



DR ROMAN ZWEIFEL (Orcid ID : 0000-0001-9438-0582)

DR FRANK J STERCK (Orcid ID : 0000-0001-7559-6572)

PROF. ARTHUR GESSLER (Orcid ID : 0000-0002-1910-9589)

PROF. MAURIZIO MENCUCCINI (Orcid ID : 0000-0003-0840-1477)

MR SIMON KNÜSEL (Orcid ID : 0000-0001-9985-7650)

MR LORENZ WALTHERT (Orcid ID : 0000-0002-1790-8563)

DR YANN SALMON (Orcid ID : 0000-0003-4433-4021)

DR ARUN BOSE (Orcid ID : 0000-0001-8581-1651)

MS LEONIE SCHÖNBECK (Orcid ID : 0000-0001-9576-254X)

Article type : Regular Manuscript

Determinants of legacy effects in pine trees - implications from an irrigation-stop experiment

Roman Zweifel¹ (ORCID: 0000-0001-9438-0582), Sophia Etzold¹, Frank Sterck^{1,2}, Arthur Gessler^{1,3} (ORCID: 0000-0002-1910-9589), Tommaso Anfodillo⁴ (ORCID: 0000-0003-2750-9918), Maurizio Mencuccini^{5,6} (ORCID: 0000-0003-0840-1477), Georg von Arx¹ (ORCID: 0000-0002-8566-4599), Martina Lazzarin^{1,7}, Matthias Haeni¹, Linda Feichtinger¹ (ORCID: 0000-0001-9176-1056), Katrin Meusburger¹ (ORCID: 0000-0003-4623-6249), Simon Knuesel¹, Lorenz Walthert¹ (ORCID: 0000-0002-1790-8563), Yann Salmon^{8,9} (ORCID: 0000-0003-4433-4021),

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the [Version of Record](#). Please cite this article as [doi: 10.1111/NPH.16582](https://doi.org/10.1111/NPH.16582)

This article is protected by copyright. All rights reserved

Arun K. Bose^{1,10} (ORCID: 0000-0001-8581-1651), Leonie Schoenbeck¹, Christian Hug¹, Nicolas De Girardi¹, Arnaud Giuggiola¹, Marcus Schaub¹ (ORCID: 0000-0002-0158-8892), Andreas Rigling¹ (ORCID: 0000-0003-1944-4042)

¹ Swiss Federal Institute for Forest, Snow and Landscape Research WSL, 8903 Birmensdorf, Switzerland

² Forest Ecology and Management Group, Wageningen University, 6701 Wageningen, Netherlands

³ Institute of Terrestrial Ecosystems, ETH Zurich, 8092 Zurich, Switzerland

⁴ Dipartimento Territorio e Sistemi Agro-Forestali, University of Padova, 35020 Legnaro, Italy

⁵ ICREA, 08010 Barcelona, Spain

⁶ CREA, Universidad Autonoma de Barcelona, 08193 Barcelona, Spain

⁷ Horticulture and Product Physiology, 6701 Wageningen University, the Netherlands

⁸ Institute for Atmospheric and Earth System Research/Physics, University of Helsinki, 00100 Helsinki, Finland

⁹ Institute for Atmospheric and Earth System Research/Forest sciences, University of Helsinki, 00100 Helsinki, Finland

¹⁰ Forestry and Wood Technology Discipline, Khulna University, 9208 Khulna, Bangladesh

Correspondence to: Roman Zweifel, roman.zweifel@wsl.ch, +41 79 703 04 91

Received: 4 December 2019

Accepted: 24 March 2020

Word count total: 6427, Introduction: 1117, M&M: 1933, Results: 1100, Discussion: 2277, number of figures: 7, number of tables: 2, supplementary figures: 3, supplementary tables: 2, supplementary methods: 2

1 **Summary**

2 • Tree responses to altered water availability range from immediate (e.g., stomatal regulation) to
3 delayed (e.g., crown size adjustment). The interplay of the different response times and
4 processes, and their effects on long-term whole-tree performance, however, is hardly
5 understood.

6 • Here we investigated legacy effects on structures and functions of mature Scots pine in a dry
7 inner-Alpine Swiss valley after stopping an 11-year lasting irrigation treatment. Measured
8 ecophysiological time series were analyzed and interpreted with a system-analytic tree model.

9 • We found that the irrigation-stop led to a cascade of downregulations of physiological and
10 morphological processes with different response times. Biophysical processes responded
11 within days, whereas needle and shoot lengths, crown transparency, and radial stem growth
12 reached control levels after up to four years only. Modelling suggested that organ and carbon
13 reserve turnover rates play a key role for a tree's responsiveness to environmental changes.
14 Needle turnover rate was found to be most important to accurately model stem growth
15 dynamics.

16 • We conclude that leaf area and its adjustment time to new conditions is the main determinant
17 for radial stem growth of pine trees since the transpiring area needs to be supported by a
18 proportional amount of sapwood, despite the growth-inhibiting environmental conditions.

19 Key words: Cambial activity, drought stress, ecological memory, irrigation experiment,
20 osmoregulation, point dendrometer, radial stem growth, TreeNet

21 Introduction

22 Physiological responses of plants in general, and trees in particular, are often explained by current
23 environmental conditions in e.g., ecophysiological models (Steppe *et al.*, 2006; Zweifel *et al.*, 2007;
24 Medlyn *et al.*, 2011), wood formation studies (Drew *et al.*, 2010; Rathgeber *et al.*, 2016; Delpierre *et*
25 *al.*, 2019) or assessments of climate-vegetation dynamics (Liu *et al.*, 2018; Ma *et al.*, 2019). However,
26 a wide range of evidence documents the limitation of this common approach accounting for
27 concurrent environmental drivers only and, instead, strongly suggests to additionally consider past
28 conditions (Anderegg *et al.*, 2015; Ogle *et al.*, 2015; Jump *et al.*, 2017; Zweifel & Sterck, 2018;
29 Kannenberg *et al.*, 2019a). This effect is commonly described with the term 'legacy effect' (Huang *et*
30 *al.*, 2018; Peltier *et al.*, 2018) and is in this work used as a generic term encompassing various carry-
31 over or lagged effects (also called ecological memory effects). As a consequence, the stronger a legacy
32 effect is, the lower becomes the predictive power of current conditions for a physiological response
33 (Meinzer *et al.*, 2013; Jump *et al.*, 2017; Zweifel & Sterck, 2018). It is thus also a measure for the
34 degree of decoupling of plant responses from the concurrent environmental conditions (Kannenberg
35 *et al.*, 2019b; Kannenberg *et al.*, 2019c).

36 There is fast-growing statistical evidence for such legacy effects (Ogle *et al.*, 2015; Jiang *et al.*, 2019;
37 Peltier & Ogle, 2019). Annual stem growth of trees, as an example, is generally not optimally
38 explicable with current year conditions ($R^2 = 20\text{-}40\%$) and including past conditions has been shown
39 to result in greater fractions of explained variance (R^2 increased by 30% and more (Ogle *et al.*, 2015).
40 But the question remains, how do legacy effects take place at a mechanistic, physiological level? In
41 contrast to statistical evidences for the importance of legacy effects, little is known about the
42 potential mechanisms. Zweifel and Sterck (2018) recently proposed an approach considering the
43 turnover rates of organs and reserves as a way to link past conditions to the current plant response.
44 They employed a model showing that differences in turnover rates can theoretically explain different
45 levels of responsiveness to current conditions. Trees with generally longer turnover rates of leaves,
46 sapwood and carbon reserves (> 5 years) were found to be less responsive to a sudden change in the
47 environmental conditions than trees with shorter organ turnover rates of 1 or 2 years. It means that
48 the former type of trees is better able to buffer short-term negative environmental impacts. However,
49 it also means that it takes longer to recover from severe impacts, in terms of re-building structures of
50 the pre-disturbance level (Zweifel *et al.*, 2000; Weber *et al.*, 2007; Galiano *et al.*, 2011; Zweifel &
51 Sterck, 2018).

