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Article *in* Ecological Monographs · January 2022

DOI: 10.1002/ecm.1507

Arun Bose
Swiss Federal Institute for Forest, Snow and Landscape Research WSL

Andreas Rigling
Swiss Federal Institute for Forest, Snow and Landscape Research WSL

Arthur Gessler
Swiss Federal Institute for Forest, Snow and Landscape Research WSL

Frank Hagedorn
Swiss Federal Institute for Forest, Snow and Landscape Research WSL

Received: 21 February 2021 | Revised: 4 October 2021 | Accepted: 18 October 2021

DOI: 10.1002/ecm.1507

ARTICLE

ECOLOGICAL MONOGRAPHS
ECOLOGICAL SOCIETY OF AMERICA

Lessons learned from a long-term irrigation experiment in a dry Scots pine forest: Impacts on traits and functioning

Arun K. Bose[1,2] | **Andreas Rigling**[1,3] | **Arthur Gessler**[1,3] | **Frank Hagedorn**[1] | **Ivano Brunner**[1] | **Linda Feichtinger**[1] | **Christof Bigler**[4] | **Simon Egli**[1] | **Sophia Etzold**[1] | **Martin M. Gossner**[1,3] | **Claudia Guidi**[1] | **Mathieu Lévesque**[4] | **Katrin Meusburger**[1] | **Martina Peter**[1] | **Matthias Saurer**[1] | **Daniel Scherrer**[1] | **Patrick Schleppi**[1] | **Leonie Schönbeck**[1,5] | **Michael E. Vogel**[1] | **Georg von Arx**[1] | **Beat Wermelinger**[1] | **Thomas Wohlgemuth**[1] | **Roman Zweifel**[1] | **Marcus Schaub**[1]

[1]Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

[2]Forestry and Wood Technology Discipline, Khulna University, Khulna, Bangladesh

[3]Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland

[4]Department of Environmental Systems Science, Forest Ecology, ETH Zurich, Zurich, Switzerland

[5]Plant Ecology Research Laboratory, School of Architecture, Civil and Environmental Engineering ENAC, École Polytechnique Fédérale de Lausanne EPFL, Lausanne, Switzerland

Correspondence
Arun K. Bose
Email: arun.bose@wsl.ch

Handling Editor: Anthony W. D'Amato

Abstract

Climate change exposes ecosystems to strong and rapid changes in their environmental boundary conditions mainly due to the altered temperature and precipitation patterns. It is still poorly understood how fast interlinked ecosystem processes respond to altered environmental conditions, if these responses occur gradually or suddenly when thresholds are exceeded, and if the patterns of the responses will reach a stable state. We conducted an irrigation experiment in the Pfynwald, Switzerland from 2003–2018. A naturally dry Scots pine (*Pinus sylvestris* L.) forest was irrigated with amounts that doubled natural precipitation, thus releasing the forest stand from water limitation. The aim of this study was to provide a quantitative understanding on how different traits and functions of individual trees and the whole ecosystem responded to increased water availability, and how the patterns and magnitudes of these responses developed over time. We found that the response magnitude, the temporal trajectory of responses, and the length of initial lag period prior to significant response largely varied across traits. We detected rapid and stronger responses from aboveground tree traits (e.g., tree-ring width, needle length, and crown transparency) compared to belowground tree traits (e.g., fine-root biomass). The altered aboveground traits during the initial years of irrigation increased the water demand and trees adjusted by increasing root biomass during the later years of irrigation, resulting in an increased survival rate of Scots pine trees in irrigated plots. The irrigation also stimulated ecosystem-level foliar decomposition rate, fungal fruit body biomass, and regeneration abundances of broadleaved tree species. However, irrigation did

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Arun K. Bose and Andreas Rigling contributed equally to this work.

not promote the regeneration of Scots pine trees, which are reported to be vulnerable to extreme droughts. Our results provide extensive evidence that tree- and ecosystem-level responses were pervasive across a number of traits on long-term temporal scales. However, after reaching a peak, the magnitude of these responses either decreased or reached a new stable state, providing important insights into how resource alterations could change the system functioning and its boundary conditions.

KEYWORDS
climate change, ecosystem properties, ecosystem resilience, functional traits, long-term irrigation, Scots pine

INTRODUCTION

Climate change including changes in temperature and precipitation regimes chronically alter resource availability in forest ecosystems (Grossiord et al., 2020; Schuldt et al., 2020; Will et al., 2013) with far-reaching biological consequences such as shifts in ecosystem structure and functioning (Estiarte et al., 2016; McDowell et al., 2020; Richardson et al., 2018; Williams et al., 2012). The direction, magnitude, and temporal trajectory of changes in ecosystem functioning may depend on how strongly the changes in environmental parameters and thus resource availability deviate from the preceding conditions (Felton et al., 2020; Smith et al., 2015; Zweifel et al., 2020) and how well the ecosystem biotic components such as trees are acclimating to the new condition (Anderegg et al., 2015; Batllori et al., 2020; Bose, Gessler, et al., 2020; Zweifel & Sterck, 2018). In forests, molecular and physiological responses to changes in resource availability or environmental conditions, usually occur immediately (Martin-StPaul et al., 2013; Timofeeva et al., 2017), while ecosystem-level responses such as changes in tree mortality and species composition take longer as they depend on altered competitive interactions among multiple species (da Costa et al., 2018; Korell et al., 2021). However, it is largely unknown whether any individual tree- and ecosystem-level change will persist and reach a new stable state or will return to the initial condition over longer time periods (Smith et al., 2015).

Individual tree or ecosystem-level responses to resource alterations can be continuous or gradual if the rate of change is similar at individual and community level (Gavinet et al., 2019; Ogaya & Peñuelas, 2007). However, the response can be delayed, both at the individual and community level due to the influences of the memory of past environmental conditions (Kannenberg, Maxwell, et al., 2019; Kannenberg, Novick, et al., 2019; Peltier et al., 2016; Zweifel et al., 2020). The individual tree-level responses can vary across species because different tree species feature different genetic and physiological traits (Nicotra et al., 2010), and thus can influence the ecosystem-level responses (Estiarte et al., 2016; Smith et al., 2015). For example, altered resource availability can change the growing conditions and can influence the competition among species in forest ecosystems (Forrester, 2014; Gomez-Aparicio et al., 2011). The changes in interspecific competition through resource alterations can benefit the growth of one species while increasing the mortality of others (Barbeta et al., 2013; Batllori et al., 2020; Kimball et al., 2014). Moreover, lack of responses over extended time periods have also been reported (Felsmann et al., 2015; LeBauer & Treseder, 2008), which could occur when only such resources are altered that are not limiting tree growth or other functions (Leuzinger et al., 2011).

Growing awareness of the impacts of extreme events and long-term changes in water availability and air temperature on forest ecosystems has stimulated a number of long-term experiments (Barbeta et al., 2013; Beier et al., 2012; Grossiord et al., 2018; Le Roncé et al., 2021; Paschalis et al., 2020). The results from these experiments revealed a large variability in patterns and magnitude of responses, because acclimation to the newly formed growth environment may depend on a multitude of factors and their respective interactions (Smith, 2011; Volaire, 2018), including the type of experimental manipulation (e.g. warming, water removal, or water addition; Wu et al., 2011), the magnitude of the manipulation (Grossiord et al., 2017), the legacy of the receiving ecosystem (Kannenberg, Maxwell, et al., 2019; Kannenberg, Novick, et al., 2019), long-term forest management (Felsmann et al., 2017), and the inherent ecosystem acclimation potential driven by species and genetic diversity (Alberto et al., 2013; Bose, Moser, et al., 2020).

