



## ARTICLE

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

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

<sup>1</sup>Swiss Federal Research Institute WSL, Birmensdorf, Switzerland

<sup>2</sup>Forestry and Wood Technology Discipline, Khulna University, Khulna, Bangladesh

<sup>3</sup>Institute of Terrestrial Ecosystems, ETH Zurich, Zurich, Switzerland

<sup>4</sup>Department of Environmental Systems Science, Forest Ecology, ETH Zurich, Zurich, Switzerland

<sup>5</sup>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](mailto: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

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

This is an open access article under the terms of the [Creative Commons Attribution](https://creativecommons.org/licenses/by/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

© 2022 The Authors. *Ecological Monographs* published by Wiley Periodicals LLC on behalf of Ecological Society of America.

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 (Voltaire, 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; Dobberty 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; Dobberty et al., 2010).

### Irrigation experiment

The 1.2-ha experimental area was initially divided into eight plots of 1000 m<sup>2</sup> 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  $\delta^{13}\text{C}$ ; ‰), 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 ( $\text{g}/\text{m}^2$ ), ingrowth (i.e., newly formed) root length density ( $\text{m}/\text{m}^2$ ), ingrowth root tip frequency (number/cm), ingrowth root biomass density ( $\text{g}/\text{m}^2$ ), and ingrowth root tissue density ( $\text{mg}/\text{cm}^3$ ) 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  $\leq 400$  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).

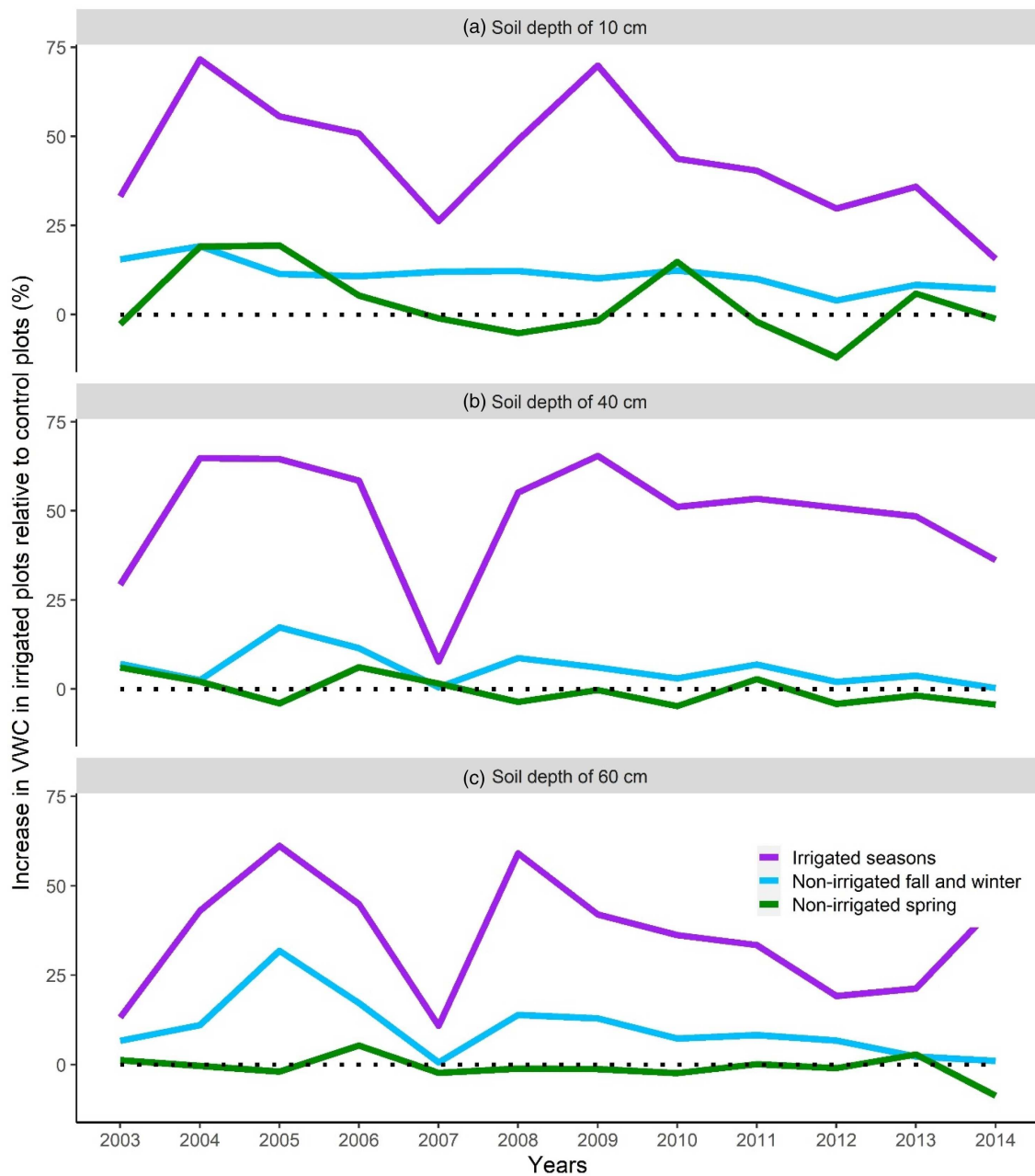
## Statistical analysis

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  $\delta^{13}\text{C}$ ) that had the highest number of measurements. For each of those four variables, we considered measurement years, treatments (control and irrigated), and the

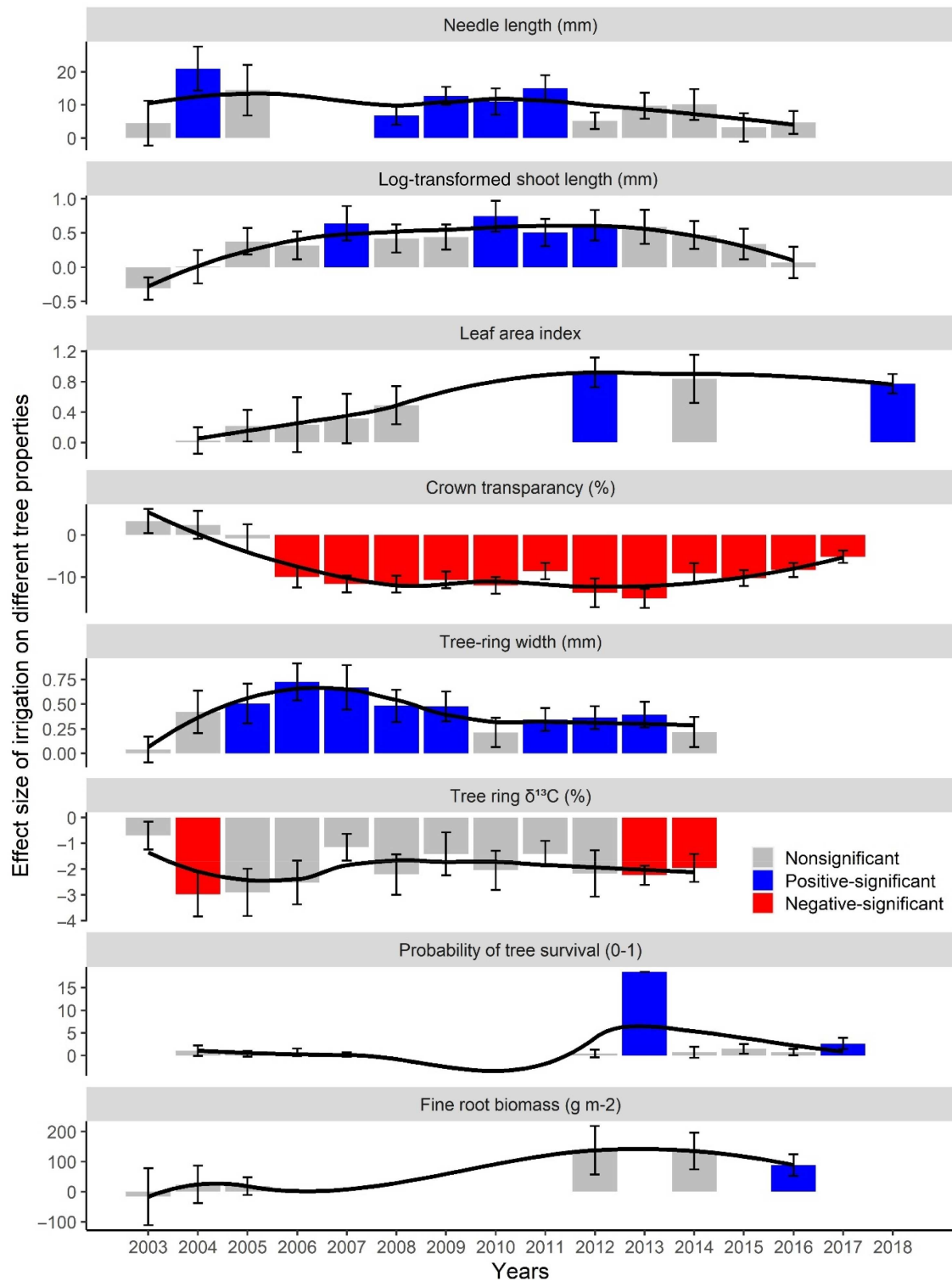


**FIGURE 1** Temporal change in soil VWC (volumetric water content) from irrigated plots relative to the control plots (%) across three different soil layers (a–c) for the irrigation periods (see Appendix S1: Table S1), non-irrigated fall–winter periods (September–February) and non-irrigated spring period (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  $\pm$  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

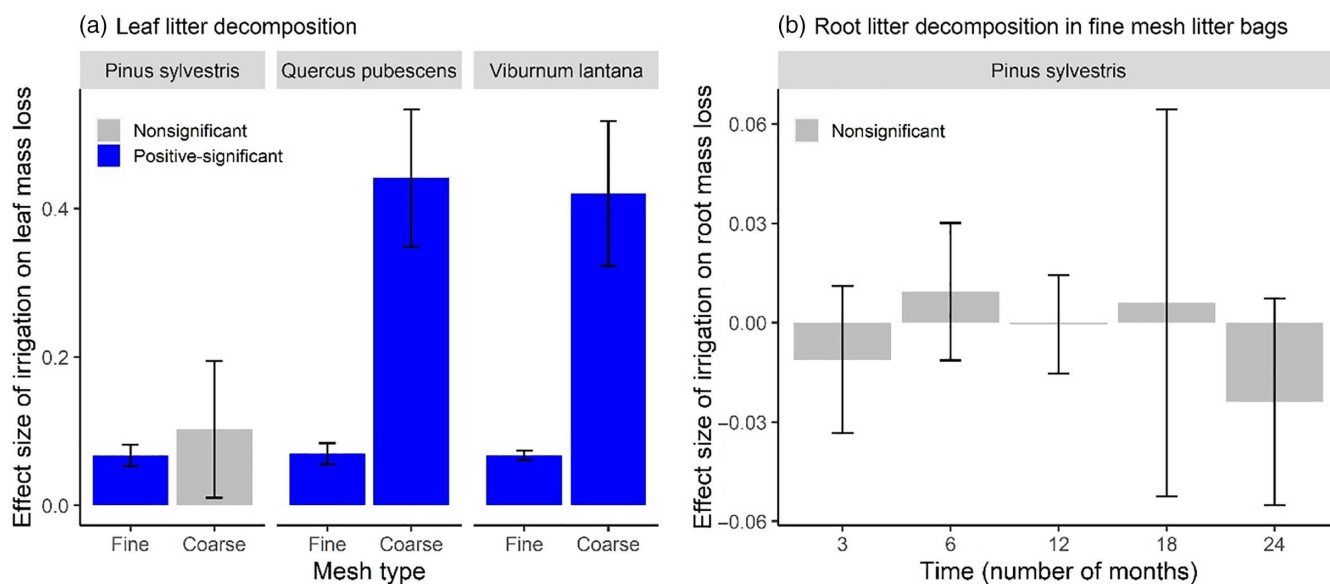
The irrigation treatment increased soil volumetric water content (VWC) across the three different soil layers from 2004 to 2014 especially during irrigated seasons (i.e., summer and parts of late spring and early fall) and non-irrigated fall–winter seasons. The magnitude of VWC increase varied across 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  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  (1 year) and needle length (1 year). The tree-ring  $\delta^{13}\text{C}$  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  $\delta^{13}\text{C}$  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).



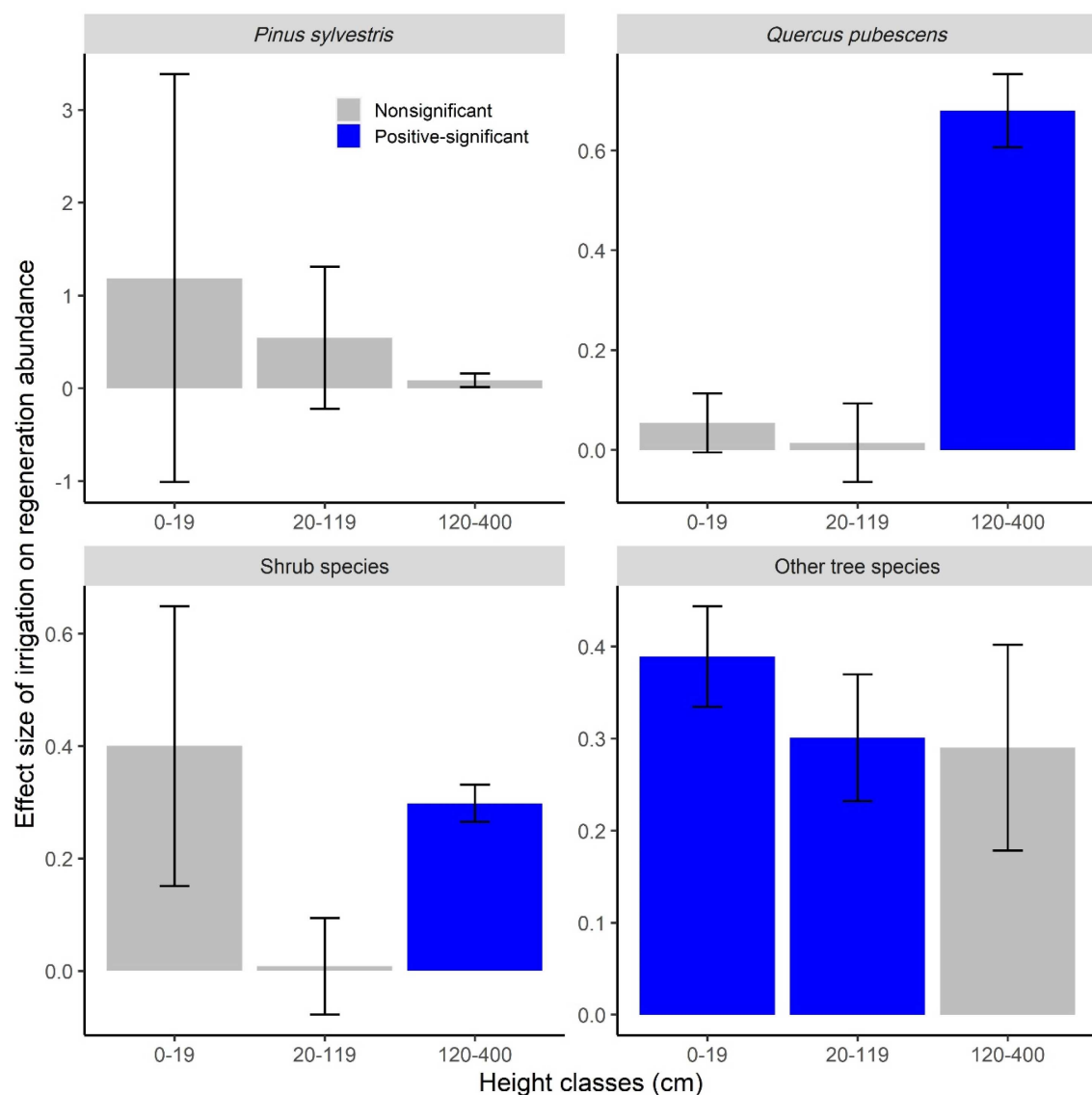
**FIGURE 3** Effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on mass loss of leaf and root litter. (a) Leaf litter mass loss of three species by the end of 140 days and (b) root litter mass loss of *Pinus sylvestris* of fine-mesh litter bags over 24 months. The error bars represent mean  $\pm$  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 ( $\text{g/m}^2$ ) 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  $\pm$  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	<i>p</i>	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 <i>Tomicus</i> abundance (ground)	GLMM (negative exponential)	−0.07	0.32	0.82	4 (measured in June)
Shoot feeding <i>Tomicus</i> abundance (ground)	GLMM (negative exponential)	−0.68	0.30	<b>0.02</b>	5 (measured in March)
Shoot feeding <i>Tomicus</i> 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 ( $\text{m}/\text{m}^2$ ), root tip frequency (number/cm), root biomass density ( $\text{g}/\text{m}^2$ ), and root tissue density ( $\text{mg}/\text{cm}^3$ ) 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).