52 The turnover rate of an organ or a reserve is defined as the time in which the underlying structure
53 (e.g., the needles of the crown, or the carbon molecules of the carbon reserve) is on average replaced.

54 Consequently, the turnover rate of needles strongly affects the adjustment time of the total leaf area
55 to changed conditions. For the sapwood, as another example, the turnover rate translates into the
56 average number of years a tree-ring remains part of the sapwood before it is turned into heartwood.
57 Therefore, this individual tree-ring with its specific number and distribution of water conducting
58 elements and thus particular hydraulic properties, can affect the water conductance of a tree for a
59 longer or a shorter time period depending on its functional life-span. The value of such an organ and
60 reserve turnover approach lies in its intrinsic capacity to mechanistically link past conditions to a
61 current plant's response (Jump *et al.*, 2017; Zweifel & Sterck, 2018).

62 Here we test this idea of linking past and present environmental conditions to current physiological
63 and morphological responses via organ and reserve turnover rates with field data from mature Scots
64 pine trees which were experimentally irrigated since 2003 and cut off from the treatment after
65 eleven years at the end of 2013 (Dobbertin *et al.*, 2010; Schönbeck *et al.*, 2018; Brunner *et al.*, 2019).
66 The setup of the Pfywald irrigation experiment allows comparing control trees that were never
67 irrigated with trees that received continued irrigation treatment until present, with trees for which
68 irrigation was recently stopped (Bose *et al.*, 2020).

69 Scots pines in this dry inner-Alpine valley (Valais) have been reported to suffer from increased
70 mortality during the past decades (Zweifel *et al.*, 2009; Rigling *et al.*, 2013; Etzold *et al.*, 2019), a
71 phenomenon caused by longer and more frequent dry periods (Bigler *et al.*, 2006; Szejner *et al.*,
72 2019). The irrigation treatment in the Pfywald experiment added about 500-600 mm water per
73 year. This doubling of the natural precipitation increased stem radial growth, leaf area, needle and
74 shoot lengths, whereas crown transparency decreased (Dobbertin *et al.*, 2010; Eilmann *et al.*, 2013;
75 Schönbeck *et al.*, 2018). Further, the irrigated trees adjusted their root production to the irrigation in
76 terms of a significantly increased fine-root biomass (Brunner *et al.*, 2009; Herzog *et al.*, 2014;
77 Brunner *et al.*, 2019). Over the 11 years of irrigation, these trees thus developed new (overbuilt)
78 structures and adjusted their carbon reserves to the growth increase (Schönbeck *et al.*, 2018).

79 We propose three alternative response types of the trees growing in the irrigation-stop plots (Fig. 1)
80 in order to discuss timing and strength of legacy effects in different organs and the interplay among
81 them at a whole-tree level. i) In the first type, the physiological and morphological variables (i.e., sap
82 flow, tree water deficit, stem growth, needle and shoot length, and crown transparency) return to the
83 respective levels of the control trees in the first year after the irrigation stop. This type of response is
84 not affected by past conditions (at least not to the extent as compared to the control) and is called
85 here a type of response with 'no legacy effect'. ii) In the second type, the different variables are
86 maintained above the level of the control for several years before returning to it. This response type

87 is called a 'positive legacy effect' because past conditions induce a positive physiological or
88 morphological response temporarily remaining above the level of the control. We hypothesize that
89 such trees may benefit from reserves accumulated during the irrigated years. Finally, in the third
90 type (iii), the physiological responses drop below the control level before returning to it. This
91 response is called 'negative legacy effect' since the past conditions alter the tree's response in a
92 negative way by shifting the process (temporarily) below the control level. This case reflects the idea
93 that the 'overbuilt irrigated trees' are less well adjusted to the reduction in soil water after the
94 irrigation-stop than control trees and therefore perform worse.

95

96

97 **Material and Methods**

98 **Site**

99 The long-term irrigation experiment is located in a Scots pine forest (*Pinus sylvestris* L.) at the
100 northwest-exposed slope close to the bottom of the Swiss Rhone valley in the driest part of the
101 Valais, (46° 18' N, 7° 36' E, 615 m a.s.l.) and close to the dry edge of distribution of Scots pine. Mean
102 annual temperature was 9.2°C and mean annual precipitation 518 mm (1971–1990, Fig. S1) (Wehren
103 *et al.*, 2010).

104 The forest is described as *Erico Pinetum sylvestris* with a mean tree height of 10.8 m, a stand density
105 of 730 stems ha⁻¹, and a basal area of 27.3 m² ha⁻¹ (Dobbertin *et al.*, 2010). A description of trees
106 equipped with dendrometer and sap flow sensors can be found in Table S1. For the irrigated plots,
107 precipitation has been approximately doubled since 2003 (additional 500-600 mm/year) by adding
108 water from a nearby channel during night of the growing season (April-October) using sprinklers of 1
109 m height (Herzog *et al.*, 2014; Bose *et al.*, 2020). End of 2013, the irrigation was stopped in the upper
110 third of each irrigated plot. The soil is a shallow Regosol characterized by low water retention
111 capacity. All plots had the same exposition.

112 **General setup**

113 We measured microclimatic variables in air and soil (data resolution: 10 min), physiological
114 variables (10 min) and crown morphological variables (annual) on trees in the different subplots: (i)
115 control plots which never were irrigated (control), (ii) treated plots with irrigation until the end of
116 2013 (irrigation-stop), and (iii) irrigated plots until the end of 2017 (irrigation).

117 Additionally, we applied a system-analytical tree model (Zweifel & Sterck, 2018) that bridges the
118 influence of past conditions to the present physiological response on an annual level (Fig. 2). The
119 model quantifies legacy effects on the organ and reserve status of a tree with the help of turnover
120 rates of leaves, sapwood and carbon reserves. Those response variables which were measured and
121 modelled (radial stem growth, needle and shoot length) were compared in order to quantify the
122 explanatory power of the 'turnover approach' to catch different patterns of legacy effects (Fig. 1).

123 **Environmental measurements**

124 Meteorological measurements were recorded 2 m above the canopy on top of a scaffold, about 13 m
125 above ground. Air temperature (Sensirion, Stäfa, Switzerland), relative humidity (Sensirion, Stäfa
126 Switzerland) and precipitation (Young tipping bucket 52203, Michigan, USA) were continuously
127 recorded at a 10 min interval. Data obtained in nearby meteorological stations of MeteoSwiss
128 (www.meteoswiss.admin.ch) were employed to fill gaps and to correct obvious instrumental errors
129 by applying filters and using simple regressions.

130 Soil water content was measured with TDRs (Tektronix 1502B cable tester) at soil depths of 10, 40
131 and 60 cm from 2002 to 2013. In spring 2014, the soil water measurement equipment was partially
132 replaced and relocated. Since 2014, 10 HS-Sensors (Decagon Devices, USA) were installed in all
133 treatments and recorded soil water content at 10 and 80 cm soil depth. Soil water content data were
134 gap-filled and homogenized for the period from 2011 to 2017 with the help of overlapping periods of
135 different soil measurement methods and devices. The logging devices used were from DecentLab
136 (DecentLab GmbH, Dübendorf Switzerland) and Campbell (CR1000, Logan, USA).