Under drier climatic conditions, trees' physiological and morphological properties are adjusted toward a water-saving strategy (Volaire, 2018), including optimal carbon gain through increased water use efficiency (Limousin et al., 2015), adjustment of mesophyll conductance (Hommel et al., 2014), higher root to shoot ratio (Brunner et al., 2015; Lloret et al., 1999), and smaller crown with reduced leaf and shoot size (Feichtinger et al., 2015; Limousin et al., 2010). The physiological and morphological legacies of growing in a dry environment could make the tree-level responses to increased water supply complex and uncertain (Limousin et al., 2009; Peltier & Ogle, 2019; Zweifel et al., 2020). For example, a delayed response to altered water supply has been reported by a number of studies (Cotrufo et al., 2011; Feichtinger et al., 2014; Rigling et al., 2003). However, most of our understanding is based on short-term studies (<5 years; Beier et al., 2012), or studies that do not have repeated measurements over a longer period of time (De Dato et al., 2006; Felsmann et al., 2017; Neary et al., 1990). In addition, the studies that observed longer term (>10 years) responses are primarily focused on individual tree-level responses such as tree growth and physiological responses (da Costa et al., 2018; Feichtinger et al., 2014). Due to the lack of long-term empirical information from manipulation experiments we are short of a basis for a more consolidated theoretical framework that could lead to a comprehensive understanding of individual and ecosystem-level responses to long-term changes in water availability.

Most common experimental treatments are a reduction of soil water availability (Gavinet et al., 2019; Grams et al., 2021; Misson et al., 2011) or the exposure of trees to increased temperature and drought (Adams et al., 2015). In this study, we examined long-term (from 2003 to 2018) tree and ecosystem-level responses to irrigation, which was performed at the very dry edge of Scots pine (*Pinus sylvestris*) distribution. Within the last decades, intensive Scots pine mortality occurred in this area (Rigling et al., 2013) indicating the extreme drought conditions limiting growth and survival. The irrigation treatment allowed us to quantify the effects of natural drought on ecosystems traits and functions as well as to track the recovery trajectories of trees and the whole forest stand released from the natural dry conditions (Brunner et al., 2009; Dobbertin et al., 2010). Thus, the alteration in environmental conditions was induced by adding water to parts of a naturally dry Scots pine forest in amounts that doubled natural precipitation during the summer months, thus releasing the forest from water restriction during the vegetation period. In this study, we aimed to provide quantitative understanding on how the direction (positive or negative) and magnitude of responses to water regime changes vary across different tree- and ecosystem-level traits. Moreover, we aimed at assessing, which ecosystem traits and functions respond immediately or with a time lag after changing water availability and if responses are transient or persisting. Ultimately, we examined if the long-term (2003–2018) drought-release period is sufficient for a dry Scots pine forest to reach a new stable state in tree and ecosystem functioning.

METHODS

Study site

The study site is located in the Rhone Valley in Switzerland (46°18′ N, 7°3′ E, 615 m above sea level). The area is one of the driest inner Alpine valleys of the European Alps, with a mean annual temperature of 10.6°C (19.6°C for June–August) and mean annual precipitation of 576 mm (174 mm for June–August) for the period 1995–2014 (data from the MeteoSwiss station Sion; MeteoSwiss, 2018). The soil is shallow and characterized by low soil volumetric water content that ranges from 0.11 to 0.47 with an average of 0.27 (based on the data from 2003 to 2014). According to the pedotransfer function of Puhlmann et al. (2009), the soil is characterized by a low available water-holding capacity of 135 mm until 0.8 m rooting depth. The irrigation treatment was applied to a 100-years-old xeric Scots pine forest. The forest is even-aged with 730 stems/ha and the overstory is dominated by Scots pine. However, pubescent oak (*Quercus pubescens* Willd.) and shrub species occupy 60% of the understory cover (Brunner et al., 2009; Dobbertin et al., 2010).

Irrigation experiment

The 1.2-ha experimental area was initially divided into eight plots of 1000 m^2 each. Four plots were randomly selected for irrigation and the four remaining plots served as non-irrigated naturally dry controls. The irrigation has been running since June 2003 and only during the night (~3.8 mm per night). Irrigation runs during the frost-free period starting from late spring to the end of the summer (see seasonal irrigation periods from 2003 to 2018 in Appendix S1: Table S1). The yearly irrigation amounts are shown in Appendix S1: Figure S1. Irrigation was not event-based and thus not aimed to increase individual precipitation events but to approximately double the average annual precipitation (~600 mm/year). The irrigation water was taken from a nearby water channel fed by the River Rhone next to the experimental area and brought into the forest stand by means of permanent sprinklers established at each irrigation treatment plot.

Analytical approach

In this study, we benefited from extensive data series collected in previous studies (Brunner et al., 2009, 2019; Dobbertin et al., 2010; Eilmann et al., 2011; Herzog et al., 2014, 2019; Schönbeck et al., 2018; von Arx et al., 2017) and in additional ongoing and unpublished studies (Appendix S1: Table S2). In these studies, various tree-level above- and belowground traits and ecosystem-level traits and functions have been determined. Using these data, we quantified effect size of the irrigation treatment by the coefficient of mixed-effect models (see details in statistical analysis) to understand how the impact of the irrigation treatment varied across tree- and ecosystem-level traits. We also examined how the effect size of the irrigation treatment changed over the 16 years monitoring period (2003–2018). For each trait, our analysis aimed to detect the initial lag period prior to a significant response and if these responses were persistent or disappeared after a certain period. The effect size of the irrigation treatment and how that varied temporally has never been published in any other study.

For aboveground tree-level traits, we analyzed tree needle length (mm), shoot length (mm), leaf area index (LAI), radial growth (i.e., tree-ring width; mm), intrinsic water use efficiency (based on tree-ring $\delta^{13}C$; ‰), non-structural carbohydrates (NSC, soluble sugars and starch) in the tree trunk, percentage of ray parenchyma, probability of tree survival (i.e., live or dead), and crown transparency (a proxy for tree vitality) (Dobbertin, 2005; Dobbertin & Brang, 2001), while fine-root biomass density (g/m^2), ingrowth (i.e., newly formed) root length density (m/m^2), ingrowth root tip frequency (number/cm), ingrowth root biomass density (g/m^2), and ingrowth root tissue density (mg/cm^3) were analyzed for tree-level belowground responses.

For ecosystem-level traits, we analyzed soil volumetric water content, stand basal area of live trees, decomposition rates of *P. sylvestris* needles and roots, *Q. pubescens* leaves, and *Viburnum lantana* L. leaves. In the decomposition experiments, aboveground litter was placed in litter bags of 0.1-mm mesh size (named fine) to exclude the soil macrofauna and of 10-mm mesh size (coarse) allowing access by the macrofauna. Belowground litter was placed in 1-mm mesh size litter bags allowing access by the mesofauna. We also analyzed the abundance of plant galls, abundance of dropped shoots killed by *Tomicus* bark beetle species, abundance and richness of ground beetles and spiders, and occurrence of shoot feeding by *Tomicus* species in the tree canopy. For better understanding the impact of drought release on the understory composition, we analyzed the abundance of natural regeneration (called in the following juveniles, i.e., seedlings and saplings of ≤400 cm height) of *P. sylvestris*, *Q. pubescens*, and other tree species combined, and shrub species. Field measurement for natural regeneration was conducted in September 2019 (i.e., 16 years after irrigation treatment application). The impact of drought release on fungal community was assessed by analyzing the abundance and biomass of mycorrhizal and saprotrophic fungi fruit bodies. Aboveground fungal abundance and biomass were assessed by recording fungal fruit body production of macromycetes (visible to the naked eye) weekly during the mushroom season (May–November) from 2003 to 2007 (see Appendix S1: Table S2 and Section S1 for data measurement protocols).

