 SPSS (IBM Corp., Armonk, NY, USA).

3. Results

3.1. Soil physical properties

For the understory removal plots, average soil temperature during the vegetation period (April to September) from 2010 to 2014 increased significantly by 19% (5 cm soil depth, mean \pm SE, 2.7 ± 0.8 °C), 15% (30 cm, 2.0 ± 0.4 °C), and 15% (60 cm, 1.9 ± 0.13 °C) compared to the control ($P < .001$, see Fig. S1). For the same period, the average VWC increased by 10% (5 cm, 0.01 ± 0.04 cm³ cm⁻³), 14% (30 cm, 0.03 ± 0.04 cm³ cm⁻³), and 16% (60 cm, 0.03 ± 0.02 cm³ cm⁻³). The variability in VWC was visibly higher than in temperature, especially for the upper soil layers (5 and 30 cm). Although annual differences in VWC between treated and control plots were always significant for the 30 and 60 cm soil layers ($P < .05$), differences in the 5 cm soil

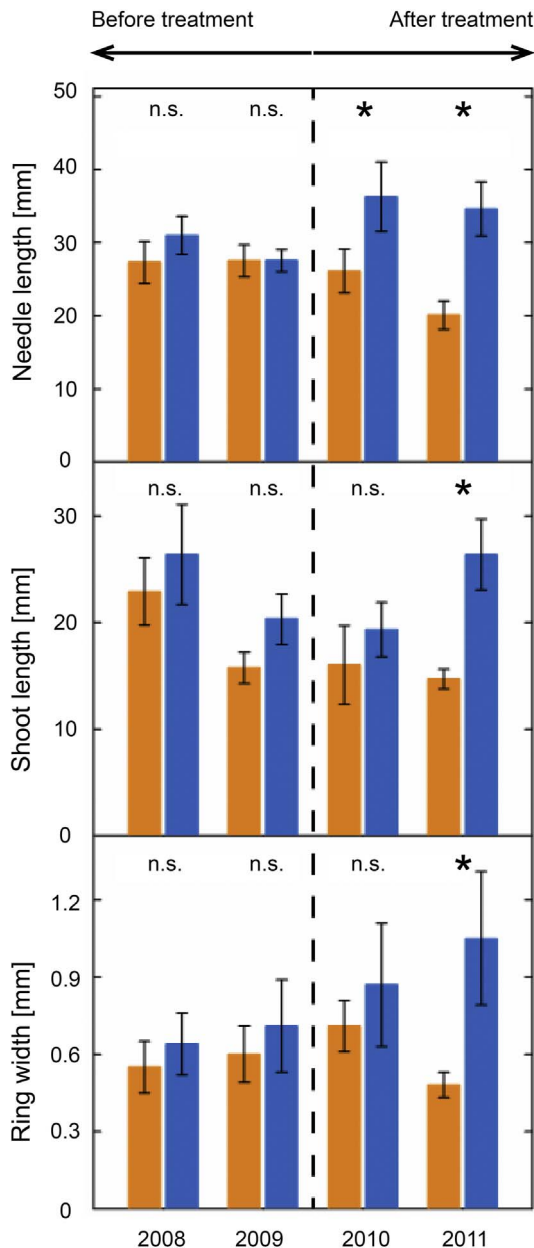


Fig. 2. Mean needle length, shoot length and tree-ring width \pm SE ($N = 6$) of the treated (understory removal, blue) and the control (orange) overstory Scots pine trees. Significant differences between the treated and the control trees were indicated (one-sided t -test, $*P < .05$). The vertical dashed line divides the time in the period before (2008–2009) and after the understory removal in April 2010.

layer were only significant for the years 2011 and 2014 (see Fig. S1).

Within the first year after the understory removal in April 2010, the soil temperature at 5 cm depth instantly increased in response to the understory removal (Fig. 1). In contrast, the VWC showed an initial drying of the 5 cm soil layer following the understory removal. Only

after June 2010, the VWC at 5 cm depth started to be higher in the treated plots than in the control plots. In contrast, the VWC at 30 cm was increasing almost instantly in response to the understory removal. For the 60 cm soil layer, no data are available for the year 2010.