137 **Physiological measurements**

138 Stem radius (SR) changes were measured with point dendrometers at breast height (ZN11-T-WP,
139 Natkon, Oetwil am See, Switzerland) on nine trees (three trees per treatment) consisting of a T-
140 shaped carbon fibre frame anchored in the stem with three stainless steel rods and a potentiometer.
141 The dendrometers, including cables and loggers, have a low temperature sensitivity of $< 0.3 \mu\text{m per}$
142 $^{\circ}\text{C}$ and SR data were not further corrected for temperature sensitivity. Further, tree water deficit-
143 induced reversible stem shrinkage and swelling (TWD) and growth-induced irreversible increment
144 (GRO) were calculated with the R package TreenetProc (Haeni *et al.*, 2020), according to the
145 approach of Zweifel *et al.* (2016) assuming no cell growth during periods of stem shrinkage.

146 Stem sap flow was measured simultaneously with Granier-type sensors (UMS/UP, Germany) on the
147 same trees where the dendrometers were mounted. The two needles of the sensors were drilled 5 cm
148 into the sapwood and insulated from direct sunlight. Data resolution was 10 min. Sapwood depth

149 was found to range between 23 and 107 mm in a sampling of 20 irrigated and 20 control trees in
150 2013 (other trees than the ones equipped with sap flow sensors). The mean sap wood width for
151 control and irrigated trees was 47 and 51 mm, respectively (Fig S2), found to be not significantly
152 different (t-test, $p > 0.05$). Sap flow was calculated from individual stem diameters and an average
153 sapwood depth of 5 cm (370-425 cm²).

154 Sensors were powered and logged by devices establishing a local mesh network around a central
155 base station with data transmission to the related online database (DecentLab GmbH, Dübendorf,
156 Switzerland).

157 **Crown morphology measurements**

158 Needle and shoot lengths were measured from 36 trees (10 control, 12 irrigated, 14 irrigation-stop).
159 Three branches from each of these trees were selected from the top and the middle parts of the
160 crown, resulting in 116 sampled branches. Shoot lengths on every branch were measured for the
161 years 2011 to 2017 and averaged for the three treatments. Needle length of each shoot was
162 determined by measuring five randomly selected needles close to the center of the shoot.

163 Annual crown transparency was assessed by a visual rating in 5% steps of all (about 800) trees of the
164 experimental area using reference photographs ranging from 0% (a fully foliated tree) to 100% (a
165 dead tree) as described by Dobbertin et al. (2005). The tree crown foliage is judged relative to the
166 optimum foliage of an average tree of the same size and species. The average crown transparency of
167 all trees within the different treatments (control, irrigation-stop, and irrigation) was used as a proxy
168 for the development of the total leaf area. System-analytical tree model

169 The model applied (Zweifel & Sterck, 2018) is based on physiological key processes such as crown
170 growth, radial stem growth and carbon reserve growth (Fig. 2). The key processes described as linear
171 functions (with weighting factors, Methods S1) are driven by environmental conditions (linearly
172 coupled to tree water relations), and the status of crown, buds, carbon reserves and sapwood of the
173 past year. We refer to this approach as a system-analytic model (Vester, 2007) in which absolute
174 mass or energy balances are not quantified, but the individual responses of system components are
175 quantified relative to each other and relative to a 'normal' response (value = zero). This approach is
176 particularly valuable to assess a system responsiveness, respectively the legacy effects of system
177 parts (organs), in our case a tree.

178 The simulation in annual steps starts with the status of buds, crown, carbon reserve, and sapwood
179 which are the result of the past environmental conditions and the related processes over time. The
180 initial status needs to be set before the first iteration. The length of time considered to affect the

181 status of organs and reserves is defined by the turnover rates determining over how many years the
182 respective structure is built and renewed, respectively. The model quantifies the current-year
183 environmental impact on all the processes involved and calculates the new status of the organs and
184 reserves at the end of the year according to the network of functions (Fig. 2, Methods S1).

185 The model input is an annual environmental index calculated from water supply (precipitation plus
186 irrigation), soil water content, air temperature, and radiation (Methods S2).

187 The model consists of linear functions with weighting factors (Methods S1) for which the input-,
188 operating- and output-ranges are limited to index values ranging from -1 (very poor status), over 0
189 (average) to +1 (very good/improved status). This way, annual changes of environmental conditions
190 (also expressed in values between -1 and +1) alter the status of structures (crown, bud, sapwood)
191 and reserves (carbon reserve) according to the linear functions, their weighting factors and their
192 turnover rates. Status values are thus always relative to an average value of zero. Values above zero
193 always mean a status or a response above the average, a value below zero a status or response below
194 the average.

195 The weighting factors (WF) for the linear functions between the status and the processes of the
196 model were parameterized (Table S2) for the control trees (never irrigated, control), for the irrigated
197 trees (irrigated), and for the trees treated with irrigation until the end of 2013 and for which
198 irrigation was removed afterwards (irrigation-stop).

199 The model was run for two scenarios for all three treatments (control irrigation, irrigation-stop) with
200 the respective parameter sets. Scenario I mimics a tree with no ecological memory in which the
201 model parameters 'turnover rate of needles', 'turnover rate of sapwood', and 'turnover rate of carbon
202 reserves' were set to 1 year (abbreviation 'NoMemo'). Scenario II (abbreviation 'Memo') mimics a
203 tree with more realistic turnover rates of needles (5 years), sapwood (50) and carbon reserves (10)
204 based on empirical findings. The number of Scots pine needle cohorts at Pfywald was measured to
205 be between three and five (data not shown). The average sapwood turnover rate was found to be
206 between 45 and 55 years (Fig. S2). Most uncertain was the estimation of the turnover rate of the
207 carbon reserve (Gessler & Treydte, 2016). The metabolically active carbon reserve was reported to
208 be 1-2 years old (Gaudinski *et al.*, 2009), whereas the average age of all stem carbon reserves was
209 found to be 10 years (Carbone *et al.*, 2013). (Richardson *et al.*, 2015) explained this finding by the
210 presence of two storage pools – a fast-turning and a slow-turning one. They assumed that the slow
211 pool, however, was large enough that it cannot be ignored as a store of reserves and that it is over
212 simplistic to assume a single pool that turns over quickly. As a consequence, we set the average
213 turnover rate of the carbon pool to 10 years.

214 **Statistical methods**

215 Stem radius data were aligned, cleaned and gap-filled for gaps < 120 min with the R-based (Team,
216 2019) package *treenetproc* (Haeni *et al.*, 2020). Data gaps equal or longer than 120 min remained in
217 the data set as NA.

218 The weighting factors (WF) of the system-analytic model were calculated in an optimization process
219 with Excel's function Solver, maximizing the determination coefficients for annual stem growth
220 (GRO), needle (NL) and shoot length (SL) between consecutive years. These three variables were
221 measured in the field as well as explicitly modelled and thus qualified to be used for the optimization
222 process. Parameterization was run in three steps grouping WF according to their direct effect onto
223 NL, SL, and GRO. In the first step the two WF directly affecting NL were parameterized by optimizing
224 the determination coefficients between measured and modelled NL. In the second and third step, the
225 same was performed with SL (2 WF) and GRO (11 WF).

226 The sensitivity of the model output to changes in the (set) turnover rates of needles, sapwood and
227 carbon reserves was tested with a stepwise variation of each of the three turnover rates (Fig. S3). The
228 average change in the output for annual stem growth was used as an indication for the model
229 sensitivity to changes in the turnover rates. The turnover rate of carbon reserves had the lowest
230 impact (weight 1) on model output, followed by sapwood turnover (2.3), and needle turnover had by
231 far the highest impact on model output (2180) (Table S3).