Statistical analysis

We examined the direction (i.e., positive or negative effect of irrigation), magnitude (i.e., effect size), and temporal trajectories (i.e., start and duration of the response and changes in effect size over time) of responses for various tree-level and ecosystem-level traits to increased water supply (Appendix S1: Table S2). We quantified the effect size of irrigation by the coefficient of the mixed-effect models, while a p value < 0.05 was used to determine statistical significance (Bose, Wagner, et al., 2021; Bose, Rigling, et al., 2021; Forrester, 2019). Each tree and ecosystem-level variable were analyzed in relation to the irrigation treatments (two levels: non-irrigated vs. irrigated). In addition to fixed effects (i.e., effects from irrigation treatments), the associated random effects were incorporated into the model (see Appendix S1: Table S2 for random effect variables). The analysis was performed separately for each year to understand the effect size of the irrigation treatment in each year. A single model with year as a predictor variable would not provide the difference between irrigation and control treatment for every year. Therefore, we would not be able to know exactly when the statistically significant response (i.e., initial lag period) occurred and if that response was transient or persisting. The linear mixed-effect modeling (Zuur et al., 2009) was performed for continuous data using the *lme* function of the R package *nlme* (Pinheiro et al., 2014; R Development Core Team, 2018). The generalized linear-mixed effect modeling was targeted at count (e.g., species abundance, regeneration abundance) and binomial (e.g., probability of tree survival and occurrence of *Tomicus* in tree canopy) data, which were performed using the *glmer* function of the R package *lme4* (Bates et al., 2017). In *glmer* modeling, the binomial family was used for binomial data, while

Poisson and negative binomial families were considered for the count data. We visually verified the assumptions of normality and variance homogeneity of the residuals. We used square-root and/or log-transformation when needed for continuous data.

For understanding the potential role of temporal autocorrelation due to repeated measurements, we performed a separate linear mixed-effect modeling analysis with and without temporal autocorrelation by including all measurement years. For this analysis, we picked four variables (tree-ring width, shoot length, crown transparency, and δ^{13}C) that had the highest number of measurements. For each of those four variables, we considered measurement years, treatments (control and irrigated), and the

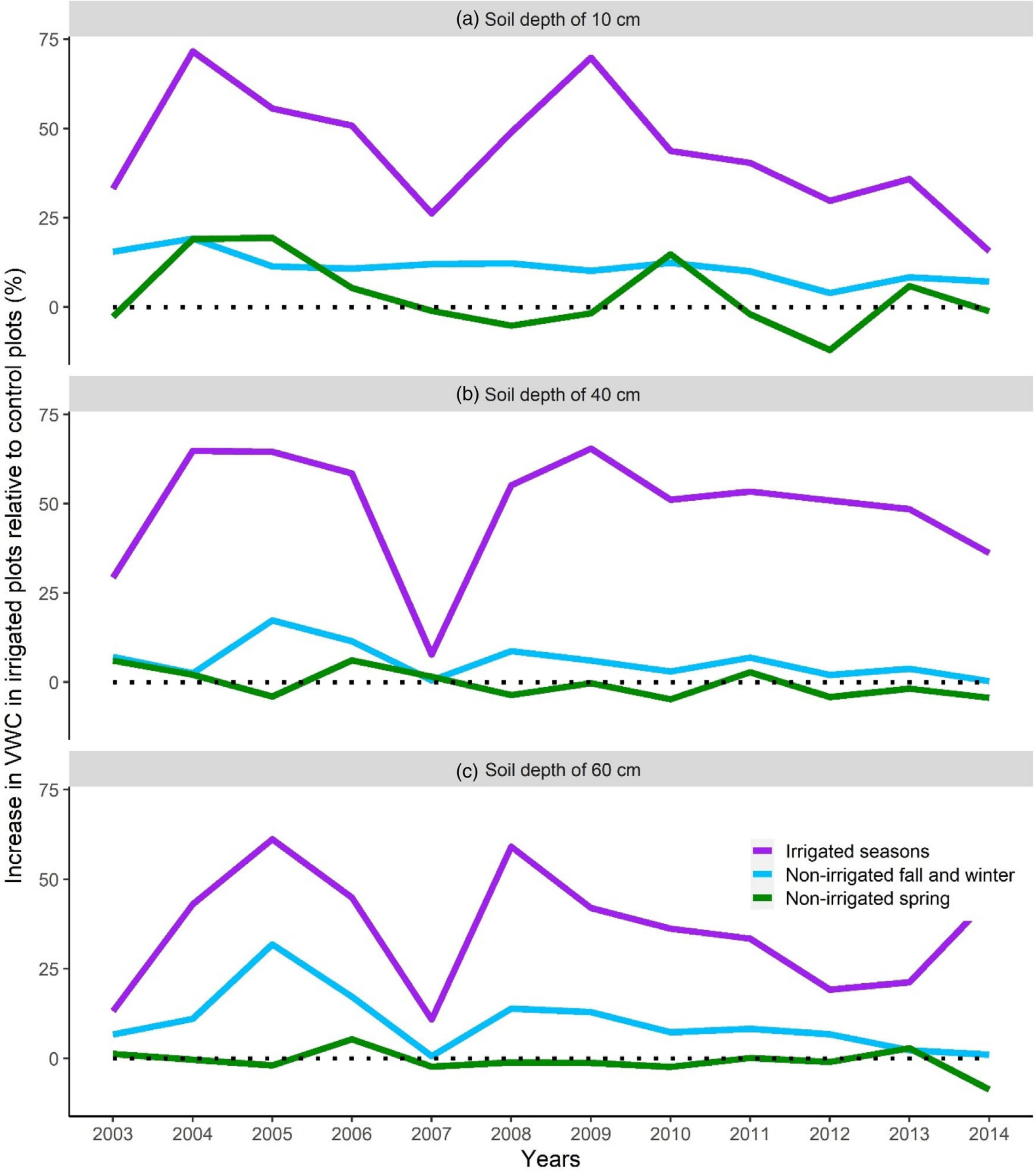


FIGURE 1 Temporal change in soil VWC (volumetric water content) from irrigated plots relative to the control plots (%) across three different soil layers (a–c) for the irrigation periods (see Appendix S1: Table S1), non-irrigated fall–winter periods (September–February) and non-irrigated spring period (March–May). The VWC values represent the average of one to four measurements conducted within a single treatment plot (irrigation or control). Thus, no statistical test was performed. Total amounts of annual precipitation and irrigation are provided in Appendix S1: Figure S1

interaction between measurement years and treatments to be fixed-effect variables while trees nested within plots were considered to be random effects. The temporal autocorrelation across measurement years was incorporated into the model by using the function *corAR1* of the R package *nlme*.