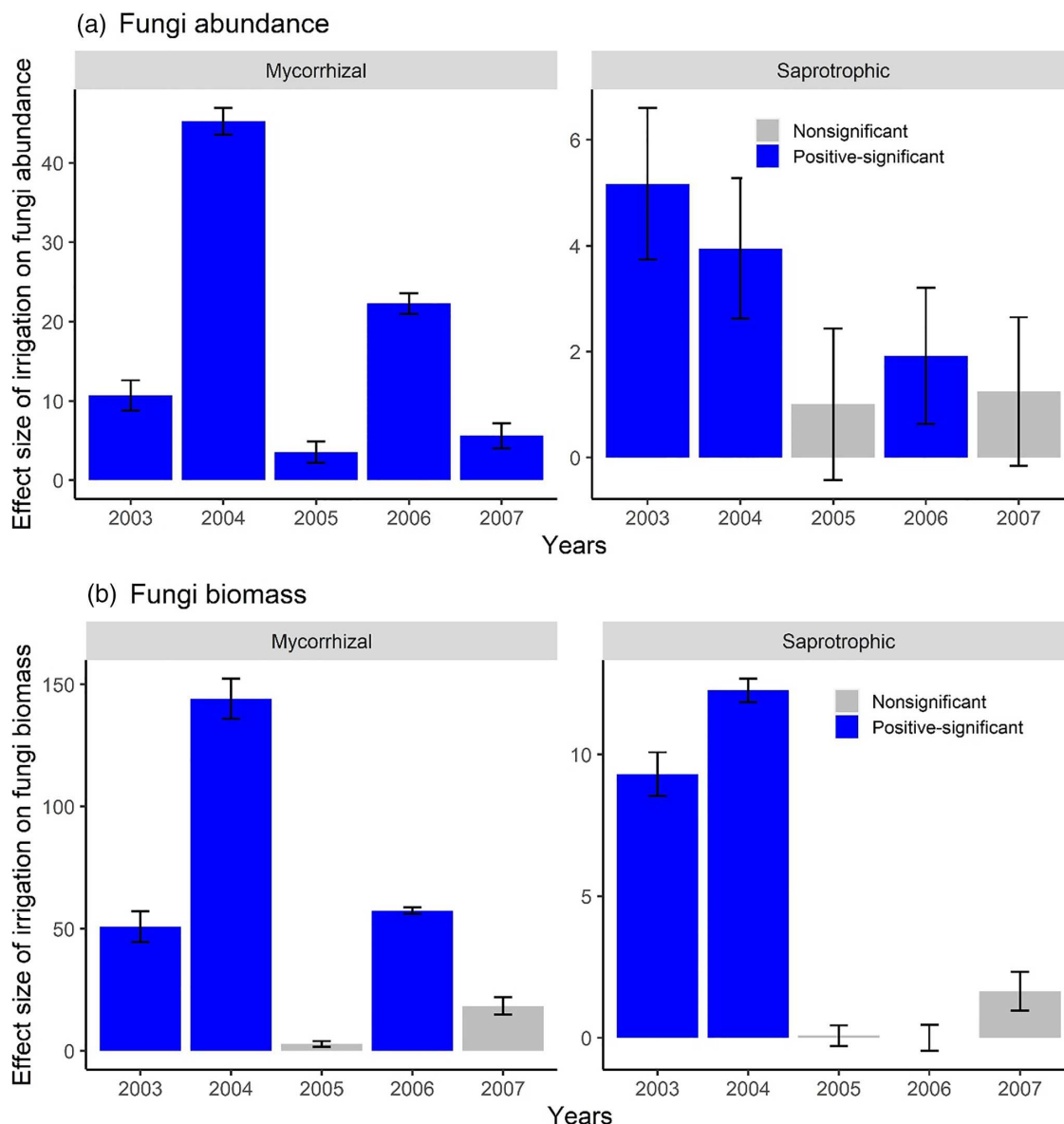
### Litter decomposition

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



**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  $\pm$  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).

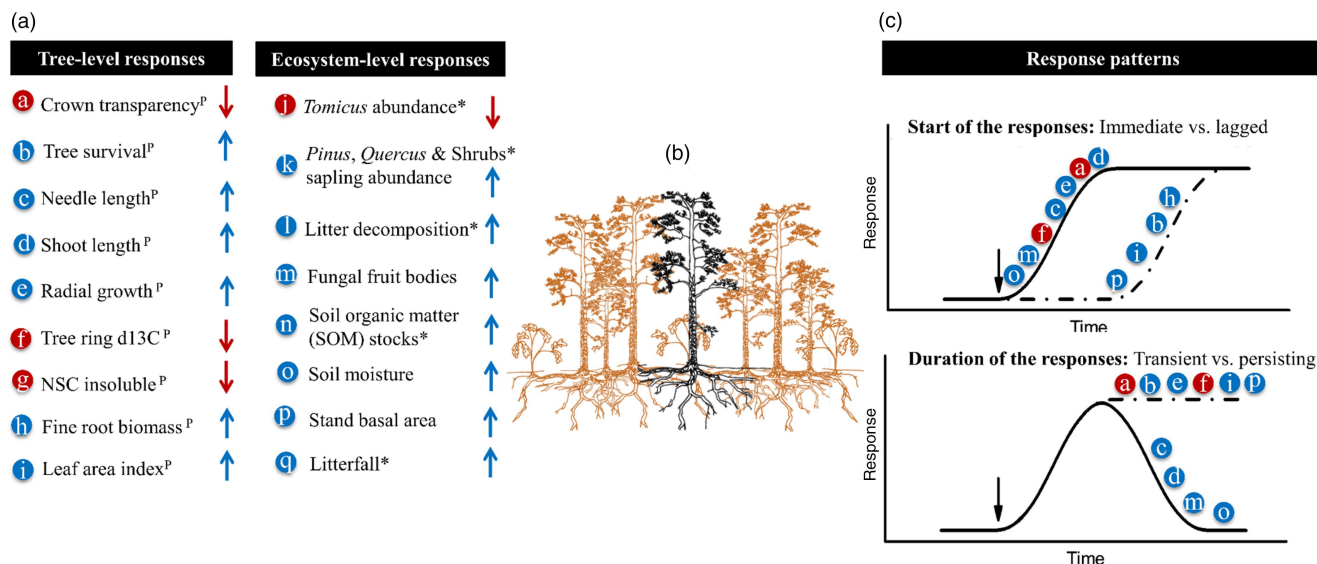
### Insect species abundance and richness

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, <sup>p</sup>*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  $\delta^{13}C$  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  $\delta^{13}C$  of tree rings. In addition,  $\delta^{13}C$  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  $\delta^{13}C$  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 heterogeneous 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; Höglberg 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 Pfywald forest irrigation experiment, which is part of the Swiss Long-term Forest Ecosystem Research Program LWF ([www.lwf.ch](http://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 Skłodowska-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. Open Access Funding provided by Lib4RI Library for the Research Institutes within the ETH Domain Eawag Empa PSI and WSL. [Correction added on 11 April after first publication: Consortium of Swiss Academic Libraries (CSAL) funding statement has been added.]

## 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.pzgmsbncd>.

## ORCID

Arun K. Bose  <https://orcid.org/0000-0001-8581-1651>

Martin M. Gossner  <https://orcid.org/0000-0003-1516-6364>

## REFERENCES

- Adams, H.D., A.D. Collins, S.P. Briggs, M. Vennetier, L.T. Dickman, S.A. Sevanto, N. Garcia-Forner, H.H. Powers, and N.G. McDowell. 2015. "Experimental Drought and Heat Can Delay Phenological Development and Reduce Foliar and Shoot Growth in Semiarid Trees." *Global Change Biology* 21(11): 4210–20.
- Alberto, F.J., S.N. Aitken, R. Alía, S.C. González-Martínez, H. Hänninen, A. Kremer, F. Lefèvre, et al. 2013. "Potential for Evolutionary Responses to Climate Change – Evidence from Tree Populations." *Global Change Biology* 19(6): 1645–61.
- Anderegg, W.R.L., C. Schwalm, F. Biondi, J.J. Camarero, G. Koch, M. Litvak, K. Ogle, et al. 2015. "Pervasive Drought Legacies in Forest Ecosystems and their Implications for Carbon Cycle Models." *Science* 349(6247): 528–32.
- Barbeta, A., R. Ogaya, and J. Peñuelas. 2013. "Dampening Effects of Long-Term Experimental Drought on Growth and Mortality Rates of a Holm Oak Forest." *Global Change Biology* 19(10): 3133–44.
- Bates, D., M. Maechler, B. Bolker, and S. Walker. 2017. lme4: Linear Mixed-Effects Models Using 'Eigen' and S4. R package version 1.1-14. <https://CRAN.R-project.org/package=lme4>
- Battlori, E., F. Lloret, T. Aakala, W.R.L. Anderegg, E. Aynekulu, D.P. Bendixsen, A. Bentouati, et al. 2020. "Forest and Woodland Replacement Patterns Following Drought-Related Mortality." *Proceedings of the National Academy of Sciences USA* 117(47): 29720.
- Beier, C., C. Beierkuhnlein, T. Wohlgemuth, J. Penuelas, B. Emmett, C. Körner, H. Boeck, J.H. Christensen, S. Leuzinger, and I.A. Janssens. 2012. "Precipitation Manipulation Experiments—Challenges and Recommendations for the Future." *Ecology Letters* 15(8): 899–911.
- Bose, A.K., A. Gessler, A. Bolte, A. Bottero, A. Buras, M. Cailleret, J.J. Camarero, et al. 2020. "Growth and Resilience Responses of