3.2. Needle, shoot and radial growth, and needle nitrogen concentration

Needle and shoot lengths as well as tree-ring widths of treated and control trees were not significantly different before the understory removal (2008, 2009; $P > .05$, Fig. 2). In response to the first shrub removal, only the needle length of treated trees was increasing significantly in 2010 ($P < .05$), while shoot length and tree-ring width were not significantly different compared to the control. Only 2 years after the initial treatment, the treated trees showed significant responses in shoot and radial growth ($P < .01$). In 2011, needles of treated trees were 72% and shoots 79% longer, and tree-ring widths 119% larger than those of the control trees. The variability in tree-ring widths increased substantially after the understory removal. In 2011, no differences in needle nitrogen concentration [N] between treated and control trees was found ($P > .05$, treated trees: $[N] = 1.24 \pm 0.15 \text{ mg g}^{-1}$; control trees: $[N] = 1.18 \pm 0.19 \text{ mg g}^{-1}$).

3.3. Seasonal course of needle water potential

Predawn needle water potential (Ψ_{wp}) of the treated and the control trees started to differ significantly at the beginning of July 2010 ($P < .05$, Fig. 3), remaining at a higher level (closer to zero) than those of the control trees, which decreased considerably particularly during dry periods. After rain events, Ψ_{wp} of both the treated and control trees increased and the differences ceased (Fig. 3). In 2010, the average Ψ_{wp} of treated Scots pine trees was -0.56 MPa (min. -0.75 MPa), whereas average Ψ_{wp} of the control trees was -0.75 MPa (min. -1.11 MPa). In 2011, the differences between the treated and the control trees became even more pronounced, with an average Ψ_{wp} of -0.75 MPa (min. -1.18 MPa) for the treated and -1.09 MPa (min. -1.85 MPa) for the control trees, respectively.

3.4. Tree water relations and radial stem growth

Measurements of sap flow and stem radius data revealed distinct differences in stomatal aperture (SA, calculated as the ratio between potential transpiration and measured sap flow), tree water deficit (TWD), and radial stem growth (GRO) between treated trees and control trees. Monthly averaged sap flow rates were consistently higher for trees in the understory removal plots (on average 49%) than in the control plots for 2011 to 2014 ($P < .05$, Fig. 4a). Differences in sap flow (Fig. 4b) and predawn water potential (Fig. 3) between treated and control trees were found to increase with time and the longer a dry period with no or little rain lasted (Fig. S1). After a heavy rain event the differences vanished for about 1 to 3 days (e.g., 5th Sep. 2011, Fig. 4c), and then restarted to diverge with increasing dryness. The differences were most pronounced in long-lasting drought periods (e.g., in August 2011, Fig. 4c). Control trees reduced sap flow to near-zero values in August 2011, whereas the understory removal trees maintained stomata more open and achieved considerably higher sap flow rates.

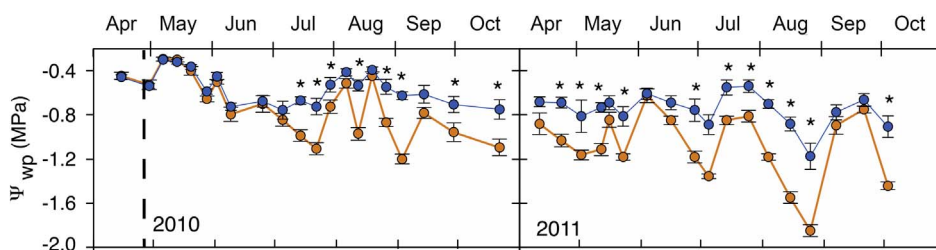


Fig. 3. Seasonal course of mean predawn needle water potential (Ψ_{wp}) \pm SE ($N = 4$) of the treated (understory removal, blue) and control (orange) overstory Scots pine trees. Differences between the treated and the control trees were indicated (repeated ANOVA, $*P < .05$). The vertical dashed line represents the time of the understory removal (April 2010).