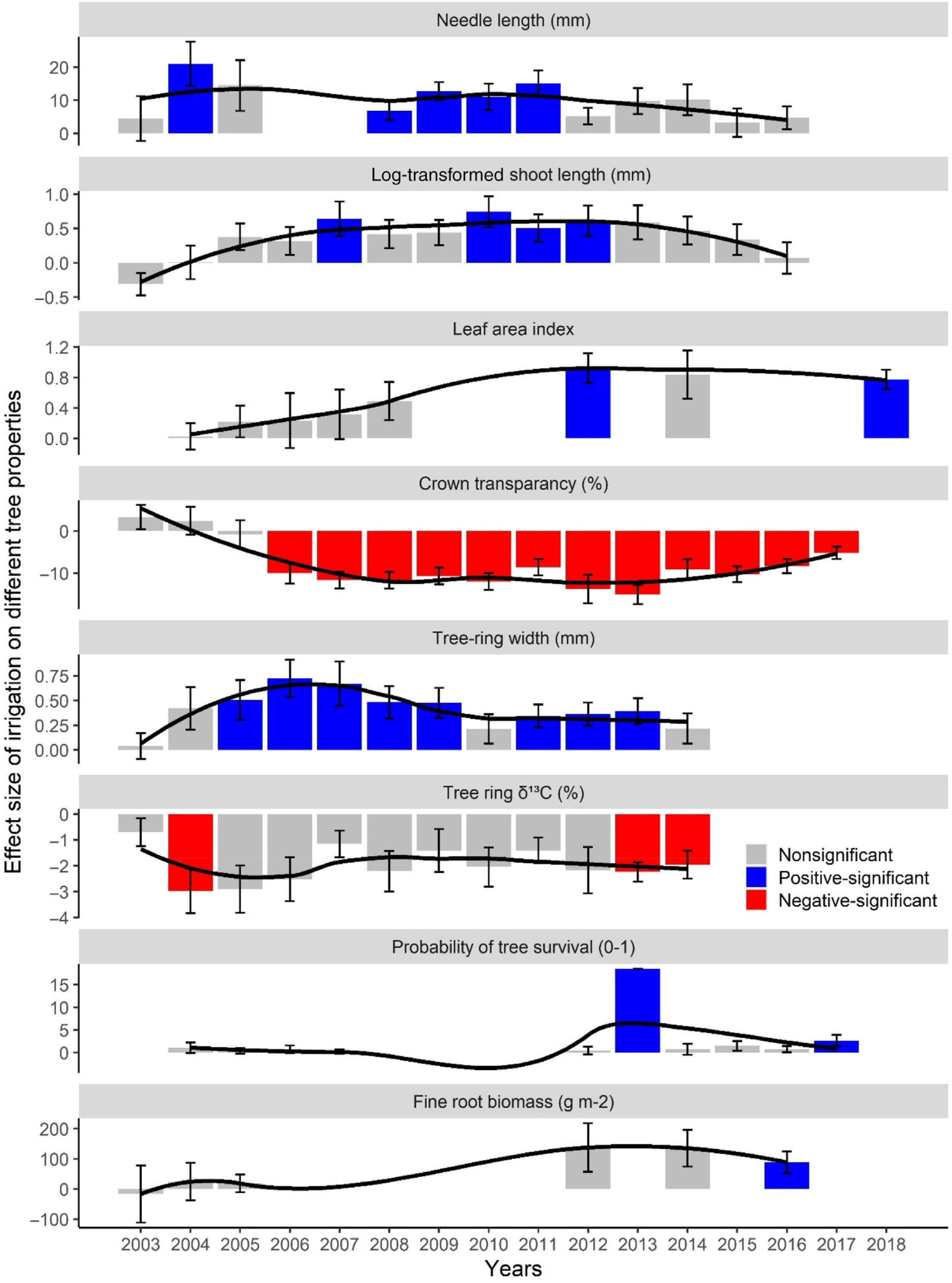


FIGURE 2 Effect size (i.e., coefficient of the mixed-effect model) of the irrigation on different tree-level properties over the course of the treatment period 2003–2018. The error bars represent the mean ± SE and the fitted line shows the locally estimated scatterplot smoothing (i.e., loess). The number of observations used for each analysis is provided in Appendix S1: Table S2. The analysis was performed separately for each year. Irrigation started in 2003

RESULTS

Soil volumetric water content

The irrigation treatment increased soil volumetric water content (VWC) across the three different soil layers from 2004 to 2014 especially during irrigated seasons (i.e., summer and parts of late spring and early fall) and non-irrigated fall–winter seasons. The magnitude of VWC increase varied across seasons and soil layers (Figure 1 and Appendix S1: Figure S2). However, the difference between irrigated and control plots in terms of VWC was not statistically tested due to lack of replicated measurements. The VWC was measured at four positions within one irrigated plot and one control plot. The increase in VWC of the irrigated plots in relation to the control plots was generally highest in irrigated seasons and lower in non-irrigated spring season (Figure 1). Although not statistically tested, the soil of the irrigated plots repeatedly became drier than that of the controls during the spring period starting in 2008. This pattern did not occur every year but was observed in all soil layers from 10 to 60 cm depth (Figure 1).

Aboveground tree-level responses

The irrigation treatment significantly increased needle length, shoot length, leaf area index (LAI), tree-ring width, and decreased crown transparency and tree-ring δ^{13}C of *P. sylvestris* trees with an initial lag of 1–4 years since treatment application (Figure 2). Irrespective of negative or positive response, the initial lag was highest for shoot length (4 years) and lowest for tree-ring δ^{13}C (1 year) and needle length (1 year). The tree-ring δ^{13}C was significantly lower already in the 1st year after the onset of the treatment for trees in irrigated plots than for trees in control plots. However, even though tree-ring δ^{13}C in the irrigated trees was always at least 5% lower compared to the control trees during 2–9 years since the treatment application, the effect was only significant again in 2013 and 2014 (Figure 2). LAI was not significantly higher in irrigated plots during the initial years (2004–2008), but during the years 2012 and 2018, which is 10 and 16 years since the onset of the treatment (Figure 2). Our mixed-effect model analysis detected no significant effect of the irrigation on the percentage of ray parenchyma, total NSC, and soluble NSC, but an initial reduction of starch concentration (Appendix S1: Figure S3).

In 2003, the year of the irrigation start, the total number of dead trees was similar in control and irrigated plots (Appendix S1: Figure S4). However, tree mortality was higher in control plots during the treatment years (2004–2017). In 2017, the total number of dead trees in control plots was 162 stems/ha compared to 30 stems/ha in irrigated plots (Appendix S1: Figure S4). The probability of tree survival was significantly higher in irrigated plots in 2013 and in 2017, however, no statistically significant difference was observed for the rest of the measurement years (Figure 2).

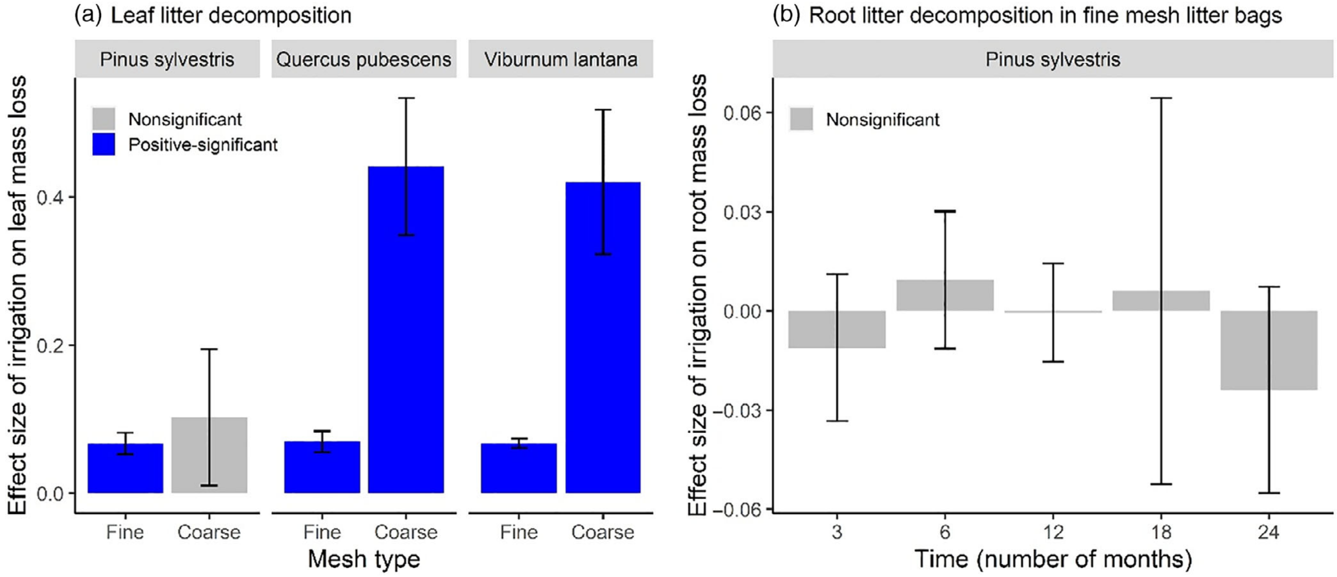


FIGURE 3 Effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on mass loss of leaf and root litter. (a) Leaf litter mass loss of three species by the end of 140 days and (b) root litter mass loss of *Pinus sylvestris* of fine-mesh litter bags over 24 months. The error bars represent mean ± SE. The number of observations used for each analysis is provided in Appendix S1: Table S2. The analysis was performed separately for each time period of root litter. The leaf litter and root litter experiments were conducted during May–September 2014 and during March 2014–March 2016, respectively, which is 11 years after irrigation treatment application

The temporal trajectories of effect size varied across tree traits (Figure 2). For example, no response to irrigation was found in terms of percent NSC and percent ray parenchyma (Appendix S1: Figure S3) while tree-ring width and crown transparency were consistently enhanced by irrigation after initial lags of various lengths (Figure 2). The effect of irrigation on needle length, shoot length, and LAI becomes insignificant in 2013 and onward except the LAI in 2018 (Figure 2). The effect size on tree crown transparency showed a declining trend after reaching a peak in 2013. The same response pattern with a decline following a peak was also found in needle length and tree-ring width (Figure 2). Our results showed that the magnitude of response (i.e., effect size) to increased water supply can be quite variable and did not increase continuously over time (Figure 2). It is important to mention that the potential role of temporal autocorrelation due to repeated measurements in our data sets was extremely minor on effect sizes (magnitude of responses) and on statistical significances (see *p* values in Appendix S1: Table S3).