- Scots Pine to Extreme Droughts across Europe Depend on Predrought Growth Conditions." *Global Change Biology* 26: 4521–37.
- Bose, A.K., B. Moser, A. Rigling, M.M. Lehmann, A. Milcu, M. Peter, C. Rellstab, T. Wohlgemuth, and A. Gessler. 2020. "Memory of Environmental Conditions across Generations Affects the Acclimation Potential of Scots Pine." *Plant, Cell & Environment* 43(5): 1288–99.
- Bose, A.K., R.G. Wagner, A.R. Weiskittel, and A.W. D'Amato. 2021. "Effect Magnitudes of Operational-Scale Partial Harvesting on Residual Tree Growth and Mortality of Ten Major Tree Species in Maine USA." *Forest Ecology and Management* 484: 118953.
- Bose, A., A. Rigling, A. Gessler, F. Hagedorn, I. Brunner, L. Feichtinger, C. Bigler, et al. 2021. "Long Term Irrigation Experiment." Dryad Dataset. <https://doi.org/10.5061/dryad.pzgmsbcnd>
- Brunner, I., C. Herzog, M.A. Dawes, M. Arend, and C. Sperisen. 2015. "How Tree Roots Respond to Drought." *Frontiers in Plant Science* 6: 547.
- Brunner, I., C. Herzog, L. Galiano, and A. Gessler. 2019. "Plasticity of Fine-Root Traits under Long-Term Irrigation of a Water-Limited Scots Pine Forest." *Frontiers in Plant Science* 10: 701.
- Brunner, I., E.G. Pannatier, B. Frey, A. Rigling, W. Landolt, S. Zimmermann, and M. Dobbertin. 2009. "Morphological and Physiological Responses of Scots Pine Fine Roots to Water Supply in a Dry Climatic Region in Switzerland." *Tree Physiology* 29(4): 541–50.
- Büntgen, U., S. Egli, J.D. Galván, J.M. Diez, J. Aldea, J. Latorre, and F. Martínez-Peña. 2015. "Drought-Induced Changes in the Phenology, Productivity and Diversity of Spanish Fungi." *Fungal Ecology* 16: 6–18.
- Choat, B., T.J. Brodribb, C.R. Brodersen, R.A. Duursma, R. López, and B.E. Medlyn. 2018. "Triggers of Tree Mortality under Drought." *Nature* 558(7711): 531–9.
- Collado, E., J.A. Bonet, J.J. Camarero, S. Egli, M. Peter, K. Salo, F. Martínez-Peña, et al. 2019. "Mushroom Productivity Trends in Relation to Tree Growth and Climate across Different European Forest Biomes." *Science of the Total Environment* 689: 602–15.
- Cotrufo, M.F., G. Alberti, I. Ingleima, H. Marjanović, D. LeCain, A. Zaldei, A. Peressotti, and F. Miglietta. 2011. "Decreased Summer Drought Affects Plant Productivity and Soil Carbon Dynamics in a Mediterranean Woodland." *Biogeosciences* 8(9): 2729–39.
- da Costa, A.C.L., L. Rowland, R.S. Oliveira, A.A.R. Oliveira, O.J. Binks, Y. Salmon, S.S. Vasconcelos, et al. 2018. "Stand Dynamics Modulate Water Cycling and Mortality Risk in Droughted Tropical Forest." *Global Change Biology* 24(1): 249–58.
- De Dato, G., G. Pellizzaro, C. Cesaraccio, C. Sirca, P.B. De Angelis, P. Duce, D. Spano, and M. Scarascia. 2006. "Effects of Warmer and Drier Climate Conditions on Plant Composition and Biomass Production in a Mediterranean Shrubland Community." *Forest Ecology* 3: 511–26.
- Dobbertin, M. 2005. "Tree Growth as Indicator of Tree Vitality and of Tree Reaction to Environmental Stress: A Review." *European Journal of Forest Research* 124(4): 319–33.
- Dobbertin, M., and P. Brang. 2001. "Crown Defoliation Improves Tree Mortality Models." *Forest Ecology and Management* 141(3): 271–84.
- Dobbertin, M., B. Eilmann, P. Bleuler, A. Giuggiola, E. Graf Pannatier, W. Landolt, P. Schleppi, and A. Rigling. 2010. "Effect of Irrigation on Needle Morphology, Shoot and Stem Growth in a Drought-Exposed *Pinus sylvestris* Forest." *Tree Physiology* 30(3): 346–60.
- Egli, S., F. Ayer, M. Peter, B. Eilmann, and A. Rigling. 2010. "Is Forest Mushroom Productivity Driven by Tree Growth? Results from a Thinning Experiment." *Annals of Forest Science* 67(5): 509–9.
- Eilmann, B., N. Buchmann, R. Siegwolf, M. Saurer, P. Cherubini, and A. Rigling. 2010. "Fast Response of Scots Pine to Improved Water Availability Reflected in Tree-Ring Width and  $\delta^{13}C$ ." *Plant, Cell & Environment* 33(8): 1351–60.
- Eilmann, B., R. Zweifel, N. Buchmann, E. Graf Pannatier, and A. Rigling. 2011. "Drought Alters Timing, Quantity, and Quality of Wood Formation in Scots Pine." *Journal of Experimental Botany* 62(8): 2763–71.
- Ellison, D., N.M. Futter, and K. Bishop. 2012. "On the Forest Cover–Water Yield Debate: From Demand- to Supply-Side Thinking." *Global Change Biology* 18(3): 806–20.
- Estiarte, M., S. Vicca, J. Peñuelas, M. Bahn, C. Beier, B.A. Emmett, P.A. Fay, et al. 2016. "Few Multiyear Precipitation–Reduction Experiments Find a Shift in the Productivity–Precipitation Relationship." *Global Change Biology* 22(7): 2570–81.
- Feichtinger, L.M., B. Eilmann, N. Buchmann, and A. Rigling. 2014. "Growth Adjustments of Conifers to Drought and to Century-Long Irrigation." *Forest Ecology and Management* 334: 96–105.
- Feichtinger, L.M., B. Eilmann, N. Buchmann, and A. Rigling. 2015. "Trait-Specific Responses of Scots Pine to Irrigation on a Short vs Long Time Scale." *Tree Physiology* 35(2): 160–71.
- Felsmann, K., M. Baudis, K. Gimbel, Z.E. Kayler, R. Ellerbrock, H. Bruehlheide, J. Bruckhoff, et al. 2015. "Soil Bacterial Community Structure Responses to Precipitation Reduction and Forest Management in Forest Ecosystems across Germany." *PLoS One* 10(4): e0122539.
- Felsmann, K., M. Baudis, Z.E. Kayler, H. Puhlmann, A. Ulrich, and A. Gessler. 2017. "Responses of the Structure and Function of the Understory Plant Communities to Precipitation Reduction across Forest Ecosystems in Germany." *Annals of Forest Science* 75(1): 3.
- Felton, A.J., A.K. Knapp, and M.D. Smith. 2020. "Precipitation–Productivity Relationships and the Duration of Precipitation Anomalies: An Underappreciated Dimension of Climate Change." *Global Change Biology* 27(6): 1127–40.
- Forrester, D.I. 2014. "The Spatial and Temporal Dynamics of Species Interactions in Mixed-Species Forests: From Pattern to Process." *Forest Ecology and Management* 312: 282–92.
- Forrester, D.I. 2019. "Linking Forest Growth with Stand Structure: Tree Size Inequality, Tree Growth or Resource Partitioning and the Asymmetry of Competition." *Forest Ecology and Management* 447: 139–57.
- Galiano, L., J. Martínez-Vilalta, and F. Lloret. 2010. "Drought-Induced Multifactor Decline of Scots Pine in the Pyrenees and Potential Vegetation Change by the Expansion of Co-Occurring Oak Species." *Ecosystems* 13(7): 978–91.
- Gao, D., J. Joseph, R.A. Werner, I. Brunner, A. Zürcher, C. Hug, A. Wang, et al. 2021. "Drought Alters the Carbon Footprint of Trees in Soils—Tracking the Spatio-Temporal Fate of  $^{13}C$ -Labelled Assimilates in the Soil of an Old-Growth Pine Forest." *Global Change Biology* 27(11): 2491–506.
- Gaudio, N., P. Balandier, S. Perret, and C. Ginisty. 2011. "Growth of Understorey Scots Pine (*Pinus sylvestris* L.) Saplings in

- Response to Light in Mixed Temperate Forest.” *Forestry: An International Journal of Forest Research* 84(2): 187–95.
- Gavinet, J., J.-M. Ourcival, and J.-M. Limousin. 2019. “Rainfall Exclusion and Thinning Can Alter the Relationships between Forest Functioning and Drought.” *New Phytologist* 223(3): 1267–79.
- Gomez-Aparicio, L., R. García-Valdes, P. Ruiz-Benito, and M.A. Zavala. 2011. “Disentangling the Relative Importance of Climate, Size and Competition on Tree Growth in Iberian Forests: Implications for Forest Management under Global Change.” *Global Change Biology* 17(7): 2400–14.
- Gosheva, S., L. Walthert, P.A. Niklaus, S. Zimmermann, U. Gimmi, and F. Hagedorn. 2017. “Reconstruction of Historic Forest Cover Changes Indicates Minor Effects on Carbon Stocks in Swiss Forest Soils.” *Ecosystems* 20(8): 1512–28.
- Grams, T.E.E., B.D. Hesse, T. Gebhardt, F. Weikl, T. Rötzer, B. Kovacs, K. Hikino, et al. 2021. “The Kroof Experiment: Realization and Efficacy of a Recurrent Drought Experiment plus Recovery in a Beech/Spruce Forest.” *Ecosphere* 12(3): e03399.
- Grossiord, C., T.N. Buckley, L.A. Cernusak, K.A. Novick, B. Poulter, R.T.W. Siegwolf, J.S. Sperry, and N.G. McDowell. 2020. “Plant Responses To Rising Vapor Pressure Deficit.” *New Phytologist* 226(6): 1550–66.
- Grossiord, C., S. Sevanto, T.E. Dawson, H.D. Adams, A.D. Collins, L.T. Dickman, B.D. Newman, E.A. Stockton, and N.G. McDowell. 2017. “Warming Combined with more Extreme Precipitation Regimes Modifies the Water Sources Used by Trees.” *New Phytologist* 213(2): 584–96.
- Grossiord, C., S. Sevanto, J.-M. Limousin, P. Meir, M. Mencuccini, R.E. Pangle, W.T. Pockman, Y. Salmon, R. Zweifel, and N.G. McDowell. 2018. “Manipulative Experiments Demonstrate how Long-Term Soil Moisture Changes Alter Controls of Plant Water Use.” *Environmental and Experimental Botany* 152: 19–27.
- Hartmann, M., I. Brunner, F. Hagedorn, R.D. Bardgett, B. Stierli, C. Herzog, X. Chen, et al. 2017. “A Decade of Irrigation Transforms the Soil Microbiome of a Semi-Arid Pine Forest.” *Molecular Ecology* 26(4): 1190–206.
- Heim, A., and B. Frey. 2004. “Early Stage Litter Decomposition Rates for Swiss Forests.” *Biogeochemistry* 70(3): 299–313.
- Herzog, C., M. Hartmann, B. Frey, B. Stierli, C. Rumpel, N. Buchmann, and I. Brunner. 2019. “Microbial Succession on Decomposing Root Litter in a Drought-Prone Scots Pine Forest.” *ISME Journal* 13(9): 2346–62.
- Herzog, C., J. Steffen, E.G. Pannatier, I. Hajdas, and I. Brunner. 2014. “Nine Years of Irrigation Cause Vegetation and Fine Root Shifts in a Water-Limited Pine Forest.” *PLoS One* 9(5): e96321.
- Högberg, P., A. Nordgren, N. Buchmann, A.F.S. Taylor, A. Ekblad, M. N. Högberg, G. Nyberg, M. Ottosson-Löfvenius, and D.J. Read. 2001. “Large-Scale Forest Girdling Shows that Current Photosynthesis Drives Soil Respiration.” *Nature* 411(6839): 789–92.
- Hommel, R., R. Siegwolf, M. Saurer, G.D. Farquhar, Z. Kayler, J.P. Ferrio, and A. Gessler. 2014. “Drought Response of Mesophyll Conductance in Forest Understory Species—Impacts on Water-Use Efficiency and Interactions with Leaf Water Movement.” *Physiologia Plantarum* 152(1): 98–114.
- Joseph, J., D. Gao, B. Backes, C. Bloch, I. Brunner, G. Gleixner, M. Haeni, et al. 2020. “Rhizosphere Activity in an Old-Growth Forest Reacts Rapidly to Changes in Soil Moisture and Shapes Whole-Tree Carbon Allocation.” *Proceedings of the National Academy of Sciences USA* 117(40): 24885.
- Jucker, T., C. Grossiord, D. Bonal, O. Bouriaud, A. Gessler, and D. A. Coomes. 2017. “Detecting the Fingerprint of Drought across Europe’s Forests: Do Carbon Isotope Ratios and Stem Growth Rates Tell Similar Stories?” *Forest Ecosystems* 4(1): 24.
- Jump, A.S., P. Ruiz-Benito, S. Greenwood, C.D. Allen, T. Kitzberger, R. Fensham, J. Martínez-Vilalta, and F. Lloret. 2017. “Structural Overshoot of Tree Growth with Climate Variability and the Global Spectrum of Drought-Induced Forest Dieback.” *Global Change Biology* 23(9): 3742–57.
- Kannenberg, S. A., J. T. Maxwell, N. Pederson, L. D’Orangeville, D. L. Ficklin, & R. P. Phillips. 2019. Drought Legacies Are Dependent on Water Table Depth, Wood Anatomy and Drought Timing across the Eastern US.
- Kannenberg, S.A., K.A. Novick, M.R. Alexander, J.T. Maxwell, D.J. P. Moore, R.P. Phillips, and W.R.L. Anderegg. 2019. “Linking Drought Legacy Effects across Scales: From Leaves to Tree Rings to Ecosystems.” *Global Change Biology* 25(9): 2978–92.
- Kimball, S., M.L. Goulden, K.N. Suding, and S. Parker. 2014. “Altered Water and Nitrogen Input Shifts Succession in a Southern California Coastal Sage Community.” *Ecological Applications* 24(6): 1390–404.
- Korell, L., H. Auge, J.M. Chase, W.S. Harpole, and T.M. Knight. 2021. “Responses of Plant Diversity to Precipitation Change Are Strongest at Local Spatial Scales and in Drylands.” *Nature Communications* 12(1): 2489.
- Le Roncé, I., J. Gavinet, J.-M. Ourcival, F. Mouillot, I. Chuine, and J.-M. Limousin. 2021. “Holm Oak Fecundity Does Not Acclimate to a Drier World.” *New Phytologist* 231(2): 631–45.
- LeBauer, D.S., and K.K. Treseder. 2008. “Nitrogen Limitation of New Primary Productivity in Terrestrial Ecosystems in Globally Distributed.” *Ecology* 89(2): 371–9.
- Leuzinger, S., Y. Luo, C. Beier, W. Dieleman, S. Vicca, and C. Körner. 2011. “Do Global Change Experiments Overestimate Impacts on Terrestrial Ecosystems?” *Trends in Ecology & Evolution* 26(5): 236–41.
- Limousin, J.-M., L. Misson, A.-V. Lavoie, N.K. Martin, and S. Rambal. 2010. “Do Photosynthetic Limitations of Evergreen Quercus Ilex Leaves Change with Long-Term Increased Drought Severity?” *Plant, Cell & Environment* 33(5): 863–75.
- Limousin, J.-M., E.A. Yezzer, N.G. McDowell, and W.T. Pockman. 2015. “Convergence in Resource Use Efficiency across Trees with Differing Hydraulic Strategies in Response to Ecosystem Precipitation Manipulation.” *Functional Ecology* 29(9): 1125–36.
- Limousin, J.M., S. Rambal, J.M. Ourcival, A. Rocheteau, R. Joffre, and R. Rodriguez-Cortina. 2009. “Long-Term Transpiration Change with Rainfall Decline in a Mediterranean Quercus ilex Forest.” *Global Change Biology* 15(9): 2163–75.
- Lloret, F., C. Casanovas, and J. Peñuelas. 1999. “Seedling Survival of Mediterranean Shrubland Species in Relation to Root:Shoot Ratio, Seed Size and Water and Nitrogen Use.” *Functional Ecology* 13(2): 210–6.
- Manzoni, S., J.P. Schimel, and A. Porporato. 2012. “Responses of Soil Microbial Communities to Water Stress: Results from a Meta-Analysis.” *Ecology* 93(4): 930–8.
- Martin-StPaul, N.K., J.-M. Limousin, H. Vogt-Schilb, J. Rodríguez-Calcerrada, S. Rambal, D. Longepierre, and L. Misson. 2013. “The Temporal Response to Drought in a Mediterranean