232 The explanatory power of the simulations was quantified with the determination coefficient of linear
233 regressions between measured and modelled means and standard errors of means per treatment.

234

235

236 **Results**

237 **Soil water content**

238 The irrigation treatment starting in 2003 considerably increased the soil water content of the treated
239 plots (Fig. 3). However, with the stop of the irrigation in 2013, the level of soil water content (orange
240 line) dropped to the same level as the control plot (red line) or even slightly below already in 2014.
241 Generally, the water content of the soil with its low water holding capacity responded quickly to
242 changes in the treatment, which became visible during periods of irrigation outages and during
243 wintertime when the irrigation was stopped.

244 **Tree water deficit**

245 The irrigation-stop trees had a significantly lower tree water deficit TWD than the control trees
246 during the irrigation period until the end of 2013 (Fig. 4). After switching off irrigation, the average
247 annual TWD of the irrigation-stop trees generally increased, however, not linearly over the entire
248 season. TWD remained reduced from March to July 2014-2016 (Fig. 4) before returning to the TWD
249 level of the control trees during the later summer months. This intra-seasonal pattern disappeared in
250 the fourth year (2017) after the irrigation-stop.

251 **Sap flow data**

252 Prior to stopping the irrigation treatment, sap flow rate of the irrigation-stop trees was strongly
253 increased during the summer months. During this time, sap flow reached values up to the double the
254 rates of the control trees, however with a wide variation among individual trees (Fig. 5). During
255 winter-time, when the irrigation was stopped, both treatments behaved in a similar way. After the
256 irrigation was stopped at the end of 2013, sap flow rates generally dropped significantly below the
257 rates of the control trees during the summer months but remained increased in spring when soil
258 water availability was generally higher than in summer (Fig. 3). This pattern persisted over the
259 entire measurement period until 2017. Interestingly, the short response time to reduced soil water
260 availability became also visible during short-term failures of the irrigation system (e.g., in
261 July/August 2011, Fig. 5): As soon as the irrigation was stopped, the sap flow of the treated trees
262 started to decrease and went markedly below the sap flow level of the control trees after about 1-2
263 weeks without irrigation. On a mean annual scale, sap flow remained downregulated below the level
264 of the control trees for all four years measured after stopping the irrigation.

265 **Radial stem growth (GRO)**

266 Radial stem growth (GRO) – deduced from SR measurement including irreversible bark and wood
267 growth – was markedly increased in the irrigated compared to the control trees (Fig. 6). On average,
268 the irrigated trees grew two to three times faster and started growth earlier than the control trees,
269 however, with considerable individual differences. GRO decreased gradually after the irrigation-stop
270 but remained significantly above the growth rate of the control trees for three more years. In the
271 fourth year after the irrigation was stopped (2017), the difference in GRO disappeared between the
272 two treatments. An interesting detail is the often occurring GRO increase towards the end of the year
273 which goes in parallel with the general soil rehydration at this time of the year (Fig. 3).

274 **Crown morphological measurements**

275 Needle length (NL) of the new cohort responded in the first year after the irrigation was stopped
276 with a marked decrease (Fig. 7b). The needles grew even shorter than the ones of the control trees
277 and kept this trend in the following years (Fig. 7b). Shoot length (SL) remained high in the first year
278 after stopping irrigation and strongly responded in the second year after the irrigation-stop (Fig. 7c).
279 SL remained markedly below the control in the following years.
280 Crown transparency (Fig. 7d) and GRO (Figs. 6, 7e) showed the most distinct delays in their
281 response. In both cases, the irrigation-stop trees needed three to four years to reach the same values
282 as the control trees.

283 **Simulated tree responses**

284 The simulations were run for all treatments (control, irrigation-stop, and irrigation) using the two
285 alternative scenarios (Memo and NoMemo). The NoMemo scenario with a model parameterization
286 not allowing for legacy effects (Table S2) was not able to accurately simulate the measurements of
287 the irrigation-stop trees and led to a consistently lower explanatory power of the response variables
288 shoot length and stem growth than the Memo scenario (Tab. 1). The only exception was with needle
289 length which was insensitive to the turnover rates of needles, sapwood and carbon reserves and
290 showed the same simulation output for both scenarios (Fig. 7, Tab. 1, Fig. S3, Tab. S3).

291 In contrast, the Memo scenario with the more realistic turnover rates of needles (5 years), sapwood
292 (50) and carbon reserves (10) was able to predict the measured annual courses of radial stem
293 growth and shoot lengths significantly better for all treatments (control, irrigation-stop, and
294 irrigation). The increased explanatory power of the Memo scenario compared to the NoMemo
295 scenario ranged between 13.8 and 52%, depending on the variable (Tab. 1).

296 Contrary to the above described measurement-model relationships, the relationship between the
297 environmental index ENV and the modelled radial stem growth (GRO) was stronger in the NoMemo
298 scenario than in the Memo one (Tab. 1) showing that increasing the memory effect (by increasing the
299 turnover rates) is reducing the responsiveness of GRO to current environmental conditions.

300 **Chronology of responses and the respective legacy effects**

301 The irrigation-stop treatment led to a reduction of the soil water content to a level comparable with -
302 or even slightly lower than - the control plots (Fig. 4), and a cascade of tree physiological and
303 morphological responses started (Figs. 5-7). On an annual timescale, needle length, sap flow, and tree
304 water deficit responded already in the first year (Tab. 2). Shoot length responded strongly in the
305 second year, while radial stem growth and crown transparency did not respond abruptly but
306 gradually, needing about four years to reach the level of the trees in the control plots (Fig. 7, Tab. 2).

307 There appeared positive and negative legacy effects as shown in Fig. 1. Radial stem growth and
308 crown transparency showed a distinct positive legacy effect (annual growth remaining above the
309 control, crown transparency remaining below the control, Figs. 6 and 7), whereas the immediate
310 biophysical responses related to tree water relations, i.e., sap flow (Fig. 5), tree water deficit (Fig. 4)
311 and also needle length (Fig. 7), responded negatively (on a mean annual scale, Tab. 2) but with
312 distinct intra-annual deviations from the annual patterns (Figs. 4-5). Shoot length responded with a
313 positive legacy effect in the first year after the irrigation-stop (shoot length growth remained larger)
314 and only negatively thereafter (shoots grew shorter than the control), i.e., shoot length responded
315 with a negative legacy effect with a one-year delay.

316

317 **Discussion**

318 **How to live with an overbuilt tree structure when soil water gets short?**

319 The investigated pine trees grew larger and denser crowns during the 11 years of irrigation
320 compared to the control trees (Dobbertin *et al.*, 2010) and the functional structures such as sapwood
321 (Schönbeck *et al.*, 2018) and roots (Brunner *et al.*, 2019) became adjusted to support this enlarged
322 crown (Enquist & Niklas, 2002; Choat *et al.*, 2012). This response demonstrates the effect of water-
323 limited conditions on tree growth on the one hand, and the general tree response to a release from
324 limiting conditions on the other hand, already documented several times also in other studies from
325 this area (Feichtinger *et al.*, 2014; Herzog *et al.*, 2014; Feichtinger *et al.*, 2015; Grossiord *et al.*, 2018).
326 The novel aspect here is how trees with an overbuilt structure deal with a water shortage after 11
327 well-watered years. Are they able to benefit from potentially accumulated reserves or do they rather
328 suffer from mal-adjusted structures? In the following, we discuss why both responses were found
329 (positive and negative legacy effects, Figs. 1 and 7), depending on the organ or reserve that is
330 considered (Tab. 2). With the help of the system-analytical tree model, we further discuss why the
331 turnover rates of organs and reserves are able to explain, at least partially, the different legacy effects
332 (Fig. 7). Finally, we speculate what processes could explain the measured fact that irrigation-stop
333 trees grow better than the control trees despite the reduced soil water availability.