Belowground tree-level response

Our mixed-effect modeling analysis showed that biomass density (g/m^2) of fine roots was significantly higher in irrigated plots than in control plots 14 years after

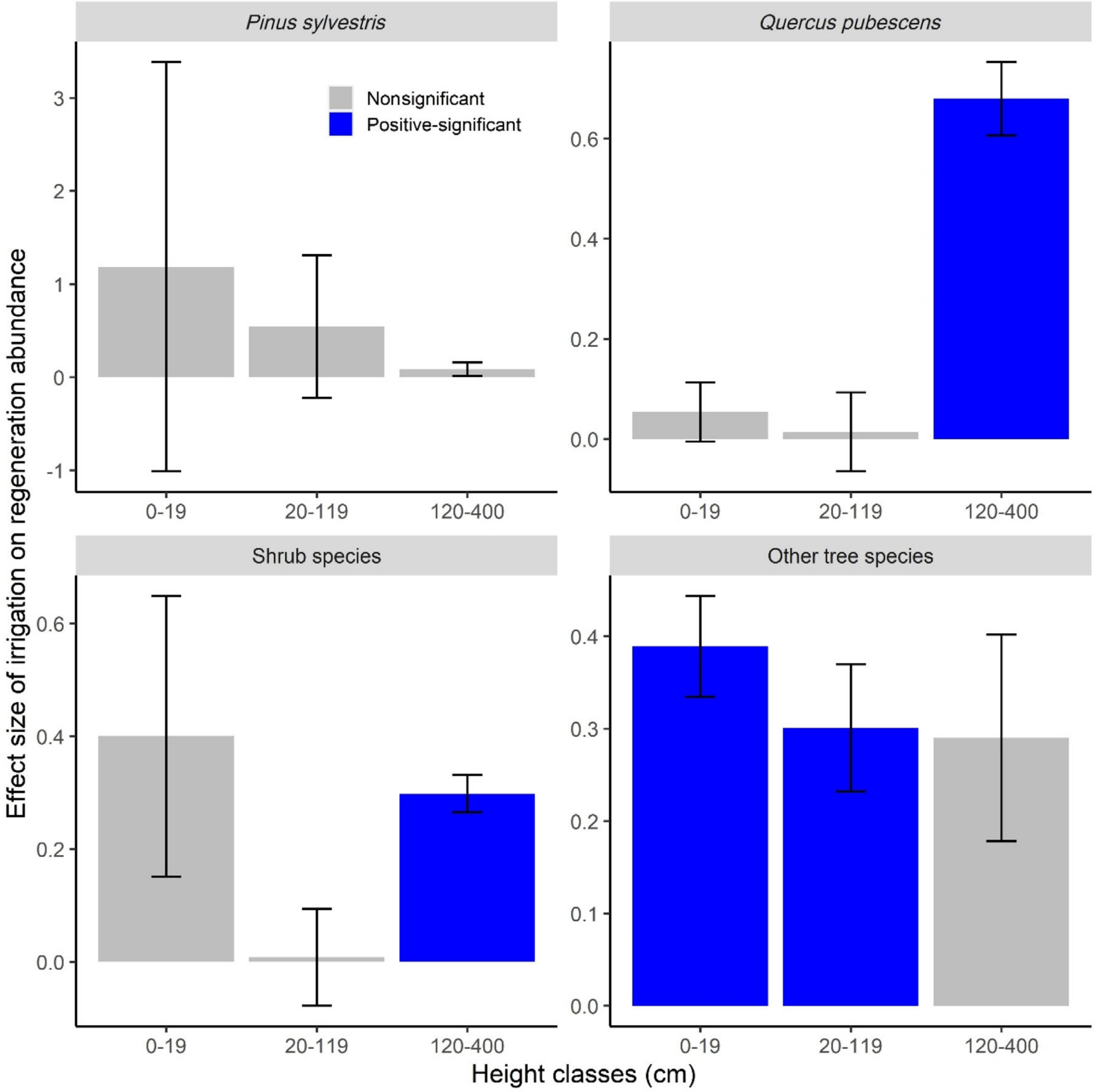


FIGURE 4 Effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on abundances of natural regeneration of *Pinus sylvestris*, *Quercus pubescens*, other tree species, and shrub species across three height classes. The error bars represent the mean ± SE ($n = 32$). The analysis was performed separately for each of the height classes. The regeneration measurement was conducted during September 2019, which is 16 years after irrigation treatment application

TABLE 1 Ecosystem-level responses: the effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on various biodiversity indicators

Biodiversity indicators	Model type	Coefficient	SE	*p*	Time since treatment onset (year)
Abundances of galls	GLMM (negative exponential)	0.30	0.51	0.56	4
Abundances of galls	GLMM (negative exponential)	−0.06	0.34	0.87	5
Shoot feeding *Tomicus* abundance (ground)	GLMM (negative exponential)	−0.07	0.32	0.82	4 (measured in June)
Shoot feeding *Tomicus* abundance (ground)	GLMM (negative exponential)	−0.68	0.30	**0.02**	5 (measured in March)
Shoot feeding *Tomicus* occurrence (canopy)	GLMM (binomial)	−0.12	0.50	0.81	13
Species richness spiders	LMM	−4.38	2.25	0.10	4
Species richness spiders	LMM	−0.64	1.97	0.76	5
Abundance spiders	LMM	−10.67	32.20	0.75	4
Abundance spiders	LMM	35.23	39.80	0.41	5
Species richness ground beetles	LMM	1.01	0.97	0.34	4
Species richness ground beetles	LMM	−0.10	1.00	0.92	5
Abundance ground beetles	LMM	18.78	8.18	0.06	4
Abundance ground beetles	LMM	20.31	17.50	0.29	5

Note: Significant effects ($p < 0.05$) are shown in boldface type. GLMM, generalized linear mixed-effect model; LMM, linear mixed-effect model.

irrigation treatment application (Figure 2). The irrigation treatment had a relatively weaker influence on fine-root biomass compared to the influence of irrigation on aboveground tree traits. The irrigation effect on fine-root biomass was not significant during the initial 1–3 years as well as 10 and 12 years after treatment application (Figure 2). We detected no significant effect on ingrowth root length density (m/m^2), root tip frequency (number/cm), root biomass density (g/m^2), and root tissue density (mg/cm^3) at 2 and 14 years after treatment application (Appendix S1: Figure S5).

Ecosystem-level responses

Stand basal area of live trees

Stand basal area of live trees was higher in irrigated plots compared to control plots throughout the study period from 2003 to 2017. We did not observe statistically significant differences ($p < 0.05$) between irrigated and control treatments until 2009; however, differences were significant from 2009 to 2017. The effect size of irrigation on stand basal area increased over time from 2009 to 2017 (Appendix S1: Figure S6).