- Evergreen Tree: Comparing a Regional Precipitation Gradient and a Throughfall Exclusion Experiment." *Global Change Biology* 19(8): 2413–26.
- Martínez-Vilalta, J., H. Cochard, M. Mencuccini, F. Sterck, A. Herrero, J.F.J. Korhonen, P. Llorens, et al. 2009. "Hydraulic Adjustment of Scots Pine across Europe." *New Phytologist* 184(2): 353–64.
- McDowell, N.G., C.D. Allen, K. Anderson-Teixeira, B.H. Aukema, B. Bond-Lamberty, L. Chini, J.S. Clark, et al. 2020. "Pervasive Shifts in Forest Dynamics in a Changing World." *Science* 368(6494): eaaz9463.
- McVean, D.N. 1961. "Experiments on the Ecology of Scots Pine Seedlings." *Empire Forestry Review* 40(4 [106]): 291–300.
- MeteoSwiss. 2018. "Federal Office of Meteorology and Climatology, IDAweb: the data portal of MeteoSwiss for research and teaching." [www.meteoschweiz.admin.ch/web/en/services/data\\_portal/idaweb.html](http://www.meteoschweiz.admin.ch/web/en/services/data_portal/idaweb.html)
- Misson, L., D. Degueldre, C. Collin, R. Rodriguez, A. Rocheteau, J.-M. Ourcival, and S. Rambal. 2011. "Phenological Responses to Extreme Droughts in a Mediterranean Forest." *Global Change Biology* 17(2): 1036–48.
- Neary, D.G., D.L. Rockwood, N.B. Comerford, B.F. Swindel, and T. E. Cooksey. 1990. "Importance of Weed Control, Fertilization, Irrigation, and Genetics in Slash and Loblolly Pine Early Growth on Poorly Drained Spodosols." *Forest Ecology and Management* 30(1): 271–81.
- Nicotra, A.B., O.K. Atkin, S.P. Bonser, A.M. Davidson, E. Finnegan, U. Mathesius, P. Poot, M.D. Purugganan, C. Richards, and F. Valladares. 2010. "Plant Phenotypic Plasticity in a Changing Climate." *Trends in Plant Science* 15(12): 684–92.
- Niinemets, Ü., and F. Valladares. 2006. "Tolerance to Shade, Drought, and Waterlogging of Temperate Northern Hemisphere Trees and Shrubs." *Ecological Monographs* 76(4): 521–47.
- Ogaya, R., and J. Peñuelas. 2007. "Tree Growth, Mortality, and Above-Ground Biomass Accumulation in a Holm Oak Forest under a Five-Year Experimental Field Drought." *Plant Ecology* 189(2): 291–9.
- Palviainen, M., L. Finér, A.M. Kurka, H. Mannerkoski, S. Piirainen, and M. Starr. 2004. "Decomposition and Nutrient Release from Logging Residues after Clear-Cutting of Mixed Boreal Forest." *Plant and Soil* 263(1): 53–67.
- Paschalis, A., S. Fatichi, J. Zscheischler, P. Ciais, M. Bahn, L. Boysen, J. Chang, et al. 2020. "Rainfall Manipulation Experiments as Simulated by Terrestrial Biosphere Models: Where Do We Stand?" *Global Change Biology* 26(6): 3336–55.
- Peltier, D.M.P., M. Fell, and K. Ogle. 2016. "Legacy Effects of Drought in the Southwestern United States: A Multi-Species Synthesis." *Ecological Monographs* 86(3): 312–26.
- Peltier, D.M.P., and K. Ogle. 2019. "Legacies of More Frequent Drought in Ponderosa Pine across the Western United States." *Global Change Biology* 25(11): 3803–16.
- Pinheiro, J., D. Bates, S. DebRoy, and D. Sarkar 2014. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-117. <https://cran.rproject.org/web/packages/nlme/index.html>
- Poorter, H., and O. Nagel. 2000. "The Role of Biomass Allocation in the Growth Response of Plants to Different Levels of Light, CO<sub>2</sub>, Nutrients and Water: A Quantitative Review." *Functional Plant Biology* 27(12): 1191–1.
- Poorter, H., K.J. Niklas, P.B. Reich, J. Oleksyn, P. Poot, and L. Mommer. 2012. "Biomass Allocation to Leaves, Stems and Roots: Meta-Analyses of Interspecific Variation and Environmental Control." *New Phytologist* 193(1): 30–50.
- Puhlmann, H., K. Von Wilpert, M. Lukes, and W. Dröge. 2009. "Multistep Outflow Experiments to Derive a Soil Hydraulic Database for Forest Soils." *European Journal of Soil Science* 60 (5): 792–806. <https://doi.org/10.1111/j.1365-2389.2009.01169.x>
- R Development Core Team. 2018. R: A Language and Environment for Statistical Computing. Vienna: R Foundation for Statistical Computing. [www.r-project.org](http://www.r-project.org)
- Reich, P.B. 2014. "The World-Wide 'Fast-Slow' Plant Economics Spectrum: A Traits Manifesto." *Journal of Ecology* 102(2): 275–301.
- Richardson, A.D., K. Hufkens, T. Milliman, D.M. Aurbrecht, M.E. Furze, B. Seyednasrollah, M.B. Krassovski, et al. 2018. "Ecosystem Warming Extends Vegetation Activity but Heightens Vulnerability to Cold Temperatures." *Nature* 560(7718): 368–71.
- Rigling, A., C. Bigler, B. Eilmann, E. Feldmeyer-Christe, U. Gimmi, C. Ginzler, U. Graf, P. Mayer, G. Vacchiano, and P. Weber. 2013. "Driving Factors of a Vegetation Shift from Scots Pine to Pubescent Oak in Dry Alpine Forests." *Global Change Biology* 19(1): 229–40.
- Rigling, A., H. Brühlhart, O.U. Bräker, T. Forster, and F.H. Schweingruber. 2003. "Effects of Irrigation on Diameter Growth and Vertical Resin Duct Production in *Pinus sylvestris* L. on Dry Sites in the Central Alps, Switzerland." *Forest Ecology and Management* 175(1): 285–96.
- Schönbeck, L., A. Gessler, G. Hoch, N.G. McDowell, A. Rigling, M. Schaub, and M.-H. Li. 2018. "Homeostatic Levels of Non-structural Carbohydrates after 13 Yr of Drought and Irrigation in *Pinus sylvestris*." *New Phytologist* 219(4): 1314–24.
- Schönbeck, L., A. Gessler, M. Schaub, A. Rigling, G. Hoch, A. Kahmen, and M.-H. Li. 2020. "Soil Nutrients and Lowered Source:Sink Ratio Mitigate Effects of Mild but Not of Extreme Drought in Trees." *Environmental and Experimental Botany* 169: 103905.
- Schuldt, B., A. Buras, M. Arend, Y. Vitasce, C. Beierkuhnlein, A. Damm, M. Gharun, et al. 2020. "A First Assessment of the Impact of the Extreme 2018 Summer Drought on Central European Forests." *Basic and Applied Ecology* 45: 86–103.
- Smith, M.D. 2011. "An Ecological Perspective on Extreme Climatic Events: A Synthetic Definition and Framework to Guide Future Research." *Journal of Ecology* 99(3): 656–63.
- Smith, M.D., K.J. La Pierre, S.L. Collins, A.K. Knapp, K.L. Gross, J. E. Barrett, S.D. Frey, et al. 2015. "Global Environmental Change and the Nature of Aboveground Net Primary Productivity Responses: Insights from Long-Term Experiments." *Oecologia* 177(4): 935–47.
- Soliveres, S., F. van der Plas, P. Manning, D. Prati, M.M. Gossner, S. C. Renner, F. Alt, et al. 2016. "Biodiversity at Multiple Trophic Levels Is Needed for Ecosystem Multifunctionality." *Nature* 536: 456.
- Taylor, B.R., C.E. Prescott, W.J.F. Parsons, and D. Parkinson. 1991. "Substrate Control of Litter Decomposition in Four Rocky Mountain Coniferous Forests." *Canadian Journal of Botany* 69(10): 2242–50.

- Timofeeva, G., K. Treydte, H. Bugmann, A. Rigling, M. Schaub, R. Siegwolf, and M. Saurer. 2017. "Long-Term Effects of Drought on Tree-Ring Growth and Carbon Isotope Variability in Scots Pine in a Dry Environment." *Tree Physiology* 37(8): 1028–41.
- Volaire, F. 2018. "A Unified Framework of Plant Adaptive Strategies to Drought: Crossing Scales and Disciplines." *Global Change Biology* 24(7): 2929–38.
- von Arx, G., A. Arzac, P. Fonti, D. Frank, R. Zweifel, A. Rigling, L. Galiano, A. Gessler, and J.M. Olano. 2017. "Responses of Sapwood Ray Parenchyma and Non-structural Carbohydrates of *Pinus sylvestris* to Drought and Long-Term Irrigation." *Functional Ecology* 31(7): 1371–82.
- Wermelinger, B., A. Rigling, D. Schneider Mathis, and M. Dobbertin. 2008. "Assessing the Role of Bark- and Wood-Boring Insects in the Decline of Scots Pine (*Pinus sylvestris*) in the Swiss Rhone Valley." *Ecological Entomology* 33(2): 239–49.
- Will, R.E., S.M. Wilson, C.B. Zou, and T.C. Hennessey. 2013. "Increased Vapor Pressure Deficit Due to Higher Temperature Leads to Greater Transpiration and Faster Mortality during Drought for Tree Seedlings Common to the Forest–Grassland Ecotone." *New Phytologist* 200(2): 366–74.
- Williams, P.A., C.D. Allen, A.K. Macalady, D. Griffin, C.A. Woodhouse, D.M. Meko, T.W. Swetnam, et al. 2012. "Temperature as a Potent Driver of Regional Forest Drought Stress and Tree Mortality." *Nature Climate Change* 3: 292.
- Wohlgemuth, T., V. Doublet, C. Nussbaumer, L. Feichtinger, and A. Rigling. 2018. "Baumartenwechsel in den Walliser Waldföhrenwäldern verstärkt nach grossen Störungen." *Schweizerische Zeitschrift für Forstwesen* 169(5): 260–8.
- Wu, Z., P. Dijkstra, G.W. Koch, J. Peñuelas, and B.A. Hungate. 2011. "Responses of Terrestrial Ecosystems to Temperature and Precipitation Change: A Meta-Analysis of Experimental Manipulation." *Global Change Biology* 17(2): 927–42.
- Wullschlegel, S.D., P.J. Hanson, and T.J. Tschaplinski. 1998. "Whole-Plant Water Flux in Understory Red Maple Exposed to Altered Precipitation Regimes." *Tree Physiology* 18(2): 71–9.
- Zuur, A.F., E.N. Leno, N.J. Walker, A.A. Saveliev, and G.M. Smith. 2009. *Mixed Effects Models and Extensions in Ecology with R*. New York: Springer-Verlag.
- Zweifel, R., E. Etzold, F. Sterck, A. Gessler, T. Anfodillo, M. Mencuccini, G. von Arx, et al. 2020. "Determinants of Legacy Effects in Pine Trees—Implications from an Irrigation-Stop Experiment." *New Phytologist* 227: 1081–96.
- Zweifel, R., and F. Sterck. 2018. "A Conceptual Tree Model Explaining Legacy Effects on Stem Growth." *Frontiers in Forests and Global Change* 1: 9. <https://doi.org/10.3389/ffgc.2018.00009>

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

**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* 92(2): e1507. <https://doi.org/10.1002/ecm.1507>



**Supporting Information.** Bose AK, Rigling A, Gessler A, Hagedorn F, Brunner I, Feichtinger L, Bigler C, Egli S, Etzold S, Gossner MM, Guidi C, Lévesque M, Meusburger K, Peter M, Saurer M, Scherrer D, Schleppi P, Schönbeck L, Vogel ME, von Arx G, Wermelinger B, Wohlgemuth T, Zweifel R, Schaub M. Lessons learned from a long-term irrigation experiment in a dry Scots pine forest: Impacts on traits and functioning. Ecological Monographs.

## Appendix S1

**Table S1.** Start and end date of the irrigation treatment received by the experimental forest from 2003 to 2018.

Year	Irrigation period	
	Start date	End date
2003	19th June	21st October
2004	15th May	26th October
2005	23rd April	4th October
2006	6th May	25th October
2007	4th May	2nd October
2008	15th May	14th October
2009	14th May	12th October
2010	17th June	1st October
2011	14th May	16th October
2012	11th May	2nd October
2013	17th May	23rd September
2014	19th May	1st October
2015	12th May	5th October
2016	30th May	26th September
2017	19th April	9th October
2018	8th May	27th September

**Table S2.** List of vegetation parameters (traits and functions) considered in this study and their respective measurement period, number of observations, and experimental design. The measurement protocols for each parameter are provided in Section S1 of the supplementary materials.

Parameters	Measurement years	Number of years since onset of irrigation	Number of observations	Experimental design and associated random effect structure	References
Needle length	Three periods: 2003 - 2005, 2008 - 2012, and 2013 - 2016	1-3 years, 6-10 years, and 11-14 years	12, 32, and 22 trees at 1st, 2nd, and 3rd periods, respectively	12 (6 control and 6 irrigated), 32 (16 each from control and irrigated), and 22 trees (12 irrigated and 10 control) at 1st, 2nd, and 3rd measurement periods, respectively were nested within 8 independent sampling units	Data of 1 <sup>st</sup> period and 3 <sup>rd</sup> are published in Dobbertin <i>et al.</i> (2010) and Zweifel et al. (2020), respectively, but the 2 <sup>nd</sup> part of the data is unpublished
Shoot length	Three periods: 2003 - 2005, 2008 - 2012, and 2013 - 2016	1-3 years, 6-10 years, and 11-14 years	12, 32, and 22 trees at 1st, 2nd, and 3rd periods, respectively	12 (6 control and 6 irrigated), 32 (16 each from control and irrigated), and 22 trees (12 irrigated and 10 control) at 1st, 2nd, and 3rd measurement periods, respectively were nested within 8 independent sampling units	Data of 1 <sup>st</sup> period and 3 <sup>rd</sup> period were published in Dobbertin et al. (2010) and Zweifel et al. (2020), respectively, but the 2 <sup>nd</sup> part of the data is unpublished
Tree ring width	2003 - 2014	1-12 years	41 trees	20 control and 21 irrigated trees were nested within 8 independent sampling units	Timofeeva et al. 2017
Tree ring $\delta^{13}\text{C}$	2003 - 2014	1-12 years	10 trees	5 control and 5 irrigated trees were nested within 5 independent sampling units	Timofeeva et al. 2017

Percentage of ray parenchyma in tree trunk	2003 - 2012	1-10 years	40 trees	20 control and 20 irrigated trees were nested within 8 independent sampling units	von Arx et al. 2017
NSC in tree trunk	2003 - 2012	1-10 years	40 trees	20 control and 20 irrigated trees were nested within 8 independent sampling units	von Arx et al. 2017
Leaf Area Index	2004 - 2018	2-16 years	8 plots	3 hemispherical photographs taken from each plot and were nested within 4 control and 4 irrigated plots	Parts of the data is published in Dobbertin et al. (2010)
Crown transparency	2003 - 2017	1-15 years	622 trees	325 control and 297 irrigated trees were nested within 8 independent sampling units	Parts of the data is published in Dobbertin et al. (2010) and in Schönbeck et al. (2018)
Stand-level basal area of live trees	2003-2017	1-15 years	622 trees	325 control and 297 irrigated trees were nested within 8 independent sampling units	Unpublished data
Probability of tree survival	2003 - 2017	1-15 years	622 trees	325 control and 297 irrigated trees were nested within 8 independent sampling units	Unpublished data
Fine root biomass	2003 – 2005, 2012, 2014, and 2016	1-3, 9, 11, and 13 years	23 trees	12 control and 11 irrigated trees were nested within 8 independent sampling units	Herzog et al. 2014; Brunner et al. 2019
Ingrowth root biomass density, root length density, root tissue density, and tip frequency	2005 and 2016	3 and 14 years	21 trees in 2005 and 12 trees in 2016	12 control and 9 irrigated trees in 2005 and 6 control and 6 irrigated trees in 2016 were nested within 8 independent sampling units	Brunner et al. 2009, 2019

Litterfall	2014	11 years	56 litter traps	56 litter traps were nested with 8 independent sampling units (7 within each sapling unit)	Unpublished data
Foliar decomposition rates	2014	11 years	96 litter bags	Litters of 3 tree species and 2 types of mesh size for each species. 8 litter bags were nested within 2 independent sampling units for each mesh size of each species	Unpublished data
Root decomposition rates	2014 - 2016	11-13 years	40 litter bags	20 litter bags were placed (nested) within 4 control plots while another 20 litters bags were placed (nested) in 4 irrigated plots	Herzog et al. 2019
Regeneration abundance	2019	16 years	32 plots	16 control and 16 irrigated plots were nested within 8 independent sampling units	Unpublished data
Fungal fruit body abundance and biomass	2003 - 2007	1-5 years	96 trees	48 control and 48 irrigated trees were nested within 8 independent sampling units	Unpublished data
Abundance of galls	2007 and 2008	4 years and 5 years	113 trees in 2007 and 153 trees in 2008	58 control trees and 55 irrigated trees in 2007 and 76 control trees and 77 irrigated trees in 2008 were nested within 8 independent sampling units	Unpublished data
Species richness and abundance of spiders	2007 and 2008	4 years and 5 years	24 plots	12 control and 12 irrigated plots were nested within 8 independent sampling units	Unpublished data
Species richness and abundance of ground beetles	2007 and 2008	4 years and 5 years	24 plots	12 control and 12 irrigated plots were nested within 8 independent sampling units	Unpublished data

Abundance of <i>Tomicus</i> based on shoots fallen to the ground due to maturation feeding	June, 2007 and March, 2008	4 years and 5 years	24 plots	12 control and 12 irrigated plots were nested within 8 independent sampling units	Unpublished data
Occurrence of <i>Tomicus</i> maturation shoot feeding in the tree canopy	2016	13 years	526 shoots	385 irrigated shoots of 43 branches of 18 trees were nested with 3 independent sampling units while 141 shoots of 18 branches of 6 trees were nested within 1 independent sampling units	Unpublished data

---



## **Section S1. Measurement protocols of different variables**

### *Natural precipitation*

The monthly precipitation data was obtained from a nearby climate station (Sion), which is located 4.8 km distance from the study site.