334 **Tree water relations – mostly negative legacy effects**

335 The first response of a tree to the sudden reduction of water is of a biophysical nature. Drought-
336 stressed trees close their stomata and thus save water (Hetherington & Woodward, 2003; Zweifel *et al.*,
337 *et al.*, 2012). The general reduction of the annual sap flow of the treated trees after the irrigation-stop

338 (Fig. 5) was thus most likely a consequence of the stomatal behavior of an oversized transpiring area,
339 suffering from a reduced water supply. On an annual timescale, the response of sap flow and tree
340 water deficit resembles a negative legacy effect (Fig. 1, Tab. 2), i.e., the downregulation of tree water
341 relations is even stronger than the one observed for the control trees which grew under a continuous
342 lack of water. However, there remained an important difference to this general annual pattern:
343 during spring and early summer, sap flow remained higher (Fig. 5) and tree water deficit remained
344 lower (Fig. 4) than in the control trees. We hypothesize that the enlarged root biomass in the
345 uppermost soil layer (Brunner *et al.*, 2019) might have led to an increased soil water uptake during
346 the time when the general soil water availability was still high in this first phase of radial stem
347 growth (Fig. 6). As a consequence, the soil dried out even faster than in the control plots (Fig. 3) and
348 sap flow dropped in the second half of the summer below the rates of the control trees (Fig. 5). Less
349 likely but not excluded is the possibility that deep roots tapped water in soil layers not covered by
350 the soil water sensors. However, if this was the case, we expected a persistent positive effect on the
351 sap flow, what was not measured.

352 **Needle and shoot lengths - negative legacy effects (with delay)**

353 New built needles responded with an immediate length reduction in the year after the irrigation was
354 stopped (negative legacy effect, i.e., needles grew shorter than the control), whereas the shoots
355 responded one year later (Fig. 7, Tab. 2, negative legacy effect with one year delay), a phenomenon
356 that has been reported for pine trees before (Dobbertin *et al.*, 2010; Feichtinger *et al.*, 2015). As an
357 explanation for the needle length reduction with drought, it has been proposed that the general
358 decrease in leaf water potentials also reduces turgor pressure in the crown and thus, turgor pressure
359 becomes limiting for needle growth (Myers, 1988; Giuggiola *et al.*, 2018; Guerin *et al.*, 2018). This
360 lowered water potential was obviously not affecting the shoot growth at the same time (Tab. 2). The
361 reason for that is not fully understood since both shoots and needles are pre-determined in the buds
362 built in the previous year (Chen *et al.*, 1996) and exposed to the same environmental conditions.
363 However, the different responses of needles and shoots may be related to their tissue-specific
364 exposures to the low water potentials or eventually with tissue-specific osmoregulation processes
365 (Lazzarin *et al.*, 2019), as hypothesized also for radial stem growth (Coussement *et al.*, 2018). The
366 model applied with the 'Memo' parameterization (Fig. 7) - inducing a strong dependency of the shoot
367 growth on conditions of the past year and thus reducing the dependency from current environmental
368 conditions - was able to simulate the legacy effect with a one-year delay. However, when cutting the
369 functional link to the past year(s) - by setting the turnover rates of needles, sapwood and carbon
370 reserves to 1 year - the model was no longer able to simulate the measured shoot lengths accurately

371 (Fig. 7, Tab. 1) and thus showing the importance of accounting for the turnover rates of organs and
372 carbon reserve in the model to explain the trees' lagged response to current conditions.

373 **Radial stem growth and total leaf area - positive legacy effects**

374 After stopping irrigation, annual stem growth and total leaf area (as indicated by measured crown
375 transparency data) clearly remained above the level of the control trees for three more years before
376 matching the control level (Fig. 7). This is assigned to a positive legacy effect (Fig. 1) and indicates
377 that this high growth rate cannot be explained by current environmental conditions alone but is
378 positively influenced by the past more favorable conditions. The 'Memo' model balanced the status of
379 the accumulated carbon reserves and particularly the enlarged total leaf area – two positive effects –
380 against the direct impact of the environment (negative effect) on radial stem growth (Tab. S2). The
381 simulation results support this statement by demonstrating that the 'Memo' model (Tab. S2) is able
382 to simulate the observed growth pattern always better than the 'NoMemo' can (Fig. 7, Tab. 1).

383 **Turnover rates of organs and reserves determine legacy effects**

384 The turnover rate of needles of the pine trees was measured to be 3-5 years at our site,
385 corresponding with the legacy effect in crown transparency and radial stem growth which lasted
386 about four years. The 'Memo' parameterization of the model assumed a turnover rate for the needles
387 of 5 years (which indicates that only about 20% of the total leaf area is replaced every year) and this
388 model parameter (Tab. S2) was found to be crucial to be able to track the observed annual stem
389 growth dynamics.

390 Interestingly, a sensitivity analysis of the 'Memo' model gave the highest correlation between model
391 output and measured radial stem growth data when a needle turnover rate of three years was used
392 (Fig. S3). This implies that the initially set needle turnover rate of 5 years could be adjusted to 3 years
393 in order to further increase the goodness-of-fit. Furthermore, the turnover rates of sapwood and
394 carbon reserves contributed to the modelling quality, however with much lower weights (Tab. S3).

395 According to our crown transparency measurements (Fig. 7), the irrigation-stop pines took about
396 four years to adjust their leaf area to the new conditions. Further, the simulation of the crown status
397 (proxy for total leaf area) indicated that the adjustment time might even be longer, since crown
398 status remained still increased after four years (of modelling) (Fig. 7). Additionally, the lag of four
399 years matched exactly the time during which measured radial stem growth rates appeared to be
400 increased in relation to the expected values from the control trees, and it was also about the duration
401 in which the needle biomass was totally renewed (needle lifetime was measured to be between 3 and

402 5 years). An argumentation that sets these facts into a causal relationship as done in our model,
403 intrinsically implies a partial decoupling of growth from current environmental conditions as clearly
404 supported by our results (Tab. 1).

405 **Leaf area determines radial stem growth**

406 'The resources grow the leaves and the leaves grow the tree' is an old saying of some foresters which
407 gets reappraised with this study. The rapid response of the needle growth to the current conditions
408 fits the first part of the statement, whereas the delayed stem growth response supports the second
409 part. Physiologically, we argue that the enlarged leaf area of the irrigation-stop trees demands an
410 adequate water supply system which can support the high potential transpiration (Anfodillo *et al.*,
411 2016). In other words, the sapwood area (particularly the annual sapwood increment) is needed to
412 support the potential evaporative demand of the crown. This balanced relationship between leaves
413 and their amount of xylem (Martinez-Vilalta *et al.*, 2009) requires a corresponding amount of xylem
414 at the stem level, also well-known as pipe model theory, which basically assumes a distinct number
415 of xylem conduits per leaf area (Shinozaki *et al.*, 1964; Mencuccini & Grace, 1996; Sterck & Zweifel,
416 2016). As a consequence, we assume a direct physiological causality between leaf area and wood
417 growth (Zweifel *et al.*, 2006; Fatichi *et al.*, 2014; Zweifel & Sterck, 2018), which can lead to an
418 increased radial stem growth despite drought. However, what mechanism is able to explain that?