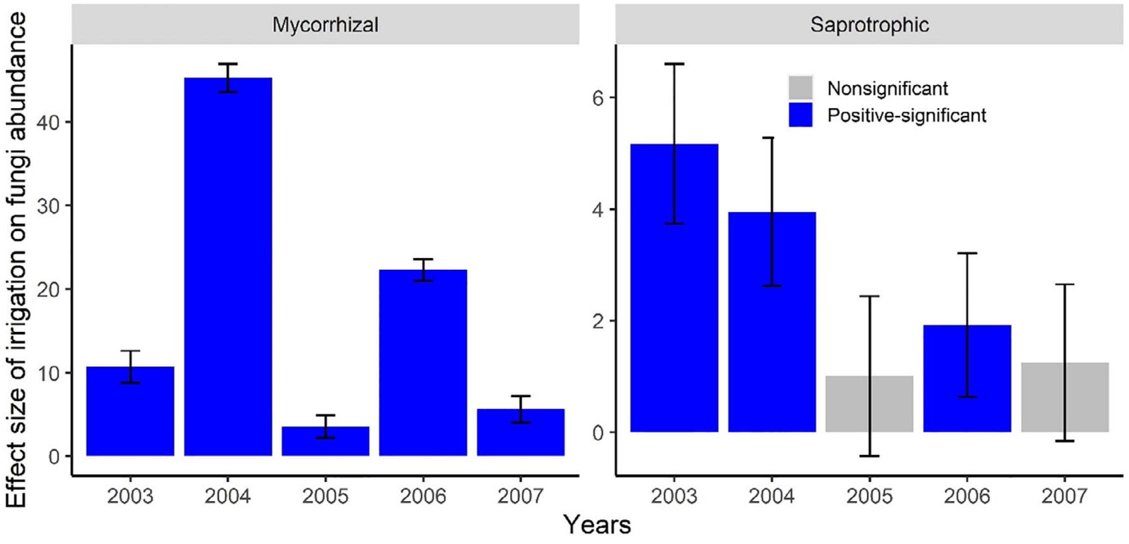
Litter decomposition

The litterfall was measured in 2014 (12 years since the onset of the irrigation treatment). Overall, irrigation treatment increased litterfall, especially in terms of the needles of *P. sylvestris*, mistletoes, shrubs, and cones. However, the litterfall in terms of *Q. pubescens* leaves and woods and barks (irrespective of species) were not significantly different between control and irrigated plots (Appendix S1: Figure S7). The litter-bag experiment carried out after 11 treatment years showed increased decomposition rates of *P. sylvestris* needles, and *Q. pubescens* and *V. lantana* leaves in the irrigation treatment. The effect size of the irrigation on mass loss was dependent on litter bag types (fine and coarse) and species. Irrigation had a larger effect on mass loss of *Q. pubescens* and *V. lantana* leaves when those were placed in the coarse-mesh litter bags (10 mm mesh size) compared to when incubated in fine-mesh litter bags (0.1 mm mesh size). In coarse-mesh litter bags, the effect size was higher for *Q. pubescens* and *V. lantana* than for *P. sylvestris* (Figure 3a). Irrigation had no significant effect on *P. sylvestris* root litter decomposition rate in fine-mesh bags over a 24-month monitoring period performed 11 years after the irrigation treatment application (Figure 3b).

Natural regeneration of woody species

Sixteen years after irrigation onset, large sized (120–400 cm in height) Scots pine was more frequent than *Q. pubescens* in both control and irrigation plots. However, *Q. pubescens* caught up in numbers on irrigated plots versus control plots, while Scots pine was not affected by irrigation. The same pattern was assessed for large-sized shrubs. Irrigation treatment had no significant

(a) Fungi abundance



(b) Fungi biomass

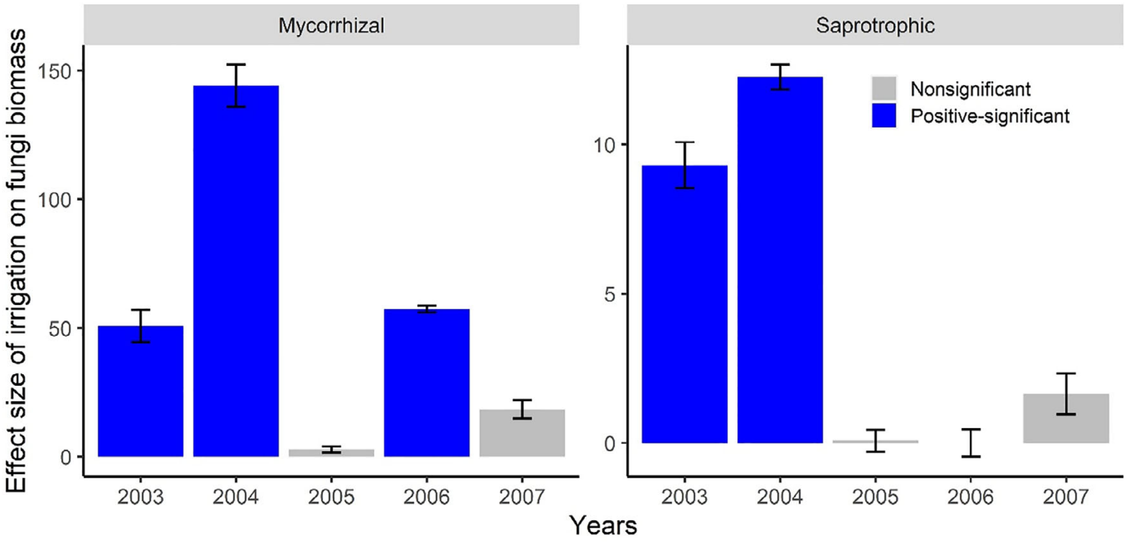


FIGURE 5 Effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on (a) abundances and (b) biomass of fungal fruit bodies from two ecological guilds (mycorrhizal and saprotrophic). The error bars represent the mean ± standard errors. The number of observations used for each analysis is provided in Appendix S1: Table S2. The analysis was performed separately for each year

influence on the abundance of *P. sylvestris* juveniles irrespective of size classes. Juveniles of tree species other than Scots pine and oak were present in far higher numbers for small (0–19 cm in height) and moderate-sized (20–119 cm in height) individuals in the irrigated plots, with *Betula pendula* and *Sorbus aria* having highest abundances (Figure 4 and Appendix S1: Figure S8).

Insect species abundance and richness

The irrigation treatment had a significant negative effect on the maturation feeding of pine shoot beetles (*Tomicus* spp.) after 5 years of treatment. However, there was no effect after 4 and 13 years of treatment (Table 1). The irrigation treatment did not have any effect neither on the abundance of gall-wasp-induced oak galls nor on the species richness and abundance of spiders and ground beetles 4 and 5 years after treatment application (Table 1).

Abundance and biomass of fungal fruit bodies

The abundances and biomass of mycorrhizal and saprotrophic fungal fruit bodies were higher in irrigated plots compared to control plots during the initial 5 years

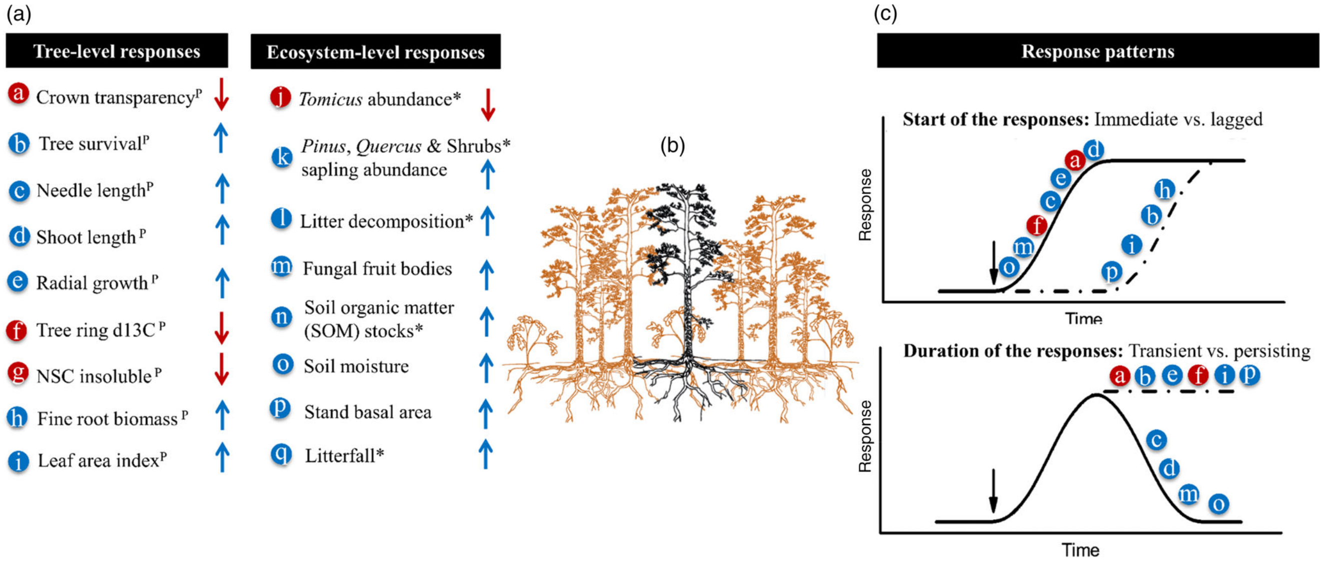


FIGURE 6 Summary scheme: (a) tree and ecosystem-level responses and (c) response patterns to the irrigation treatment (arrow: start of treatment). Negative responses are depicted in red and positive responses in blue, ^{P}*Pinus sylvestris*; variables that do not have repeated measurements over time are indicated by the symbol * and variables that did not show clear indication of response type (immediate vs. lagged or transient vs. persisting) are not included in panel c. Immediate, response occurred within 1–5 years; lagged, response occurred after 5 years; transient, statistically significant ($p < 0.05$) response disappeared over time; and persisting, response stayed statistically significant over time. Panel (b) illustrates the *Pinus sylvestris* forest type and tree level (black tree) versus the ecosystem level (brownish trees)