### *Soil volumetric water content*

Soil volumetric water content (VWC) was measured hourly in one out of four control and in one out of four irrigated plots using the Time Domain Reflectometry (Tektronix 1502B cable tester, Beaverton, OR, USA) with three to four depth replicates per plot. The measurements were conducted at three different soil depths: 10, 40 and 60 cm. In the period from 2003 to 2014, the VWC sensors occasionally had measurement failures. In total missing VWC values amount to 28.1% of the time series. These gaps were filled by simulated VWC using the process-based soil-vegetation-atmosphere-transport model LWFBrook90 (Hammel & Kennel, 2001) recently implemented in an R environment (Schmidt-Walter *et al.*, 2020). LWFBrook90 is a modification of the well-known Brook90 model (Federer, 2002) which simulates daily transpiration, interception, soil and snow evaporation, streamflow and soil water fluxes through a soil profile covered with vegetation. The water movement in the ground results from the numerical solution of the Richards equation via the Mualem-van Genuchten parameters. These hydraulic parameters were predicted from measured soil texture, bulk density and organic matter content per soil horizon using the pedotransfer function of Puhlmann *et al.* (2009). The daily meteorological forcing data was derived from the adjacent MeteoSwiss Sion and measured irrigation amounts. The measured VWC from 2003 to 2014 was used to calibrate the sensitive model parameters (Schmidt-Walter *et al.*, 2020). Parameters with maximum Kling-Gupta efficiency (KGE) were selected for the simulation to gapfill missing values. For the control sites, KGEs of 0.65, 0.65, and 0.62 were achieved for 10, 40 and 60 cm soil depth, respectively. The irrigation plots model

performance was lower but can still be considered behavioural (Knoben *et al.*, 2019) with KGE values of 0.41, 0.55, and 0.32 for 10, 40 and 60 cm soil depth, respectively.

For quantifying the impact of irrigation on soil VWC, we quantified the VWC in irrigated plots relative to control plots in percentage using the following formula:

$$\frac{(VWC \text{ in irrigated plots} - VWC \text{ in control plots})}{VWC \text{ in control plots}} \times 100$$

We quantified this index separately for each measurement year starting from 2003 to 2014 based on the data availability across the three soil layers.

#### *Needle and shoot length*

In April 2006, six trees from control and six trees from irrigated plots were randomly selected. Five main shoot leaders were selected from the branches, and shoot lengths were measured to the millimetre going back to the year 2003. Within each annual shoot, 20 needles were selected close to the centre of each annual shoot for needle length measurement (see details in Dobbertin *et al.*, 2010). The second sampling for needle and shoot data was conducted in 2012. 16 trees from control and 16 trees from irrigated plots were selected randomly. From each tree, two branches were selected, and shoot lengths were measured to the millimetre going back to the year 2008. The needle length was measured following the same procedure described in Dobbertin *et al.* (2010). In 2017, 12 trees of irrigated and 10 trees of control were selected for needle and shoot length measurements. This third phase of measurement used the same procedure as before for needle and shoot length (Zweifel *et al.*, 2020).

#### *Leaf Area Index (LAI)*

From 2004 to 2018, we took hemispherical pictures at the three points along the main axis of each plot at the end of each vegetation period. These points were marked by stakes and used each measurement year. A digital camera (Coolpix 4500, Nikon, Tokyo) with a fish-eye lens (Nikon FC-E8) was fitted to self-levelling gimbals (SLM2, Delta-T, Cambridge,

UK) mounted on a tripod at 1 m above ground. The detail of the measurement protocol is provided in Dobbertin et al. (2010).

#### *Tree ring width*

In 2014 after the end of the growing season, 20 trees from non-irrigated and 21 trees from irrigated treatments were cored using a 5 mm increment borer (Haglöf, Långsele, Sweden) at 1 m height from the base (Timofeeva *et al.*, 2017). Tree-ring width (TRW) was measured using a Lintab system with a precision of 0.01 mm, using the TSAP-Win software V.3.5 (Rinntech, Heidelberg, Germany) (Eilmann *et al.*, 2010), and dated with existing TRW chronologies from the study site using the software COFECHA (Grissino-Mayer, 2001).

#### *Carbon isotope ratios*

Five trees from each non-irrigated and irrigated treatments were used for  $\delta^{13}\text{C}$  measurements of individual tree rings (Timofeeva *et al.*, 2017). Individual rings were separated using a surgical scalpel under a Wild M8 stereomicroscope. The separated rings were then cut into small pieces and packed into teflon filter bags for subsequent chemical treatment (Ankom Technology, Macedon, NY, USA). Cellulose was extracted according to Boettger *et al.* (2007) with homogenization according to Laumer *et al.* (2009) using an ultrasonic treatment with a HD3100 sonotrode (Hielscher, Berlin, Germany). The cellulose samples were measured using a high-temperature pyrolysis method with subsequent analysis on an isotope-ratio mass-spectrometer (delta Plus XP, Thermo; instrument precision 0.2%). Carbon isotope ratios are reported against Vienna Pee Dee Belemnite (VPDB). Individual tree-ring  $\delta^{13}\text{C}$  values were corrected back to preindustrial conditions to account for the Suess effect (McCarroll & Loader, 2004).

### *Percentage of ray parenchyma and Percentage of NSC*

In March 2013, 20 adult Scots pine trees per irrigation and control treatment of similar age and size were randomly selected with an experimental design that consists of five trees from each replicated treatment plots ( $5 \times 8 = 40$  trees) (von Arx *et al.*, 2017). Tissue for NSC measurement was extracted from all sampled trees by taking four 5-mm stem cores at breast height from the north, east, south and west side of the tree. The stem cores were then kept on dry ice in a cooler immediately after the extraction. Cores were then microwaved at 600 W for >90 s for eliminating enzymatic activity (Popp *et al.*, 1996) and subsequently air-dried in an oven at 65 °C for 3 days. In May 2013, one 10-mm increment core was extracted adjacent to the NSC samples for quantifying the ray abundance.

High-resolution images of anatomical samples were used for quantifying the percentage of ray parenchyma of 40 stem cores. For this purpose, cross-sections of <15 µm thickness perpendicular to the axially oriented tracheids were cut from the 10-mm cores with a microtome (Gärtner *et al.*, 2015), placed on a slide, and stained with Alcian blue (1% solution in acetic acid) and safranin (1% solution in ethanol). This staining procedure results in blue unligified (parenchyma) and red lignified (tracheid) cells. The cross-sections were then dehydrated using a series of ethanol solutions of increasing concentrations, washed with xylol, and then preserved by embedding them into Eukitt glue (Gärtner & Schweingruber, 2013).

Overlapping images covering the entire samples were captured with a Nikon D90 digital camera mounted on a Nikon Eclipse 50i optical microscope with 1009 magnification and merged to a single image using PTGUI v8.3.10 Pro (New House Internet Services B.V., Rotterdam, the Netherlands). All rays of the outermost 20 years (comprising 10 years before and 10 after the onset of irrigation) were then quantified in the merged images as described previously (von Arx *et al.*, 2015). In short, rays and the annual ring borders were manually

outlined using a tailored clone of ROXAS v1.6 (von Arx & Carrer, 2014). The final sample width ranged from 7 to 9 mm, resulting in mean PERPAR (percentage of ray volume) values being within  $\pm 5\text{--}6\%$  (rel. 95% confidence interval) of the true values (von Arx et al., 2015).

Increment cores for NSC measurements were cut in 5-year segments starting from the bark for the outer 20 years (resulting in two pre- and two post-treatment segments), and a fifth segment including all remaining sapwood rings (between 7 and 57 rings). Five-year segments were chosen to provide sufficient wood material for reliable NSC measurements, because of the generally small growth rates in Scots pine trees. Corresponding segments from different cores of the same tree were then pooled and milled. Extraction of NSC followed the anthrone technique (Olano *et al.*, 2006). This technique provides an estimate of NSC content per wood dry weight (%NSC), distinguishing between the contribution of soluble mono and oligosaccharides and non-soluble carbohydrates (starch). % NSC was calculated for each tree and radial segment by adding soluble and insoluble carbohydrate contribution.

#### *Crown transparency and tree mortality*

Crown transparency and tree mortality (i.e., live or dead) was measured once a year from 2003. Crown transparency inventory was conducted by visual rating of the crown transparency (also termed percentage of defoliation) using reference photographs ranging from 0% (i.e., a fully foliated tree) to 100% (i.e., a dead tree) (Dobbertin et al., 2010; Schönbeck et al., 2018). We created four crown transparency classes for this analysis such as <34%, 34-66%, >66-99%, and 100% transparency.

#### *Probability of tree survival*

Tree survival was quantified as a binary variable (1 if alive, 0 otherwise). Each tree was monitored and recorded as live or dead once a year from 2003. We quantified probability of survival or death between successive measurements from 2003 to 2017.

### *Fine roots biomass from soil cores*

For fine root sampling, three trees were selected from each plot (n=8; four irrigated and four control). Overall, twelve trees from the control and nine trees from the irrigation-treatment were considered in the analysis. Two soil cores per tree were taken in April/May in 2003, 2004, 2005, 2012, 2014, and 2016 (Brunner *et al.*, 2019; Brunner *et al.*, 2009; Herzog *et al.*, 2014). After sampling, the soil cores were packed in plastic bags and stored at a 4 °C temperature until they were analysed. The soil cores were then washed in a sieve for separating roots from the soil. The sorted fine roots were then dried at 60 °C temperature for 3 days, and then weighed for the biomass. Fine roots were calculated per cm<sup>3</sup> of soil for making a comparison across the measurement years (Brunner *et al.*, 2019).

### *Ingrowth of fine roots*

The first phase of ingrowth core sampling was established in April 2003. Glass-fiber-netting cylinders (11 cm in height, 5 cm in diameter, with a 5 mm mesh size) were installed with the ingrowth cores inserted into the holes of the cylinders where soil core samples had been taken previously for the fine-root biomass (Brunner *et al.*, 2009). The ingrowth cores were refilled with sieved topsoil from outside the plots. The ingrowth cores were harvested with a large soil corer 8.5 cm in diameter in May 2005 (i.e., 2 years after the core installation). After harvest, the ingrowth cores were packed undisturbed in plastic bags and stored in the laboratory at 4 °C temperature until they were analysed. The fine roots were then separated from the cores and stored in tap water in a refrigerator until fine-root morphology and architecture was analysed (Brunner *et al.*, 2009). The second phase of ingrowth core sampling was established in April 2014 using the identical ingrowth cores as before. The ingrowth cores were then harvested in spring 2016. However, trees other than those from the first series were used, and three ingrowth cores per tree instead of two were



installed. In total, six trees were selected from control plots treatment and six trees from irrigated plots.

The ingrowth of fine roots from 2005 and 2016 sampling were scanned for morphological characteristics before drying and weighing. The scanned pictures were then analysed using the WinRHIZO software package (version 4.1c, Regent Instruments Inc., Quebec, Canada) for morphological and architectural traits such as length, diameter, root volume, tips, and forks. The measured fine-root traits were root biomass density ( $\text{g m}^{-2}$ ), root length density ( $\text{m m}^{-2}$ ), mean diameter (mm), tip frequency ( $\text{n cm}^{-1}$ ), and root tissue density ( $\text{mg cm}^{-3}$ ). Biomass and length were calculated per soil area and to a soil depth of 10 cm (topsoil), tips to the root length, and root tissue density to the fine-root volume (Brunner et al., 2019; Brunner et al., 2009).

#### *Natural regeneration*

Field measurement was conducted in September 2019 (i.e., 16 years after irrigation treatment application). Two circular regeneration inventory plots of 50  $\text{m}^2$  each was established, both under canopy gaps as well as under canopy shelters in each replicated irrigation treatment plots. This makes 4 regeneration inventory plots (i.e., 2 under canopy gaps and 2 under canopy shelters)  $\times$  8 irrigation treatment plots (i.e., 2 treatments  $\times$  4 replications) = 32 plots. Regeneration inventory plots (i.e., total four plots within each irrigation treatment plot) were nested within irrigation treatment plots (i.e., total eight plots) which were incorporated as random effects in the mixed-effect models. The regeneration inventory measures every individual by their species and size (i.e., height). The regeneration height was characterized by three categories 0-19 cm, 20-119 cm, and 120-400 cm.

#### *Species richness and abundance of ground beetles and spiders*

Three pitfall funnel traps ( $\varnothing 15$  cm) were installed in each of the eight plots in the 4th (2007) and 5th (2008) seasons after the onset of the irrigation experiment. They were

arranged in the form of an isosceles triangle with each trap being 6 m away from the plot borders. The distances between the traps within each plot were 19 m (2x) and 28 m. Traps were active from April to September and emptied monthly. Subsequently, the catches were sorted to higher taxonomic level and ground beetles (Carabidae) and spiders (Araneae) were identified to species level by taxonomic specialists.

#### *Abundance of oak galls*

In each plot, 20 randomly distributed oak trees with >1 cm stem diameter and <4 m height were assessed for the presence of galls from gall wasps (Hym., Cynipidae). The most frequent galls were *Neuroterus quercusbaccarum* (L.), *Cynips quercusfolii* L., and *Andricus foecundatrix* (Hartig). The surveys were done at the end of September in the years 2007 and 2008, respectively.

#### *Shoot feeding of pine shoot beetles (Tomicus spp.)*

Along a 66 m long and 2 m wide transect between the three pitfall traps in each plot (see section “*Species richness and abundance of ground beetles and spiders*” above) all shoots fallen to the ground due to maturation feeding (shoot feeding) by the two pine shoot beetles *T. minor* and *T. piniperda* were counted. The first survey was made in 2007 and all collected shoots were removed. Therefore, this survey summed up the shoot feeding of the last 1-2 years. The second survey from 2008 included only the shoot feeding of one year.