419 **Radial stem growth despite drought stress – towards an explanation**

420 We propose two speculative explanations for the increased radial stem growth rates despite the
421 drought stress conditions in the irrigation-stop treatment: i) the enlarged root biomass (Herzog *et al.*,
422 2014; Brunner *et al.*, 2019) improved the water uptake capacity, and ii) osmoregulation actively
423 increased turgor pressure in the cambium in order to reach the threshold for cell growth (Hsiao & Xu,
424 2000; Coussement *et al.*, 2018). The first point (i) is discussed in the second paragraph of the
425 discussion and could explain the more efficient water uptake with higher sap flow rates and lower
426 tree water deficits allowing these trees to keep cellular turgor pressure high enough to allow for cell
427 division and cell enlargement (Lockhart, 1965; Petit *et al.*, 2011; Ortega *et al.*, 2012).

428 ii) A second effect we speculate about here is related to cellular osmoregulation in the bark including
429 the cambium (e.g., O'Brien *et al.*, 2014; Lintunen *et al.*, 2016) implying an active investment in
430 growth during drought. Turgor pressure in living tissues is not only determined by physical
431 conditions i.e., the dryness of air and soil, but is also affected by active biological processes, such as
432 the increase of the osmotic potential in cells by sugar loading (Badalotti *et al.*, 2000; De Schepper &

433 Steppe, 2010; De Schepper & Steppe, 2011; Barraclough *et al.*, 2018; Barraclough, A.D. *et al.*, 2019;
434 Barraclough, A. D. *et al.*, 2019; Lazzarin *et al.*, 2019; Michelot-Antalik *et al.*, 2019). We speculate that
435 the irrigation-stop trees avoided the low turgor pressure in the cambium with the mobilization of
436 osmotically active compounds. Recent work at the same research site showed, indeed, that such
437 active osmoregulation might take place in pine trees (Mencuccini *et al.*, 2017; Lazzarin *et al.*, 2019).
438 However, it was not particularly measured for the irrigation-stop trees and the osmoregulation effect
439 was mainly measured in the branches and not in the stem (Lazzarin *et al.*, 2019).

440 Proposing an osmoregulation mechanism also raises the question whether these additional
441 resources for keeping high growth rates are available and for how long they could last. There is
442 evidence that the irrigated trees had more reserves available than the control trees. A recent study of
443 pine trees at the same site showed an overall increase of non-structural carbohydrates (NSC) in the
444 stems of irrigated trees (von Arx *et al.*, 2017) and Schönbeck *et al.* (2018) found stem growth and
445 NSC being positively related to total leaf area, which was larger for the irrigated trees compared to
446 the control. We hypothesize that the irrigation-stop trees relied on the additional carbon reserves
447 and kept the reduction of available energy for extra growth under drought conditions in balance with
448 the rate of reduction of the leaf area. As long as a tree is able to keep its radial stem growth high with
449 an extra investment of energy to support the large crown, it may be able to reduce its crown size
450 slowly. Obviously, no reserve is infinite and becomes exhausted somewhen. At this time, the tree's
451 leaf area should be reduced to a size that is in balance with the new dry conditions.

452 **Conclusions**

453 The sudden reduction in soil water availability after the irrigation-stop did not lead to a rapid
454 decrease in radial stem growth of pine trees, as we expected. Instead, radial stem growth was found
455 to be in line with a slow reduction of the leaf area, taking four years of time to reach the level of the
456 never irrigated control trees. From a functional point of view, we conclude that leaf area imposes
457 radial stem growth in order to keep the balance between transpiring surface and supporting
458 sapwood.

459 The modelling results suggest turnover rates of organs and carbon reserve as important
460 determinants of legacy effects on trees. Particularly, crown size and stem growth seem to be strongly
461 determined by past conditions and processes due to the needle lifetime of about four years, affecting
462 the direct growth response to current environmental conditions. In other words, we showed that the
463 biological pre-disposition of a pine tree is able to strongly decouple growth from current
464 environmental conditions. Further we propose that an osmoregulation mechanism may help to

465 explain the increased radial stem growth despite the suddenly reduced availability of soil water.
466 Future work is called to particularly focus on the species-specific aspects of these findings.

467

468 **Author contributions**

469 Roman Zweifel¹ (idea, paper concept, data acquisition, data analyses, modelling, interpretation of
470 results, writing)

471 Sophia Etzold¹ (data analyses, interpretation of results, writing)

472 Frank Sterck^{1,2} (modelling, interpretation of results, writing)

473 Arthur Gessler^{1,3} (interpretation of results, writing)

474 Tommaso Anfodillo⁴ (interpretation of results, writing)

475 Maurizio Mencuccini^{5,6} (interpretation of results, writing)

476 Georg von Arx¹ (data acquisition, interpretation of results, writing)

477 Martina Lazzarin^{1,7} (data acquisition, interpretation of results, writing)

478 Matthias Haeni¹ (data acquisition, data analyses, interpretation of results, writing)

479 Linda Feichtinger¹ (data acquisition, data analyses, interpretation of results, writing)

480 Katrin Meusburger¹ (data acquisition, data analyses, interpretation of results, writing)

481 Simon Knuesel¹ (data analyses, interpretation of results, writing)

482 Lorenz Walthert¹ (interpretation of results, writing)

483 Yann Salmon^{8,9} (interpretation of results, writing)

484 Arun K. Bose¹ (interpretation of results, writing)

485 Leonie Schoenbeck¹ (interpretation of results, writing)

486 Christian Hug¹ (data acquisition, interpretation of results, writing)

487 Nicolas De Girardi¹ (data acquisition, interpretation of results, writing)

488 Arnaud Giuggiola¹ (data acquisition, interpretation of results, writing)

489 Marcus Schaub¹ (fund rising infrastructure, interpretation of results, writing)

490 Andreas Rigling¹ (idea research infrastructure, research coordination, fund rising infrastructure,
491 interpretation of results, writing)

492

493 **Acknowledgments**

494 We thank the forestry services of the Pfynwald and the Wasserwerk Chippis for providing the land
495 for the research site and part of the infrastructure. We particularly thank Konrad Egger (Forest
496 Region Leuk) for his continuous technical support. We acknowledge the involved networks TreeNet,
497 Swiss Long-term Forest Ecosystem Research Programme LWF, MeteoSwiss, the Integrated Carbon
498 Observation System ICOS, and Swiss ForestLab for data and technical support. Further we
499 acknowledge the financial support by the Federal Office for the Environment FOEN, (00.0365.PZ I
500 0427-0562, 09.0064.PJ/R301-0223), the Swiss National Science Foundation SNF (20FI21_148992,
501 20FI_173691), the Natural Environment Research Council NERC (#NE/I011749/11), and the
502 Academy of Finland (#1312571, #323843).