since treatment application (Figure 5a, b). However, the irrigation effect on biomass of saprotrophic fruit bodies was not significant from 2005 to 2007 (Figure 5b). The effect sizes were slightly higher for both measures of mycorrhizal fungi than for saprotrophs (although not statistically tested; Figure 5a, b).

DISCUSSION

The 16-years-long irrigation experiment allowed us to track the recovery trajectories in trees and the whole ecosystem released from the natural dry conditions. Several (published and unpublished) studies have documented responses of various tree and ecosystem-level traits to irrigation, thus providing a unique empirical basis for a synthesis to identify key general patterns of responses to increased water availability. To our knowledge there is no comparable long-term and extensive data set on the effects of the release of natural drought available in the published literature. While global change scenarios project an increase in the frequency and intensity of drought periods and have, thus, stimulated rainfall exclusion experiments (Adams et al., 2015; Grams et al., 2021) our approach, i.e., increasing the water availability, has its own advantages. First, by comparing a natural system with a system where water limitation has been lifted, we can identify the impacts of the natural drought conditions on trees. Second and most importantly, and thus the focus of this study, we can assess the recovery trajectories of previously drought-exposed trees over long time periods. We found that the initial lag period prior to significant response varies largely across tree and ecosystem-level traits (Figures 2 and 6). This indicates that the memory effect of dry conditions before irrigation in determining tree- and ecosystem-level responses is not uniform but parameter specific (Zweifel et al., 2020). In addition, the significant responses to increased water availability disappeared in a number of traits (e.g., needle length and shoot length) within a short period but stayed significant over a long period (>10 years) in some other traits (e.g., radial growth, crown transparency, and stand basal area; Figure 6). In the paragraphs below, we discuss implications and potential underlying mechanisms of these findings.

While a number of traits including tree-ring width and crown transparency showed slowly increasing but persistent responses (Figure 6), there was a rapid irrigation effect in tree-ring δ^{13}C values (Figure 2), resulting from an increased stomatal conductance through enhanced water availability (Eilmann et al., 2010). Adjustment of stomatal conductance is generally the initial reaction toward changes in water availability (Wullschleger et al., 1998), which is then visible in the δ^{13}C of tree rings. In addition, δ^{13}C appears to be more sensitive to changes in water conditions than tree-ring width (Jucker et al., 2017), which is confirmed by our results that tree-ring δ^{13}C decreased significantly in the first year after irrigation while tree-ring width responded with a 2-years delay (Figure 2). After reaching the peak in 2006, the effect size of irrigation on tree-ring width declined in the following years. This declining trend after reaching the peak was also observed in needle length, shoot length, and crown transparency (Figure 2), which may indicate that the water supply at a constant rate over the years did not meet the progressively increasing water demand from increasing vegetation activities (Ellison et al., 2012). This is supported by the fact that soil volumetric water contents during non-irrigated seasons in irrigated plots compared to control plots showed a continuous decrease throughout the years (although not statistically tested; Figure 1).

Our results might indicate that increased water availability in the long term changed tree and ecosystem properties in a way that a new balance between soil water availability and water demand is reached that changed the boundary conditions of the system (Beier et al., 2012; da Costa et al., 2018). This might lead to increased stress when the system is brought back to the initial conditions (i.e., when irrigation is stopped) due to the legacy effects of irrigated conditions (Zweifel et al., 2020). Otherwise, if the irrigation is continued, the ecosystem might become after some time (in the future) comparably vulnerable as the control, approaching a similar hydraulic safety margin as before (Choat et al., 2018; Jump et al., 2017). For example, working in drought-exposed tropical forest in the Amazon, da Costa et al. (2018) showed that although tree mortality increased soil water availability to surviving trees, the increased transpiration rate from surviving trees resulted the use of 100% of the available water. They further demonstrated that this forest could again become vulnerable to drought-induced tree mortality if the drought is associated with a mild temperature increase as the forest's water demand would substantially exceed the water supply.

Our analysis showed that 100-years-old Scots pine trees were able to regain vigor when they were provided with the double amount of natural precipitation through irrigation (Appendix S1: Figure S4). The irrigated trees adjusted their crowns by increasing shoot length, needle length, and leaf area and decreasing crown transparency. The high crown transparency can partly be attributed to tree death in the dry control plots. The lower survival rate of adult trees in control plots compared to irrigated plots from 10 years since the start of the irrigation treatment indicates that the naturally dry conditions were unfavorable for the adult trees (Figure 2 and Appendix S1: Figure S4). Overall, tree-ring width of the irrigated trees was 59% higher than of the control trees and ecosystem-level basal area of live trees was consistently higher in irrigated plots compared to control plots since the year 2009 (Appendix S1: Figure S6). The higher ecosystem-level basal area in irrigated plots has resulted from increased growth of irrigated trees and increased mortality of control trees.

Our results indicate that the initial response of the trees to increased water supply was from aboveground compartments and trees took a longer ($\geq$14 years) time to significantly increase their fine-root biomass (Figures 2 and 6). This finding might be in line with plants' drought responses in general (Poorter et al., 2012) and might follow the concept of functional equilibrium by Poorter and Nagel (2000). According to this concept, trees generally prioritize biomass allocation to roots compared to leaves when the limiting factor for growth is below ground (nutrients and water). During the initial years of irrigation, the increased water supply reduced water limitation and, therefore, biomass allocation to roots was probably not a priority for these trees, which instead displayed rapid and strong responses of aboveground traits and functions (Figure 2). However, these increased values for aboveground traits (needle, shoot, and crown areas) clearly increased the water demand (Zweifel et al., 2020) during the following years and, hence, trees might have adjusted biomass allocation priorities toward the development of root biomass (Figure 2) to meet the increased water demand from aboveground. This trade-off of fast and slow responses between above- and belowground traits provides valuable insights about trait economic strategies of Scots pine trees for acclimation to changing water availability (Feichtinger et al., 2015; Reich, 2014; Volaire, 2018).

Although irrigated trees had higher fine-root biomass (on average) in 2012 and 2014, our analysis identified that this higher fine-root biomass was not significantly different compared to trees in control treatment (Figure 2). These results indicate a high spatial variability across irrigation plots on root traits in the top soil layer, probably at least partly due to the heterogenous rocky substrate in the top soil layer at our study site (Brunner et al., 2009). In addition, the heterogeneous distribution of the tree species and understory plants is mirrored in their belowground organs and contribute to the heterogeneity of root density. However, it is clear that the amount of fine-root biomass has been increasing (although differing in magnitude) over time across all irrigated plots, which may indicate that a saturation of fine-root biomass in the top soil is yet to be reached, and may imply that water is a strong driver of fine-root growth in this forest type (Brunner et al., 2015). This is supported by recent findings from studies conducted at the same site. These studies showed that the proportion of newly assimilated C allocated to the belowground organs (roots and rhizosphere) in Scots pine is significantly higher under increased soil water availability (Joseph et al., 2020), leading to a stronger overlap of the belowground (i.e., root) system between adjacent trees (Gao et al., 2021).