This ground-based study was complemented by a study in pine crowns carried out in 2016 using scaffolds. We analysed 71 canopy shoots from 24 trees which were accessible from the five scaffolds.

#### *Litterfall*

Litterfall was sampled by placing litter traps of 0.5 m x 0.5 m continuously on the soil surface. In each of the eight replicated plots (4 control and 4 irrigated), seven litter traps were randomly distributed. Litter samples were collected in November 2014.

### *Foliar decomposition rates*

The decomposition rate of organic matter was measured through the mass loss of *Pinus sylvestris* needles and *Quercus pubescens* and *Viburnum lantana* leaves over 140 days. The needles/leaves were filled in two types of litter bags with different mesh sizes, allowing the access of only microfauna in a fine mesh and meso as well as macrofauna in a coarse mesh. The fine mesh bags consist of mesh size 0.1 x 0.1 mm, while the coarse mesh bags consist mesh size of 10 x 10 mm. The fine mesh bags were made of nylon cloth material from Frank Eckerd GmbH, while the coarse mesh bags were made of a polyester net from Eckert Waldkirch, Germany. All mesh bags were approximately 10 x 10 cm in size. For litter materials, the needles were collected from litter traps, while the leaves were picked from the soil surface. The litter (leaves and needles) was dried at 40 °C for 72 hours and kept dry in desiccators. All leaves were cut into pieces of approximately uniform size (~2 x 2 cm). The needles were left untreated. All litter was well mixed within its litter type and 1 g ± 0.02 g was put in each numbered litter bag. Each litter type was separated into the two origins (control and irrigation) and into the two-mesh sizes (fine and coarse) which means four treatments per litter type and thus overall 12 (4 × 3 species) treatments.

The experimental design consists 2 types of mesh bags (fine and coarse) × 2 irrigation treatments (control and irrigation) × 8 replication treatment plots × 6 dates of measurements (0, 10, 40, 80, 110, and 140) = 192 litter bags for each species (*P. sylvestris*, *Q. pubescens*, and *V. lantana*). The bags were arranged in groups in a subplot, 8 bags × 3 species = 24 bags in a subplot. We used a total of 24 subplots. The litter bags were directly placed on the surface soil (A-horizon). A distance of 20 to 30 cm was kept between two bags. The bags were placed between 3<sup>rd</sup> - 6<sup>th</sup> of May 2015. The litter samples were collected at six different dates over the 140 days. The litter of the collected samples were removed and were again dried at 40 °C for 72 hours and the residual litter material was cleaned from mineral soil and

deposits from irrigation with a brush before weighing. The dry and clean litter was weighed again to determine the mass loss.

#### *Root decomposition rate*

Root samples were extracted using a spade in autumn 2013 and stored in plastic bags. In laboratory, the roots were then washed on a sieve under running water. Roots < 2 mm in diameter were considered for the decomposition experiment. The root samples were then air dried and kept at room temperature. In February 2014, 1 mm mesh sized litterbags of size 10 × 10 cm were filled with 1 g of airdried root materials. The litterbags were made of a nylon mesh (Sefar Petex, Sefar AG, Heiden, Switzerland). The 1 mm mesh size generally allows the mesofauna (e.g., mites, springtails) to enter in the litterbags, but not the macrofauna such as earthworms. At the end of March 2014, each root-filled litterbag was buried in the same plot from where root materials were collected. In order to destructively sample the litterbags at five different time points (i.e., 3, 6, 12, 18, and 24 months), five litterbags per time-point and plot were tied together with a nylon cord and buried horizontally between the O and A layers at 5 cm depth measured from the surface (O layer). In total, 240 litterbags were buried. Litterbags of each time point were excavated carefully and stored in plastic bags and cool boxes during transportation to the laboratory. In the laboratory, the roots were carefully cleaned with a fine brush to remove adhesive soil, frozen in liquid nitrogen, and freeze-dried. Subsequently, roots from the same plot and time point were pooled, dry weights were measured, and samples were then stored at -20 °C until further processing. From the remaining root litter mass, the decomposition rate was quantified (see details in Herzog *et al.*, 2019).

#### *Fungal abundance and biomass*

Above-ground fungal abundance and biomass was assessed by recording fungal fruit body production of macromycetes (visible to the naked eye) weekly during the mushroom

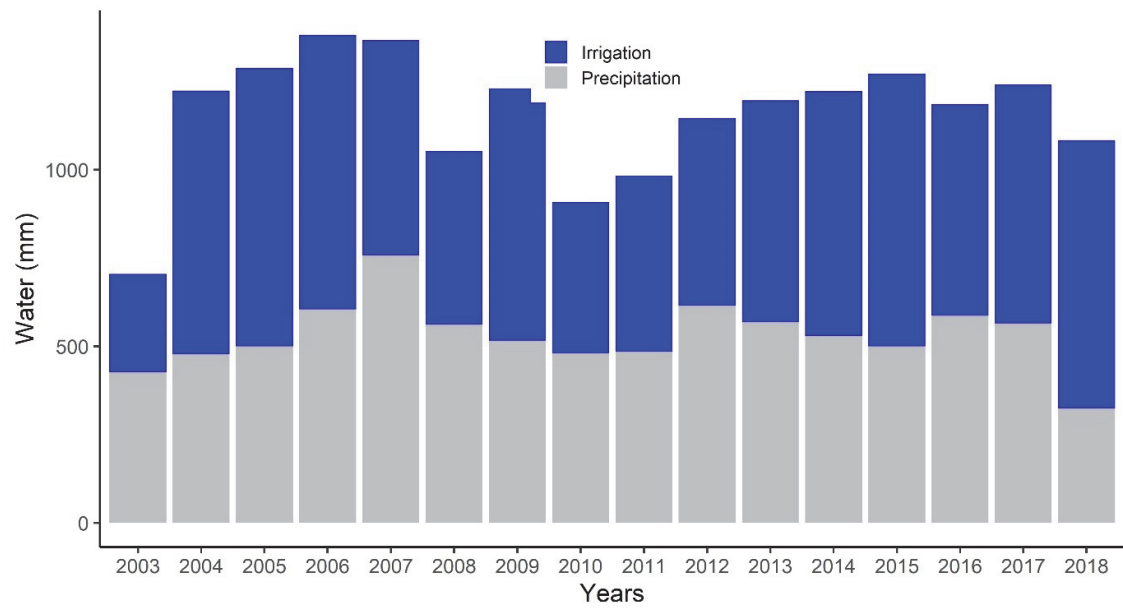
season (May – November) from 2003 to 2007. Within each treatment plot, 12 trees were selected and all epigeous soil-inhabiting macromycetes within a radius of 2 m around the trunks were counted, weighted, macro- and microscopically identified to species or genus level and assigned to two ecological guilds based on their lifestyle as saprotrophs or ectomycorrhizal symbionts.

**Table S3.** Comparing model outputs (estimate and *p*-value) with and without temporal autocorrelation. For each response variable (radial growth,  $\delta^{13}\text{C}$ , and shoot length), a linear mixed-effect model was performed, measurement year, treatments (control and irrigated), and the interaction between measurement year and treatments were considered as fixed effects while trees nested within plots were considered as random effects. The temporal autocorrelation across measurement years was included by using the *corARI* function of *nlme* package in R.

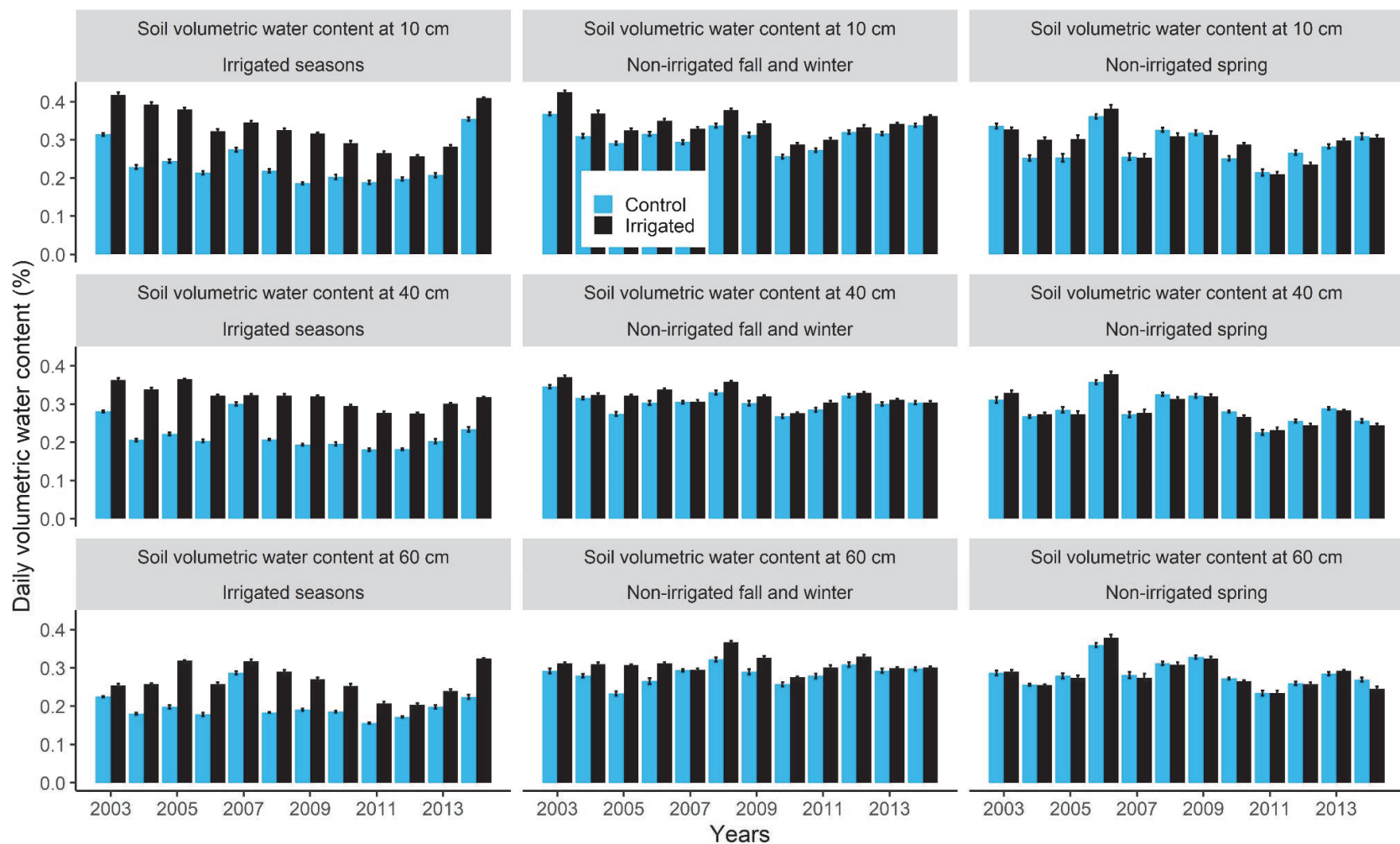
Treatment effect comparison across measurement years. (Control vs irrigated in 2003 was considered as the reference)	Tree-ring width (mm)				Tree-ring $\delta^{13}\text{C}$ (‰)				Log-transformed shoot length (mm)				Crown transparency (%)			
	With temporal autocorrelation		Without temporal autocorrelation		With temporal autocorrelation		Without temporal autocorrelation		With temporal autocorrelation		Without temporal autocorrelation		With temporal autocorrelation		Without temporal autocorrelation	
	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value	Estimate	<i>p</i> -value
Control vs irrigated in 2004	0.381	0.000	0.381	0.000	-1.92	0.000	-1.92	0.000	0.36	0.002	0.37	0.000	1.177	0.192	1.174	0.335
Control vs irrigated in 2005	0.492	0.000	0.492	0.000	-1.82	0.001	-1.82	0.000	0.74	0.000	0.74	0.000	4.218	0.000	4.209	0.000
Control vs irrigated in 2006	0.706	0.000	0.706	0.000	-1.43	0.006	-1.43	0.005	0.56	0.000	0.57	0.000	13.659	0.000	13.664	0.000
Control vs irrigated in 2007	0.644	0.000	0.644	0.000	-0.40	0.434	-0.40	0.426	0.82	0.000	0.86	0.000	15.077	0.000	15.070	0.000
Control vs irrigated in 2008	0.445	0.000	0.445	0.000	-1.07	0.044	-1.07	0.035	0.60	0.000	0.64	0.000	15.117	0.000	15.117	0.000
Control vs irrigated in 2009	0.429	0.000	0.429	0.000	-0.57	0.267	-0.57	0.259	0.62	0.000	0.66	0.000	14.066	0.000	14.072	0.000
Control vs irrigated in 2010	0.167	0.188	0.167	0.119	-1.15	0.026	-1.15	0.023	0.93	0.000	0.96	0.000	15.371	0.000	15.383	0.000
Control vs irrigated in 2011	0.298	0.021	0.298	0.006	-0.65	0.202	-0.65	0.194	0.69	0.000	0.72	0.000	12.001	0.000	12.022	0.000
Control vs irrigated in 2012	0.319	0.015	0.319	0.003	-1.19	0.022	-1.19	0.019	0.80	0.000	0.83	0.000	17.642	0.000	17.704	0.000
Control vs irrigated in 2013	0.342	0.009	0.342	0.001	-1.43	0.006	-1.43	0.005	-	-	-	-	18.610	0.000	18.787	0.000