503

504 **References**

- 505 **Anderegg WRL, Schwalm C, Biondi F, Camarero JJ, Koch G, Litvak M, Ogle K, Shaw JD,**
506 **Shevliakova E, Williams AP, et al. 2015.** Pervasive drought legacies in forest ecosystems and
507 their implications for carbon cycle models. *Science* **349**(6247): 528-532.
- 508 **Anfodillo T, Petit G, Sterck F, Lechthaler S, Olson ME. 2016.** Allometric trajectories and stress: a
509 quantitative approach. *Frontiers in Plant Science* **7**(1681): 1-6.
- 510 **Badalotti A, Anfodillo T, Grace J. 2000.** Evidence of osmoregulation in *Larix decidua* at Alpine treeline
511 and comparative responses to water availability of two co-occurring evergreen species. *Annals of*
512 *Forest Science* **57**(7): 623-633.
- 513 **Barracough AD, Cusens J, Zweifel R, Leuzinger S. 2019.** Environmental drivers of stem radius change
514 and heterogeneity of stem radial water storage in the mangrove *Avicennia marina* (Forssk.) Vierh.
515 *Agricultural and Forest Meteorology* **280**: 1-12.
- 516 **Barracough AD, Zweifel R, Cusens J, Leuzinger S. 2018.** Daytime stem swelling and seasonal reversal
517 in the peristaltic depletion of stored water along the stem of *Avicennia marina* (Forssk.) Vierh. *Tree*
518 *Physiology* **38**(7): 965-978.
- 519 **Barracough AD, Zweifel R, Cusens J, Leuzinger S. 2019.** Disentangling the net: concomitant xylem and
520 over-bark size measurements reveal the phloem-generated turgor signal behind daytime stem
521 swelling in the mangrove *Avicennia marina*. *Functional Plant Biology* **46**(5): 393-406.
- 522 **Bigler C, Braeker OU, Bugmann H, Dobbertin M, Rigling A. 2006.** Drought as inciting mortality factor
523 in Scots pine stands of the Valais, Switzerland. *Ecosystems* **9**: 330-343.
- 524 **Bose AK, Moser B, Rigling A, Lehmann MM, Milcu A, Peter M, Rellstab C, Wohlgenuth T, Gessler**
525 **A. 2020.** Memory of environmental conditions across generations affects the acclimation potential
526 of scots pine. *Plant, Cell and Environment* <https://doi.org/10.1111/pce.13729>: 1-12.
- 527 **Brunner I, Herzog C, Galiano L, Gessler A. 2019.** Plasticity of fine-root traits under long-term irrigation
528 of a water-limited Scots pine forest. *Frontiers in Plant Science* **10**(701): 1-10.
- 529 **Brunner I, Pannatier EG, Frey B, Rigling A, Landolt W, Zimmermann S, Dobbertin M. 2009.**
530 Morphological and physiological responses of Scots pine fine roots to water supply in a dry
531 climatic region in Switzerland. *Tree Physiology* **29**(4): 541-550.
- 532 **Carbone MS, Czimczik CI, Keenan TF, Murakami PF, Pederson N, Schaberg PG, Xu XM,**
533 **Richardson AD. 2013.** Age, allocation and availability of nonstructural carbon in mature red
534 maple trees. *New Phytologist* **200**(4): 1145-1155.
- 535 **Chen HJ, Bollmark M, Eliasson L. 1996.** Evidence that cytokinin controls bud size and branch form in
536 Norway spruce. *Physiologia Plantarum* **98**(3): 612-618.

- 537 **Choat B, Jansen S, Brodribb TJ, Cochard H, Delzon S, Bhaskar R, Bucci SJ, Feild TS, Gleason SM,**
538 **Hacke UG, et al. 2012.** Global convergence in the vulnerability of forests to drought. *Nature*
539 **491(7426): 752-755.**
- 540 **Coussement JR, De Swaef T, Lootens P, Roldan-Ruiz I, Steppe K. 2018.** Introducing turgor-driven
541 growth dynamics into functional-structural plant models. *Annals of Botany* **121(5): 849-861.**
- 542 **De Schepper V, Steppe K. 2010.** Development and verification of a water and sugar transport model using
543 measured stem diameter variations. *Journal of Experimental Botany* **61(8): 2083-2099.**
- 544 **De Schepper V, Steppe K. 2011.** Tree girdling responses simulated by a water and carbon transport
545 model. *Annals of Botany* **108(6): 1147-1154.**
- 546 **Delpierre N, Lireux S, Hartig F, Camarero JJ, Cheaib A, Cufar K, Cuny H, Deslauriers A, Fonti P,**
547 **Gricar J, et al. 2019.** Chilling and forcing temperatures interact to predict the onset of wood
548 formation in Northern Hemisphere conifers. *Global Change Biology* **25(3): 1089-1105.**
- 549 **Dobbertin M, Eilmann B, Bleuler P, Giuggiola A, Pannatier EG, Landolt W, Schleppei P, Rigling A.**
550 **2010.** Effect of irrigation on needle morphology, shoot and stem growth in a drought-exposed
551 *Pinus sylvestris* forest. *Tree Physiology* **30(3): 346-360.**
- 552 **Drew DM, Downes GM, Battaglia M. 2010.** CAMBIUM, a process-based model of daily xylem
553 development in Eucalyptus. *Journal of Theoretical Biology* **264(2): 395-406.**
- 554 **Eilmann B, Dobbertin M, Rigling A. 2013.** Growth response of Scots pine with different crown
555 transparency status to drought release. *Annals of Forest Science* **70(7): 685-693.**
- 556 **Enquist BJ, Niklas KJ. 2002.** Global allocation rules for patterns of biomass partitioning in seed plants.
557 *Science* **295(5559): 1517-1520.**
- 558 **Etzold S, Zieminska K, Rohner B, Bottero A, Bose AK, Ruehr NK, Zingg A, Rigling A. 2019.** One
559 century of forest monitoring data in Switzerland reveals species- and site-specific trends of climate-
560 induced tree mortality. *Frontiers in Plant Science* **10(307): 1-19.**
- 561 **Fatichi S, Leuzinger S, Korner C. 2014.** Moving beyond photosynthesis: from carbon source to sink-
562 driven vegetation modeling. *New Phytologist* **201(4): 1086-1095.**
- 563 **Feichtinger LM, Eilmann B, Buchmann N, Rigling A. 2014.** Growth adjustments of conifers to drought
564 and to century-long irrigation. *Forest Ecology and Management* **334: 96-105.**
- 565 **Feichtinger LM, Eilmann B, Buchmann N, Rigling A. 2015.** Trait-specific responses of Scots pine to
566 irrigation on a short vs long time scale. *Tree Physiology* **35(2): 160-171.**
- 567 **Galiano L, Martinez-Vilalta J, Lloret F. 2011.** Carbon reserves and canopy defoliation determine the
568 recovery of Scots pine 4 yr after a drought episode. *New Phytologist* **190(3): 750-759.**
- 569 **Gaudinski JB, Torn MS, Riley WJ, Swanston C, Trumbore SE, Joslin JD, Majdi H, Dawson TE,**
570 **Hanson PJ. 2009.** Use of stored carbon reserves in growth of temperate tree roots and leaf buds:
571 analyses using radiocarbon measurements and modeling. *Global Change Biology* **15(4): 992-1014.**

