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



Arnaud Giuggiola^{a,b}, Roman Zweifel^a, Linda M. Feichtinger^a, Pierre Vollenweider^a, Harald Bugmann^b, Matthias Haeni^a, Andreas Rigling^{a,b,*}

^a Swiss Federal Research Institute for Forest, Snow and Landscape WSL, Forest Dynamics, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
^b ETH Zürich, Institute of Terrestrial Ecosystems, Universitätsstrasse 16, 8092 Zürich, Switzerland

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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 CO_2 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 centurylong 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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^{*} Corresponding author at: Swiss Federal Research Institute for Forest, Snow and Landscape WSL, Forest Dynamics, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland. *E-mail address*: andreas.rigling@wsl.ch (A. Rigling).

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 \pm 43.7 mm and 11.5 \pm 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; Ancey 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; Ancey 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 \pm 0.2 m²m⁻² for the treated and 2.6 \pm 0.3 m²m⁻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 Download English Version:

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