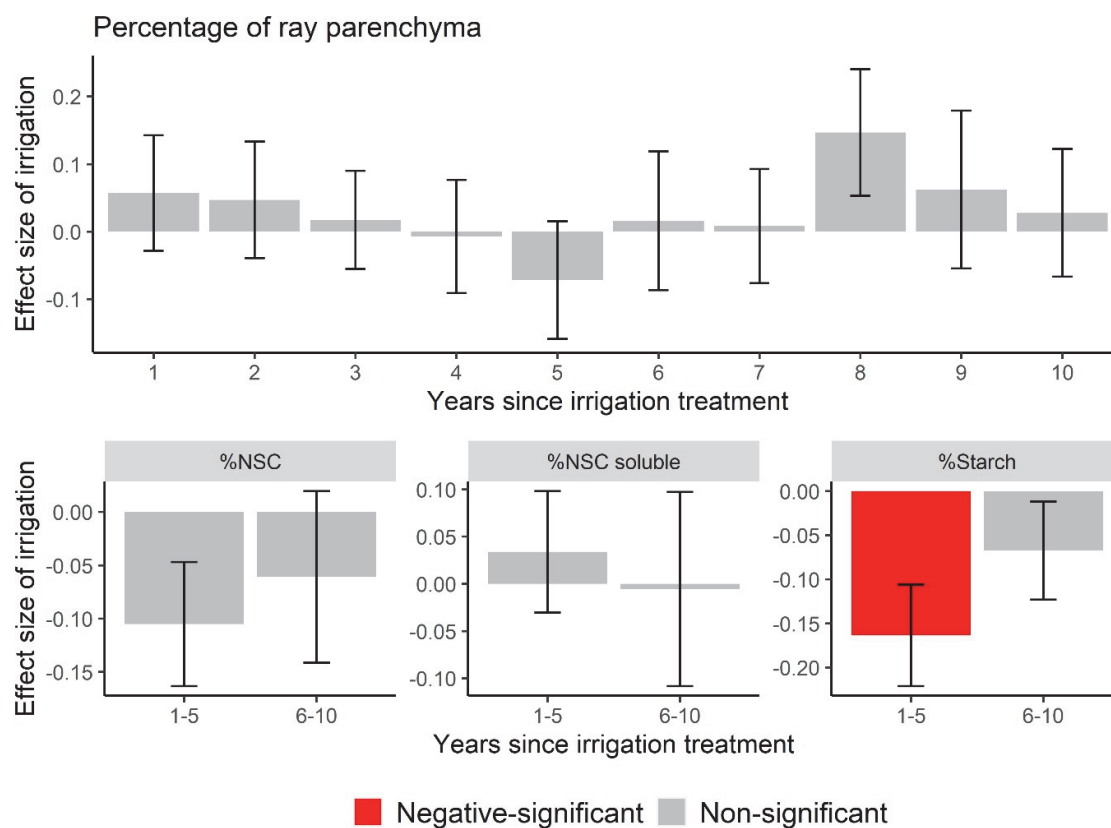
Control vs irrigated in 2014	0.157	0.236	0.157	0.142	-1.22	0.018	-1.22	0.016	-	-	-	-	15.458	0.000	15.277	0.000
Control vs irrigated in 2015	-	-	-	-	-	-	-	-	-	-	-	-	16.651	0.000	16.811	0.000
Control vs irrigated in 2016	-	-	-	-	-	-	-	-	-	-	-	-	15.743	0.000	15.828	0.000
Control vs irrigated in 2017	-	-	-	-	-	-	-	-	-	-	-	-	13.486	0.000	13.431	0.000



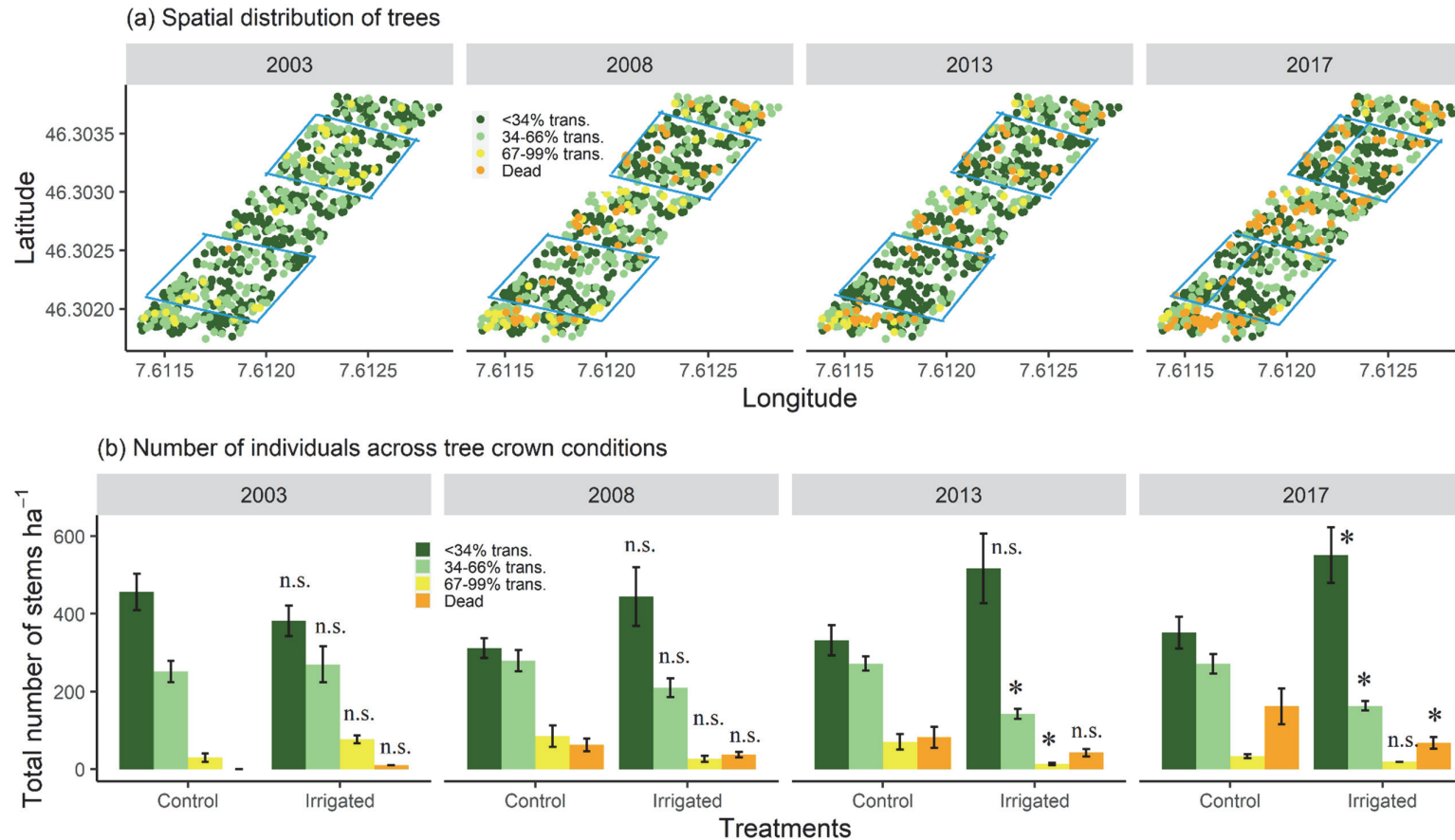
**Figure S1.** Total amount of precipitation in the control plots and the additional water in the irrigated plots.



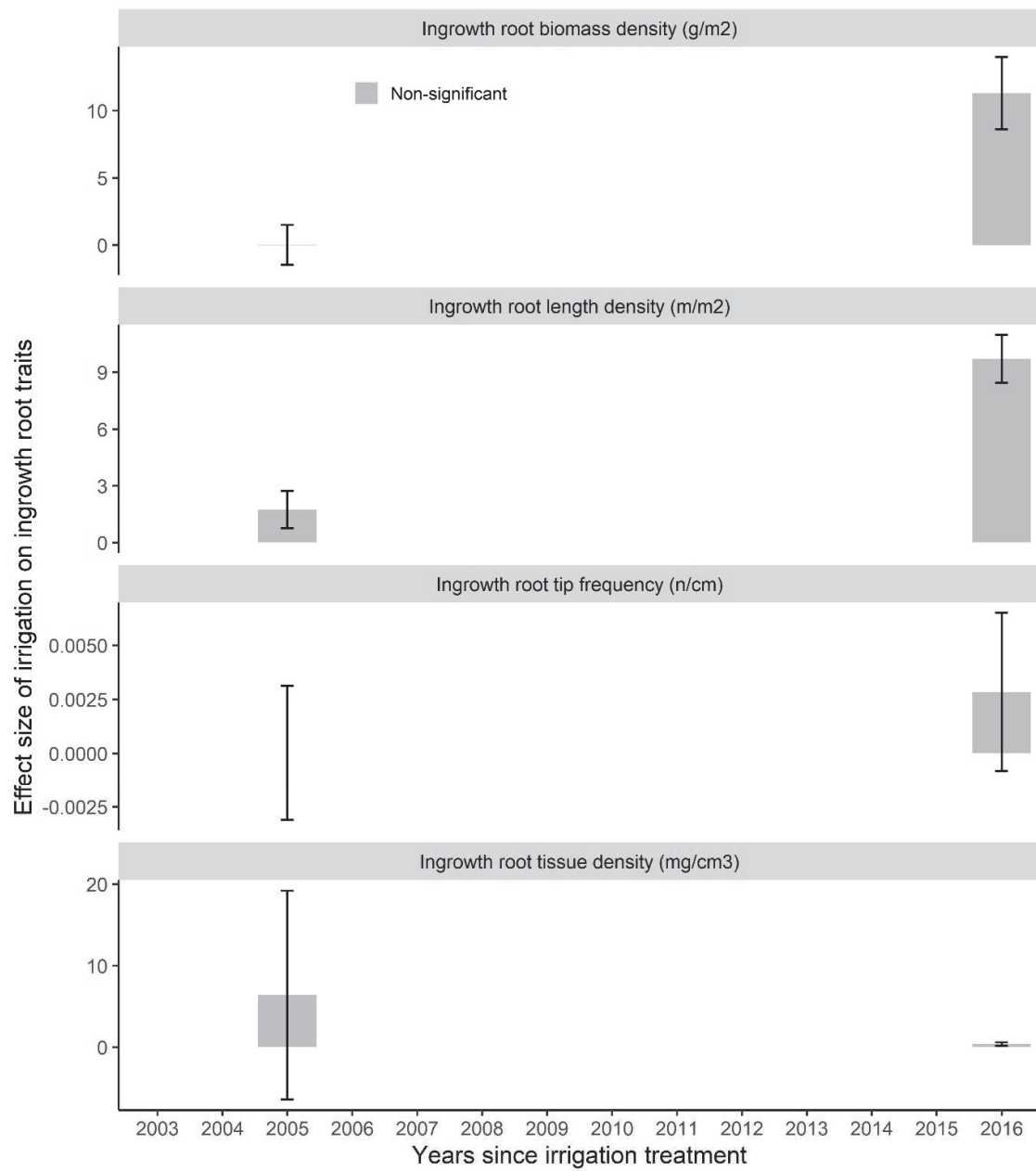
**Figure S2.** Soil volumetric water content (%) in irrigated and control plots across three different soil layers for the irrigation periods (see Table S1), non-irrigated fall-winter periods (September-February) and non-irrigated spring period (March-May). The VWC values represent the average of 1-4 measurements conducted within a single treatment plot (irrigation or control). Thus, no statistical test was performed. The standard errors were calculated from daily VWC data. Total amounts of annual precipitation and irrigation are provided in Figure S1 of the supplementary materials.



**Figure S3.** Effect size (i.e., coefficient of the mixed-effect model) of irrigation treatment on percentage of ray parenchyma and NSC (non-structural carbohydrates) in the trunks of Scots pine. The grey bar indicates non-significant effect of irrigation treatment ( $>0.05$ ). The error bars represent mean $\pm$ standard errors. The number of observations used for each analysis is provided in Table S2. The analysis was performed separately for each time period.

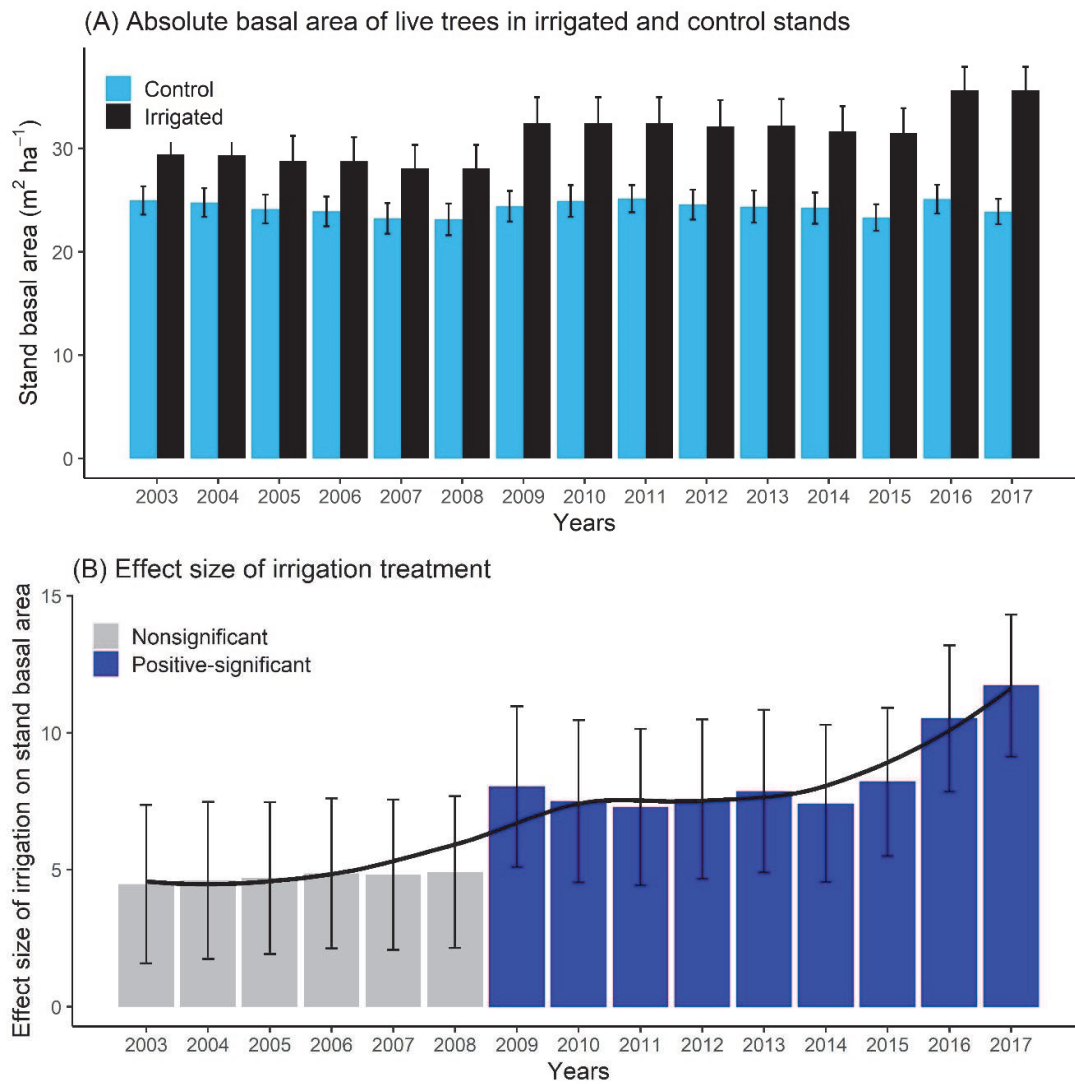


**Figure S4.** (a) The changes in crown transparency (trans) in irrigated (squares) and non-irrigated plots over time since irrigation treatment application; (b) The changes in number of tree individuals across four crown transparency classes over time since irrigation treatment application. 0% trans indicates full foliage while 100% trans indicates full defoliation or dead. In Fig. a, the entire blue squared areas are irrigated plots (two plots within each of those two squares). The remain areas are control plots (n=4). In 2017, the total number of stems ha<sup>-1</sup> in irrigated plots is lower than that of previous measurement years, this is due to change in plot size starting after the growing season 2013 when approx. one-third of the area of each irrigated plot was converted to an irrigation-stop treatment. This reduced plot size, i.e., changes in individual tree-level expansion factor affected the quantification of stems ha<sup>-1</sup> in irrigated plots. In Fig b, \* and n.s. indicate statistically significant and non-significant difference between irrigated and control treatments, respectively.