Our results from the litter decomposition experiment with aboveground foliage revealed a strong role of irrigation on the litter mass loss placed in coarse-mesh litter bags (Figure 3a), where macrofauna could contribute to the decomposition process. The mass loss in fine-mesh litter bags excluding macrofauna and hence only occurring through fungi, bacteria and microfauna was less affected by the irrigation treatment. These results indicate that increased water supply through irrigation may stimulate macrofaunal activity (such as earthworms) more strongly than the one of fungi and/or bacteria (Manzoni et al., 2012). Although the irrigation treatment had a significant positive effect on mass loss of foliar litter associated with fine-mesh litter bags, Herzog et al. (2019) as well as our analysis detected an insignificant irrigation effect on mass loss of root litters in fine-mesh litter bags in the same study site (Figure 3b). Slower decomposition rates of roots compared to needles has also been reported by other studies (Heim & Frey, 2004; Palviainen et al., 2004; Taylor et al., 1991). The divergent moisture response of litter decomposition above and below ground may lead to an altered depth distribution of soil organic matter (SOM). While a faster decomposition of aboveground litter reduces C stocks in the litter layer, the unchanged root decomposition in conjunction with an increased root production may lead to greater SOM stocks in the mineral soils. On longer time scales, this pattern may enhance C storage in soils with an increasing water supply as has been observed for Swiss forest soils with increasing mean annual precipitation (Gosheva et al., 2017).

Soil fungal communities are key in ecosystem functioning such as litter decomposition and nutrient dynamics (Soliveres et al., 2016). The irrigation treatment led to an immediate and strong increase of the abundance and biomass of mycorrhizal and saprotrophic fungal fruit bodies (Figure 5). A significant dependency of mushroom production on precipitation and soil moisture availability have been noted previously and is particularly pronounced in semiarid regions (Büntgen et al., 2015; Collado et al., 2019). A stronger effect on mycorrhizal fungi, which rely on carbon supply for fruit-body production from their host plant (Egli et al., 2010; Högberg et al., 2001), might be explained by an indirect effect via improved tree condition and higher assimilate allocation of Scots pine below ground with higher soil water availability (Joseph et al., 2020). The strong effects on aboveground biomass of the fungal community were somewhat in contrast to belowground microbial biomass and diversity, where mycelia remained unaffected by irrigation (Hartmann et al., 2017). However, there was a strong change in community composition after 10 years of irrigation at our field site (Hartmann et al., 2017) and irrigation stimulated microbial activities. This was attributed to enhanced water supply induced primary production and C input into the soil (Hartmann et al., 2017).

Although we detected no significant influence of irrigation treatment on most of our insect diversity indicators such as abundance of oak galls, spiders, and ground beetles, the frequency of pine shoot beetle (*Tomicus* spp.) feeding was lower in irrigated trees 5 years after treatment application. Pine shoot beetles are known to contribute to tree mortality by their larval feeding (Wermelinger et al., 2008). For their maturation feeding, the adult beetles seem to prefer weakened trees as prevalent in the control plots.

Scots pine has been frequently reported as a vulnerable tree species to extreme drought (Martínez-Vilalta et al., 2009; Schönbeck et al., 2020). The long-term irrigation treatment applied in Scots pine dominated forests did not increase the abundance of its natural regeneration (Figure 4). Although Scots pine is occupying >90% of the canopy, the current abundance (0–400 cm) of *Q. pubescens* juveniles is higher compared to Scots pine at both control and irrigated plots. In more detail, however, the higher number refers to small juveniles (0–120 cm) and point to a current shift toward the broadleaved species irrespective of irrigation treatments (i.e., irrigation or naturally dry). This agrees with the findings of other studies conducted in the Rhone valley in Switzerland (Rigling et al., 2013) and in southern Europe (Galiano et al., 2010). Among the established juveniles (120–400 cm), Scots pine is more frequent than oak in both control and irrigated plots. This is in agreement with Wohlgemuth et al. (2018), which indicates other processes in this height class to constrain the successful establishment of oak. Our results largely reflect the successional dynamics that naturally occurs in such forest types (Wohlgemuth et al., 2018), in which early-successional Scots pine (McVean, 1961; Niinemets & Valladares, 2006) might, in the long term, be naturally replaced by oak species (Rigling et al., 2013) unless the latter is transiently constrained during establishment by other factors such as, e.g., browsing or frost (both not examined here). If at all, our irrigation treatment might indirectly affect the regeneration dynamics by increasing crown size and density of the adult trees, which reduced the light availability at the understory and thus likely benefit more shade tolerant broadleaved species compared to shade intolerant Scots pine (Gaudio et al., 2011).

CONCLUSION

By examining 30 individual tree- and ecosystem-level traits, our analyses provide how response magnitude, direction of responses, temporal trajectories of responses, and initial lag period prior to significant responses vary across traits of individual trees and the whole ecosystem to increased water availability (Figure 6). For example, we detected transient responses in a number of tree-level (e.g., needle length, shoot length) and ecosystem-level traits (e.g., fungal fruit bodies, soil water), where significant responses either decreased in magnitude or became nonsignificant over time (Figure 6). In addition, we found rapid and stronger responses from aboveground traits (which, however, varied across traits) compared to belowground traits. These responses from aboveground tree (e.g., tree radial growth, crown transparency), and ecosystem traits (e.g., stand basal area) equilibrated over time (Figure 2 and 6; Appendix S1: Figure S6), which is probably due to the lack of progressively increasing water supply indicating changes in boundary conditions after long-term manipulation. The increased values for aboveground traits during the initial treatment years increased the water demand and trees adjusted to the new conditions by increasing root biomass after 14 years of the treatment application. We showed that 100-years-old Scots pine trees are still able to regain its vigor after decadal drought stress if watered for a longer period (>5 years) indicating the importance of moist periods (years, decades) for forest resilience in a climate-change-induced increasingly dryer future. We emphasize the need to expand our understanding of combined ecosystem-level responses including net ecosystem exchange, microbial activities, and nutrient cycling. This is essential for understanding how and why ecosystem properties may differ in their sensitivities over time to water manipulation.

ACKNOWLEDGMENTS

A. K. Bose was supported by a Marie Skłodowska-Curie Individual Fellowship (PROJECT ID: 749051-REFOREST). The study is based on data from the long-term Pfynwald forest irrigation experiment, which is part of the Swiss Long-term Forest Ecosystem Research Program LWF (www.lwf.ch) and the project TreeNet funded by the Federal Office for the Environment FOEN (funds: 00.0365. PZ I0427-0562, 09.0064.PJ/R301-0223). Arthur Gessler acknowledges support from the Swiss National Science Foundation SNF (310030_189109). Ivano Brunner acknowledges support from SNF (31003A_149507). Claudia Guidi acknowledges funding from the Marie Sklodowska-Curie grant agreement No. 846134. We thank Christian Hug, Peter Bleuler, Flurin Sutter, Simpal Kumar, Ulrich Wasem, Elisabeth Graf Pannatier, and Matthias Haeni for their valuable supports in data collection and preparation. We also thank François Ayer for fungal fruit body inventory, Doris Schneider Mathis for her assistance in the field and Anne-Catherine Grandchamp and Xavier Heer for insect identifications. Furthermore, we acknowledge the long-term help by Konrad Egger and his team from the Forstrevier Leuk, the Burgerschaft Leuk, and the HYDRO Exploitation SA. The study is dedicated to Matthias Dobbertin, the visionary initiator of this long-term irrigation experiment, who passed away in 2012.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The raw data (Bose, Rigling, et al., 2021) are available from Dryad at https://doi.org/10.5061/dryad.pzgmsbcnd.

ORCID

Arun K. Bose https://orcid.org/0000-0001-8581-1651
Martin M. Gossner https://orcid.org/0000-0003-1516-6364

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How to cite this article: Bose, Arun K., Andreas Rigling, Arthur Gessler, Frank Hagedorn, Ivano Brunner, Linda Feichtinger, Christof Bigler, et al. 2022. “Lessons Learned from a Long-Term Irrigation Experiment in a Dry Scots Pine Forest: Impacts on Traits and Functioning.” *Ecological Monographs* e1507. https://doi.org/10.1002/ecm.1507