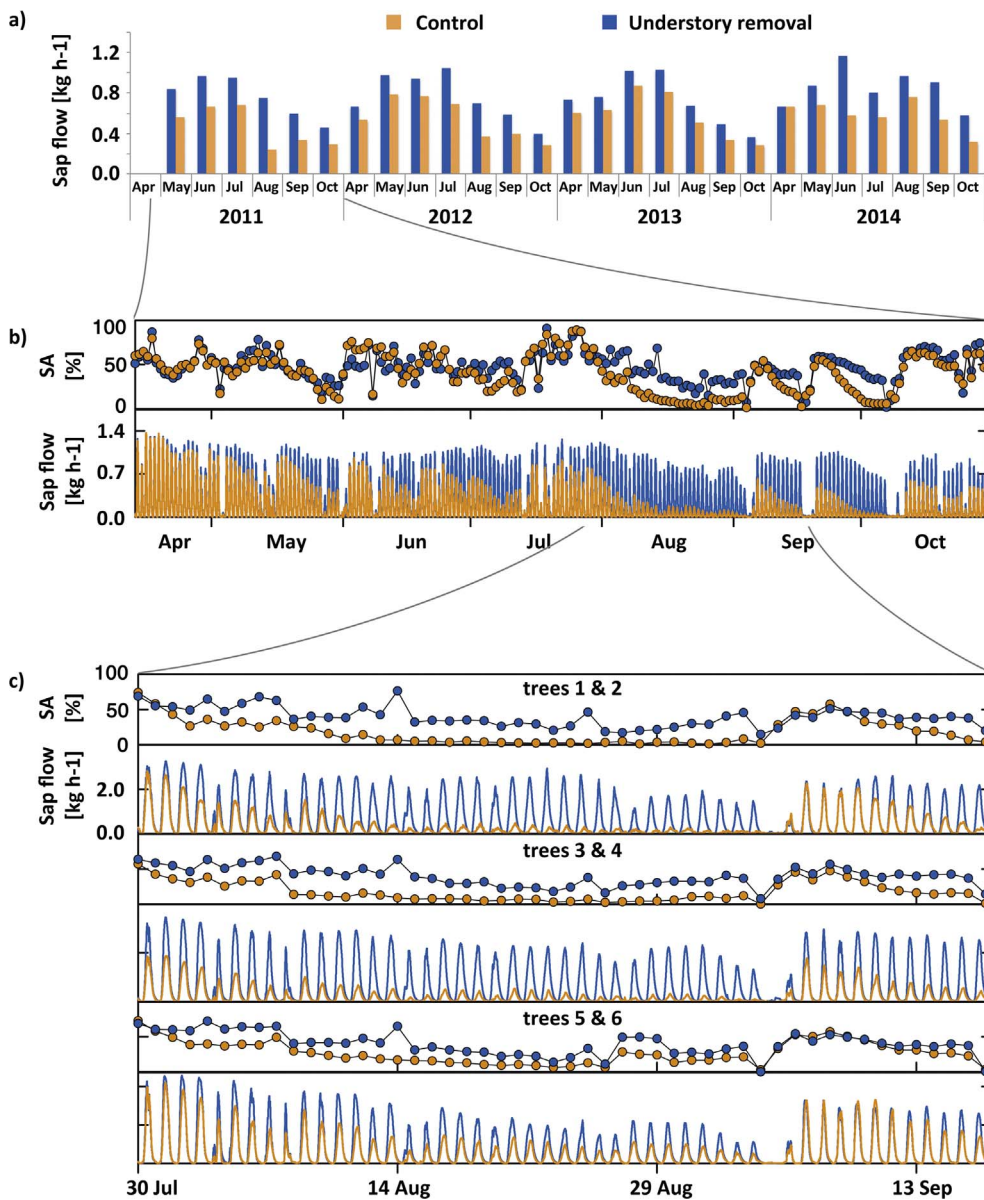


Fig. 4. Tree water relations of the treated (understory removal, blue) and the control (orange) overstory Scots pine trees. (a) Monthly averaged sap flow rates for the treated and the control trees for four years (Apr to Oct only). (b) Daily averaged stomatal aperture percentages (SA, 0 = fully closed stomata, 1 = fully open stomata), and sap flow rates for the treated and the control trees over the exceptionally dry vegetation period 2011. (c) Pairwise depiction of sap flow rates and daily averaged stomatal aperture (10 min resolution) of the individual trees during the driest period over 49 days in 2011.

Differences in sap flow were found to be quite small in winter and spring (data not shown).

Radial stem growth showed the most remarkable differences between treatment and control (Fig. 5a): radial growth of the treated trees was on average 4.6 times higher than of the control trees for 2011 to 2014 ($P < .001$). In contrast to the treated trees, some of the control trees did not grow at all in some years (e.g., trees 4 and 6 in 2012; tree 2 in 2013; cf. Fig. 5a). Trees in the understory removal plots grew better as well as they also started to grow earlier and terminated later in fall (Fig. 5a).