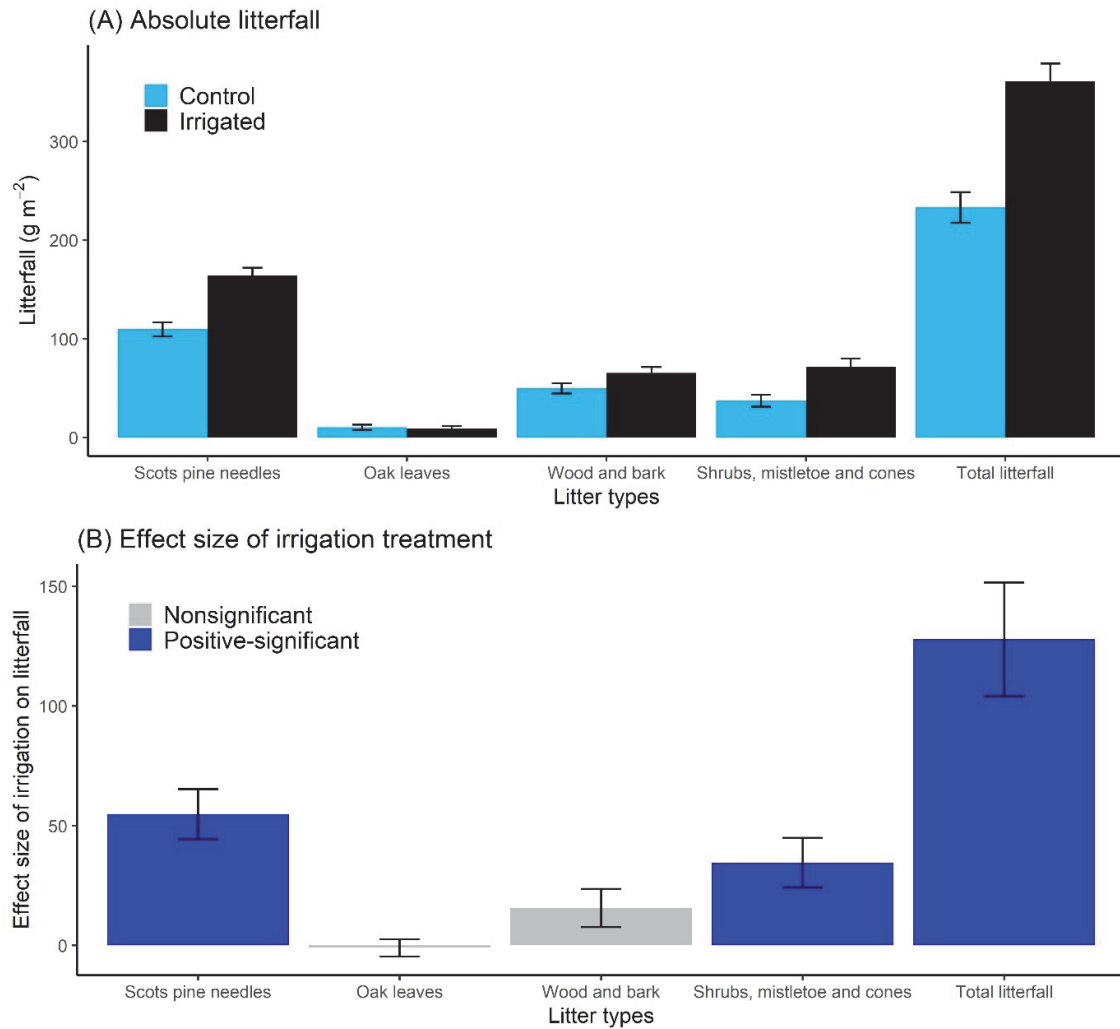


**Figure S5.** Effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on ingrowth (newly formed) root traits. The grey bar indicates non-significant effect of irrigation treatment ( $>0.05$ ). The error bars represent mean  $\pm$  standard errors. The number of observations used for each analysis is provided in Table S2. The analysis was performed separately for each time period.

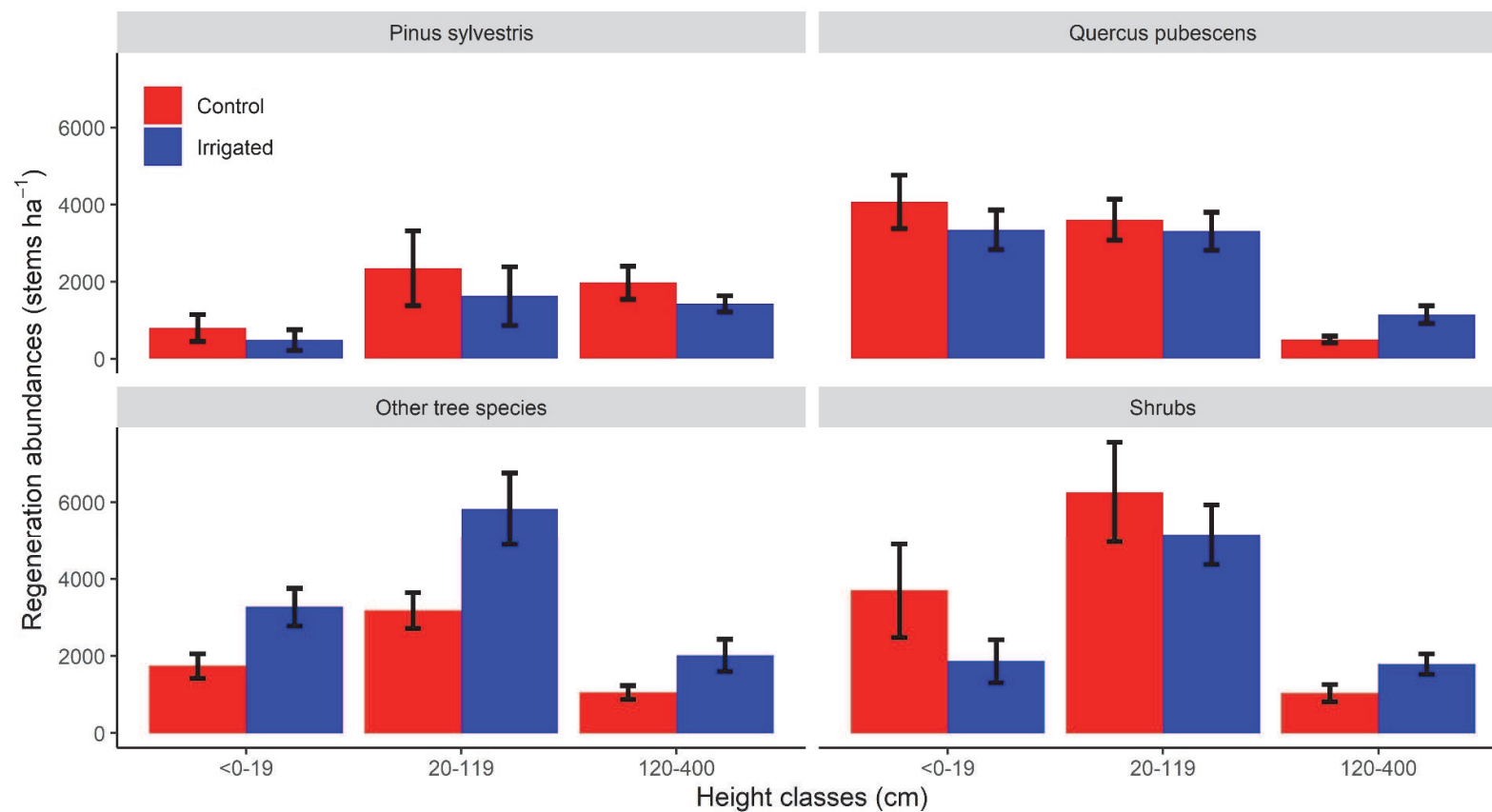




**Figure S6.** Irrigation effect on stand-level basal area of live trees. (A) Absolute stand-level basal area of live trees in irrigated and control plots from 2003 to 2017, and (B) Effect size (i.e., coefficient of the mixed-effect model) of the irrigation on stand-level basal area of live trees from 2003 to 2017. The error bars represent the mean  $\pm$  standard errors and the fitted line shows the locally estimated *smoothing* (i.e., *loess*). The number of observations used for each analysis is provided in Table S2. The analysis was performed separately for each year. Irrigation started in 2003.



**Figure S7.** Irrigation effect on litterfall. The litterfall samples were collected in November 2014. (A) Absolute litterfall in control and irrigated plots, and (B) Effect size (i.e., coefficient of the mixed-effect model) of the irrigation treatment on litterfall. The error bars represent the mean  $\pm$  standard errors.



**Figure S8.** Descriptive statistics of absolute regeneration abundances (stems  $\text{ha}^{-1}$ ) across height classes of four different species types located in irrigated and control plots. The measurement was performed after 16 years since the onset of the irrigation treatment. The error bars represent mean  $\pm$  standard errors.

## References

- Boettger, T., Haupt, M., Knöller, K., Weise, S., Waterhouse, J., Rinne, K., Loader, N., Sonninen, E., Jungner, H., Masson Delmotte, V., et al. (2007). Wood cellulose preparation methods and mass spectrometric analyses of  $\delta^{13}\text{C}$ ,  $\delta^{18}\text{O}$ , and nonexchangeable  $\delta^2\text{H}$  values in cellulose, sugar, and starch: an interlaboratory comparison. *Analytical Chemistry*, 79(12), 4603-4612.
- Brunner, I., Herzog, C., Galiano, L., & Gessler, A. (2019). Plasticity of fine-root traits under long-term irrigation of a water-limited Scots pine forest. *Frontiers in Plant Science*, 10, 701.
- Brunner, I., Pannatier, E. G., Frey, B., Rigling, A., Landolt, W., Zimmermann, S., & Dobbertin, M. (2009). Morphological and physiological responses of Scots pine fine roots to water supply in a dry climatic region in Switzerland. *Tree Physiology*, 29(4), 541-550.
- Dobbertin, M., Eilmann, B., Bleuler, P., Giuggiola, A., Graf Pannatier, E., Landolt, W., Schleppi, P., & Rigling, A. (2010). Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed *Pinus sylvestris* forest. *Tree Physiology*, 30(3), 346-360.
- Eilmann, B., Buchmann, N., Siegwolf, R., Saurer, M., Cherubini, P., & Rigling, A. (2010). Fast response of Scots pine to improved water availability reflected in tree-ring width and  $\delta^{13}\text{C}$ . *Plant, Cell & Environment*, 33(8), 1351-1360.
- Federer, C. A. (2002). BROOK 90: A simulation model for evaporation, soil water, and streamflow. <http://www.ecoshift.net/brook/brook90.htm>.
- Gärtner, Gärtner, H., Lucchinetti, S., & Schweingruber, F. H. (2015). A new sledge microtome to combine wood anatomy and tree-ring ecology. *IAWA journal*, 36(4), 452-459.

- Gärtner, H., & Schweingruber, F. H. (2013). Microscopic Preparation Techniques for Plant Stem Analysis. *Kessel Publishing House, Remagenm, Germany*.
- Grissino-Mayer, H. D. (2001). Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res*, 57, 205–221.
- Hammel, K., & Kennel, M. (2001). Charakterisierung und analyse der wasserverfügbarkeit und des wasserhaushalts von waldstandorten in bayern mit dem simulationsmodell BROOK90. Frank.
- Herzog, C., Hartmann, M., Frey, B., Stierli, B., Rumpel, C., Buchmann, N., & Brunner, I. (2019). Microbial succession on decomposing root litter in a drought-prone Scots pine forest. *The ISME Journal*, 13(9), 2346-2362.
- Herzog, C., Steffen, J., Pannatier, E. G., Hajdas, I., & Brunner, I. (2014). Nine years of irrigation cause vegetation and fine root shifts in a water-limited pine forest. *PloS one*, 9(5), e96321.
- Knoben, W. J. M., Freer, J. E., & Woods, R. A. (2019). Technical note: Inherent benchmark or not? Comparing Nash–Sutcliffe and Kling–Gupta efficiency scores. *Hydrology and Earth System Science*, 23(10), 4323-4331.
- Laumer, W., Andreu, L., Helle, G., Schleser, G. H., Wieloch, T., & Wissel, H. (2009). A novel approach for the homogenization of cellulose to use micro-amounts for stable isotope analyses. *Rapid Communications in Mass Spectrometry*, 23(13), 1934-1940.
- McCarroll, D., & Loader, N. J. (2004). Stable isotopes in tree rings. *Quaternary Science Reviews*, 23(7), 771-801.
- Olano, J. M., Menges, E. S., & Martínez, E. (2006). Carbohydrate storage in five resprouting Florida scrub plants across a fire chronosequence. *New Phytologist*, 170(1), 99-106.

- Popp, M., Lied, W., Meyer, A. J., Richter, A., Schiller, P., & Schwitte, H. (1996). Sample preservation for determination of organic compounds: microwave versus freeze-drying. *Journal of Experimental Botany*, 47(10), 1469-1473.
- Puhlmann, H., Von Wilpert, K., Lukes, M., & Dröge, W. (2009). Multistep outflow experiments to derive a soil hydraulic database for forest soils. *European Journal of Soil Science*, 60(5), 792-806.
- Schmidt-Walter, P., Trotsiuk, V., Meusburger, K., Zacios, M., & Meesenburg, H. (2020). Advancing simulations of water fluxes, soil moisture and drought stress by using the LWF-Brook90 hydrological model in R. *Agricultural and Forest Meteorology*, 291, 108023.
- Schönbeck, L., Gessler, A., Hoch, G., McDowell, N. G., Rigling, A., Schaub, M., & Li, M.-H. (2018). Homeostatic levels of nonstructural carbohydrates after 13 yr of drought and irrigation in *Pinus sylvestris*. *New Phytologist*, 219(4), 1314-1324.
- Timofeeva, G., Treydte, K., Bugmann, H., Rigling, A., Schaub, M., Siegwolf, R., & Saurer, M. (2017). Long-term effects of drought on tree-ring growth and carbon isotope variability in Scots pine in a dry environment. *Tree Physiology*, 37(8), 1028-1041.
- von Arx, G., Arzac, A., Fonti, P., Frank, D., Zweifel, R., Rigling, A., Galiano, L., Gessler, A., & Olano, J. M. (2017). Responses of sapwood ray parenchyma and non-structural carbohydrates of *Pinus sylvestris* to drought and long-term irrigation. *Functional Ecology*, 31(7), 1371-1382.
- von Arx, G., Arzac, A., Olano, J. M., & Fonti, P. (2015). Assessing conifer ray parenchyma for ecological studies: Pitfalls and guidelines. *Frontiers in Plant Science*, 6, 1016.
- von Arx, G., & Carrer, M. (2014). ROXAS – A new tool to build centuries-long tracheid-lumen chronologies in conifers. *Dendrochronologia*, 32(3), 290-293.



Zweifel, R., Etzold, E., Sterck, F., Gessler, A., Anfodillo, T., Mencuccini, M., von Arx, G., Lazzarin, M., Haeni, M., Feichtinger, L., et al. (2020). Determinants of legacy effects in pine trees - implications from an irrigation-stop experiment. *New Phytologist*, 227, 1081-1096.