Tree water deficit (TWD) summed up over the vegetation period (April to September) was on average 30% lower for the treated than for the control trees (pooled data for the years 2011 to 2014, $P < .05$). For 2011 to 2013, this difference was apparent also on the annual scale, albeit statistically not significant ($P > .05$, Fig. 5b). In the unusually rainy summer of 2014, this tendency was no longer visible and differences in TWD between the treated and the control trees disappeared. The latter contrasts with the growth response of the treated and the control trees in 2014, which remained on a similar level as in the years before. Higher TWD was exponentially linked to generally lower

growth (Fig. 6). Additionally, the control trees responded with lower growth rates to a given TWD compared to the understory removal trees.

4. Discussion

4.1. Understory removal in a xeric Scots pine forest

The removal of the understory in a drought-prone Scots pine forest and the subsequent weeding over 5 years led to fundamental changes in soil microclimate (Fig. 1), tree growth (Fig. 2) and physiology of overstory Scots pine trees (Figs. 3 and 4). Overall, the growth of the treated trees was many times higher than of the control trees. The treated trees adjusted their crowns by increasing shoot and needle length (Fig. 2), and thus also their leaf area. Furthermore, the treated trees had higher predawn leaf water potential (Fig. 3), reduced tree water deficit (Fig. 5), higher stomatal conductance, and consequently increased transpiration (measured as stem sap flow) and assimilation (assumption based on more open stomata) compared to the control. This had multiple consequences, as discussed below.

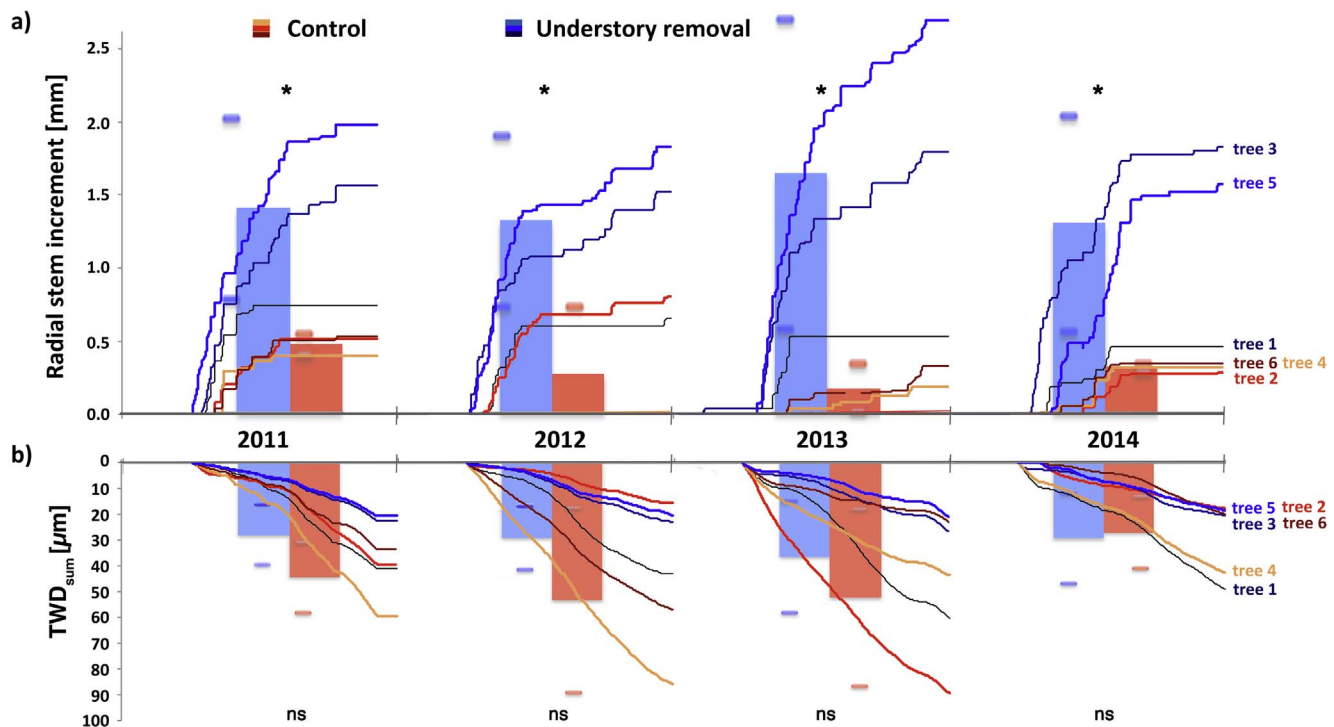


Fig. 5. Results from the stem radius change measurements of the treated (understory removal, cold colours) and the control (warm colours) overstory Scots pine trees. (a) Cumulative growth of three trees in the control plots and three trees in the understory removal plots (line graph) and the average values (column graph) with standard deviations (horizontal lines). Differences between the treated and the control trees were indicated (one-sided *t*-test, **P* < .05). (b) Summed up tree water deficits (10 min values between April and September divided by the number of measurements) of the same six trees (line graph) and the average values (column graph) with standard deviations (horizontal lines).

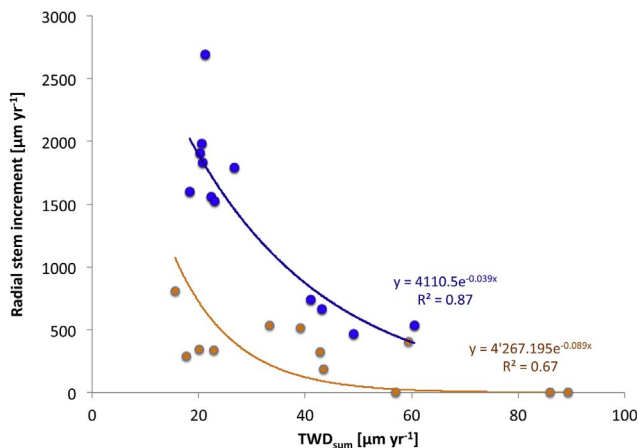


Fig. 6. Exponential relationship between annual radial increment of the overstory Scots pine trees and the sum of tree water deficit during the vegetation period (TWD_{sum}, summed up data from April to September of the years 2011 to 2014 divided by the number of measurements). Every dot represents the value of an individual tree per year. Blue symbols refer to the treated trees (understory removal, trees 1, 3, 5) and orange symbols refer to the control trees (trees 2, 4, 6). For the exponential regressions: *y* = annual increment, and *x* = TWD_{sum} (*P* < .05).

4.2. Changes in the soil microclimate

The understory removal led not only to an increase in soil temperature but also to an increase in soil water content (Fig. 1). We therefore posit that the increase in evaporation was smaller than the reduction in water loss by transpiration of the removed understory. This finding is supported by a similar experiment in a mixed loblolly-shortleaf pine (*Pinus taeda* L. and *Pinus echinata* Mill.) stand at a dry site in the USA (Zahner, 1958). However, Matsushima and Chang (2007) observed an increase in soil temperature but not in soil moisture after a removal of the understory vegetation in a white spruce (*Picea glauca*

Moench Voss) stand in the Boreal Plain in Canada. Their contrasting findings may be explained by a cooler and wetter climate at their site. In fact, wet sites were found to be generally less sensitive to a removal of the understory than dry sites (Kelty et al., 1987). Therefore, it seems logical that a potential benefit of an understory removal and thus an increase in water availability for the overstory trees is much higher at dry sites than at sites where water is not or hardly limiting.

4.3. Growth increases

In response to the understory removal and with a delay of one year, the radial growth of the treated trees increased by almost five times compared to the control and remained at this high level for the length of the study (Figs. 2 and 4). The treated trees did not only grow more, they also seem to start growing earlier than the control trees (Fig. 5a). Temperature is usually assumed to be the main driver for the beginning of tree growth in spring (Menzel and Fabian, 1999; Menzel et al., 2006) and in fact, soil temperature was found to be generally higher in the understory removal plots (Fig. 1).

In parallel to the increased wood growth, shoot lengths significantly increased one year after the understory removal (Fig. 2). This is in line with other studies on Scots pine in Valais (Dobbertin et al., 2010; Feichtinger et al., 2015), which showed that shoot length substantially depends on previous year's summer and autumn water availability. Thus, the longer shoots observed for the treated trees can most likely be explained by a (delayed) response to increased soil water availability of the previous year (Fig. 1) induced by the understory removal.

In contrast to the shoot growth, the needle elongation of Scots pine is known to be positively related to the water availability in current spring (Dobbertin et al., 2010; Feichtinger et al., 2015). This is in agreement with our findings showing significantly longer needles for the treated trees in the initial year of the understory removal (Fig. 2). Soil moisture availability in the 30 cm layer was higher for the treated trees than for the control trees from about May 2010, directly enhancing needle elongation. Light conditions in the canopy were hardly

altered by the understory removal, and thus we conclude that the observed morphological changes in Scots pine occurred in response to higher soil water availability, rather than changes in light.

4.4. Improvement in tree water relations

For the overstory Scots pine trees without understory, the higher soil water availability (Fig. 1) led to higher leaf water potentials (Fig. 2), lower tree water deficits (Fig. 5), and higher sap flow compared to the control (Fig. 4). These differences were particularly pronounced during periods of no or little rainfall (e.g. in August 2011, Fig. 4). Scots pine is known to respond to low water availability by closing its stomata at the cost of decreased carbon assimilation (Zweifel et al., 2007). When the soil water content was low, especially in August, we observed a decrease in the stomatal aperture for both control and treated trees. However, while the control trees had to close their stomata completely during these dry periods, the trees without understory were able to maintain a certain stomatal aperture. The stomata of the treated trees were on average about 50% more open than those of the control trees. These findings are in line with earlier studies on Scots pine at drought-prone sites, which showed that under hot and dry conditions in Valais this species reaches the edge of its physiological niche (Zweifel et al., 2006, 2009; Rigling et al., 2013). Increases in stomatal aperture following a removal of the understory vegetation were also found for Japanese red pine (*Pinus densiflora* Siebold & Zucc.) (Kume et al., 2003) and Erman's birch (*Betula ermanii* Cham.) (Kobayashi, 2006) in Japan, and for Monterey pine (*Pinus radiata* D.Don) in New Zealand (Miller et al., 1998). However, in contrast to these studies we found no increase in nitrogen of current-year needles (2011) in response to the understory removal in the first 2 years (data not shown). Repeating these assessments in 2014, however, led to significantly lower N concentrations in the treated trees, mainly due to the impact of lowered N concentrations in older needles.

4.5. Land-use change increases competition for water

Studies investigating the effects of climate change on tree performance are manifold, while less studies exist considering the effects of climate change together with land-use changes on tree growth and physiology. For the sub-boreal tree species Scots pine, many investigations have shown a decline at its southern dry distribution limit in the Mediterranean (Martínez-Vilalta and Piñol, 2002) and in inner-Alpine dry valleys (Oberhuber et al., 2001; Vacchiano et al., 2011; Rigling et al., 2013). This decline was discussed as being triggered by an increase in the severity of heat and drought events over the past decades (Allen et al., 2010). In parallel to these climatic changes, also land-use practices changed in many areas worldwide (e.g., Houghton, 1994; Caspersen et al., 2000; Tasser et al., 2007; Zaehle et al., 2007; Gimmi et al., 2010). In the Swiss Rhône valley (Valais), changes in land use, such as the abandonment of forest grazing by domestic ungulates and litter harvesting, have increased the density of many forests (Gimmi et al., 2010). Our results clearly show that an increase of understory density markedly increases competition for water among mature overstory Scots pine trees. Thus it may have exacerbated observed drought-induced decline processes (e.g., Rigling et al., 2013). Hence, our study demonstrates the need for a careful disentangling of climate and land-use change processes as they may evolve in parallel and potentially intensify their impact on the ecosystems. By contrast, our findings suggest a positive feedback effect of forest grazing on the growth and vitality of overstory Scots pine trees in xeric forest ecosystems induced by higher soil water availability. Moreover, fertilization by ungulate droppings could also contribute to this trend, but this effect could not be assessed experimentally in our study. Practically speaking, reducing the understory density by applying controlled grazing may be a suitable forest management practice in drought-prone areas to reduce the risk of drought-induced mortality for isohydric tree species like Scots pine.

Acknowledgements

The study was embedded in the project MOUNTLAND and financially supported by the Competence Center Environment and Sustainability (CCES) of the ETH-Domain, Switzerland. We dedicate this study to our friend and colleague Matthias Dobbertin, who tragically passed away. The authors thank Dominic Langhammer and Martin Schmidt for field and laboratory assistance, and Fabien Hiltbrand for technical assistance during the processing of soil and climate data. They are also indebted to Agroscope (Nyon, Switzerland) for kindly providing the meteorological data. We are grateful to the forest service of the Canton Valais, to Forst Region Leuk and to the community of Salgesch for the technical support and permissions.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2017.11.002>.

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