- 572 **Gessler A, Treydte K. 2016.** The fate and age of carbon - insights into the storage and remobilization
573 dynamics in trees. *New Phytologist* **209**(4): 1338-1340.
- 574 **Giuggiola A, Zweifel R, Feichtinger LM, Vollenweider P, Bugmann H, Haeni M, Rigling A. 2018.**
575 Competition for water in a xeric forest ecosystem - Effects of understory removal on soil micro-
576 climate, growth and physiology of dominant Scots pine trees. *Forest Ecology and Management*
577 **409**: 241-249.
- 578 **Grossiord C, Sevanto S, Limousin JM, Meir P, Mencuccini M, Pangle RE, Pockman WT, Salmon Y,**
579 **Zweifel R, McDowell NG. 2018.** Manipulative experiments demonstrate how long-term soil
580 moisture changes alter controls of plant water use. *Environmental and Experimental Botany* **152**:
581 19-27.
- 582 **Guerin M, Martin-Benito D, von Arx G, Andreu-Hayles L, Griffin KL, Hamdan R, McDowell NG,**
583 **Muscarella R, Pockman W, Gentine P. 2018.** Interannual variations in needle and sapwood traits
584 of *Pinus edulis* branches under an experimental drought. *Ecology and Evolution* **8**(3): 1655-1672.
- 585 **Haeni M, Knüsel S, M. W, Peters RL, Zweifel R 2020.** treenetproc - clean, process and visualise
586 dendrometer data. R package version 0.1.4. Github repository:
587 <https://github.com/treenet/treenetproc>.
- 588 **Herzog C, Steffen J, Pannatier EG, Hajdas I, Brunner I. 2014.** Nine years of irrigation cause vegetation
589 and fine root shifts in a water-limited pine forest. *Plos One* **9**(5): 1-11.
- 590 **Hetherington AM, Woodward FI. 2003.** The role of stomata in sensing and driving environmental
591 change. *Nature* **424**: 901-908.
- 592 **Hsiao TC, Xu LK. 2000.** Sensitivity of growth of roots versus leaves to water stress: biophysical analysis
593 and relation to water transport. *Journal of Experimental Botany* **51**(350): 1595-1616.
- 594 **Huang MT, Wang XH, Keenan TF, Piao SL. 2018.** Drought timing influences the legacy of tree growth
595 recovery. *Global Change Biology* **24**(8): 3546-3559.
- 596 **Jiang P, Liu HY, Piao SL, Ciais P, Wu XC, Yin Y, Wang HY. 2019.** Enhanced growth after extreme
597 wetness compensates for post-drought carbon loss in dry forests. *Nature Communications* **10**(195):
598 1-9.
- 599 **Jump AS, Ruiz-Benito P, Greenwood S, Allen CD, Kitzberger T, Fensham R, Martinez-Vilalta J,**
600 **Lloret F. 2017.** Structural overshoot of tree growth with climate variability and the global
601 spectrum of drought-induced forest dieback. *Global Change Biology* **23**(9): 3742-3757.
- 602 **Kannenber SA, Maxwell JT, Pederson N, D'Orangeville L, Ficklin DL, Phillips RP. 2019a.** Drought
603 legacies are dependent on water table depth, wood anatomy and drought timing across the eastern
604 US. *Ecology Letters* **22**(1): 119-127.

- 605 **Kannenberg SA, Novick KA, Alexander MR, Maxwell JT, Moore DJP, Phillips RP, Anderegg WRL.**
606 **2019b.** Linking drought legacy effects across scales: From leaves to tree rings to ecosystems.
607 *Global Change Biology* **25**: 2978–2992.
- 608 **Kannenberg SA, Novick KA, Phillips RP. 2019c.** Anisohydric behavior linked to persistent hydraulic
609 damage and delayed drought recovery across seven North American tree species. *New Phytologist*
610 **222**(4): 1862-1872.
- 611 **Lazzarin M, Zweifel R, Anten N, Sterck FJ. 2019.** Does phloem osmolality affect diurnal diameter
612 changes of twigs but not of stems in Scots pine? *Tree Physiology* **39**(2): 275-283.
- 613 **Lintunen A, Paljakka T, Jyske T, Peltoniemi M, Sterck F, von Arx G, Cochard H, Copini P, Caldeira**
614 **MC, Delzon S, et al. 2016.** Osmolality and non-structural carbohydrate composition in the
615 secondary phloem of trees across a latitudinal gradient in Europe. *Frontiers in Plant Science* **7**.
- 616 **Liu ZH, Ballantyne AP, Poulter B, Anderegg WRL, Li W, Bastos A, Ciais P. 2018.** Precipitation
617 thresholds regulate net carbon exchange at the continental scale. *Nature Communications* **9**.
- 618 **Lockhart JA. 1965.** An analysis of irreversible plant cell elongation. *Journal of Theoretical Biology* **8**:
619 264-275.
- 620 **Ma J, Xiao XM, Miao RH, Li Y, Chen BQ, Zhang Y, Zhao B. 2019.** Trends and controls of terrestrial
621 gross primary productivity of China during 2000-2016. *Environmental Research Letters* **14**(8).
- 622 **Martinez-Vilalta J, Cochard H, Mencuccini M, Sterck FJ, Herrero A, Korhonen JFJ, Llorens P,**
623 **Nikinmaa E, Poyatos R, Ripullone F, et al. 2009.** Hydraulic adjustment of Scots pine across
624 Europe. *New Phytologist* **184**: 353–364.
- 625 **Medlyn BE, Duursma RA, Eamus D, Ellsworth DS, Prentice IC, Barton CVM, Crous KY, de Angelis**
626 **P, Freeman M, Wingate L. 2011.** Reconciling the optimal and empirical approaches to modelling
627 stomatal conductance. *Global Change Biology* **17**(6): 2134-2144.
- 628 **Meinzer FC, Woodruff DR, Eissenstat DM, Lin HS, Adams TS, McCulloh KA. 2013.** Above- and
629 belowground controls on water use by trees of different wood types in an eastern US deciduous
630 forest. *Tree Physiology* **33**(4): 345-356.
- 631 **Mencuccini M, Grace J. 1996.** Developmental patterns of above-ground hydraulic conductance in a Scots
632 pine (*Pinus sylvestris*) age sequence. *Plant Cell Environ* **19**(8): 939-948.
- 633 **Mencuccini M, Salmon Y, Mitchell P, Holtta T, Choat B, Meir P, O'Grady A, Tissue D, Zweifel R,**
634 **Sevanto S, et al. 2017.** An empirical method that separates irreversible stem radial growth from
635 bark water content changes in trees: theory and case studies. *Plant Cell and Environment* **40**(2):
636 290-303.
- 637 **Michelot-Antalik A, Granda E, Fresneau C, Damesin C. 2019.** Evidence of a seasonal trade-off between
638 growth and starch storage in declining beeches: assessment through stem radial increment, non-
639 structural carbohydrates and intra-ring $\delta^{13}\text{C}$. *Tree Physiology* **39**(5): 831-844.

- 640 **Myers BJ. 1988.** Water-stress integral - a link between short-term stress and long-term growth. *Tree*
641 *Physiology* 4(4): 315-323.
- 642 **O'Brien MJ, Leuzinger S, Philipson CD, Tay J, Hector A. 2014.** Drought survival of tropical tree
643 seedlings enhanced by non-structural carbohydrate levels. *Nature Climate Change* 4(8): 710-714.
- 644 **Ogle K, Barber JJ, Barron-Gafford GA, Bentley LP, Young JM, Huxman TE, Loik ME, Tissue DT.**
645 **2015.** Quantifying ecological memory in plant and ecosystem processes. *Ecology Letters* 18(3):
646 221-235.
- 647 **Ortega JKE, Munoz CM, Blakley SE, Truong JT, Ortega EL. 2012.** Stiff mutant genes of *Phycomyces*
648 affect turgor pressure and wall mechanical properties to regulate elongation growth rate. *Frontiers*
649 *in Plant Science* 3(99): 1-12.
- 650 **Peltier DMP, Barber JJ, Ogle K. 2018.** Quantifying antecedent climatic drivers of tree growth in the
651 Southwestern US. *Journal of Ecology* 106(2): 613-624.
- 652 **Peltier DMP, Ogle K. 2019.** Legacies of more frequent drought in ponderosa pine across the western
653 United States. *Global Change Biology* 25: 3803–3816.
- 654 **Petit G, Anfodillo T, Carraro V, Grani F, Carrer M. 2011.** Hydraulic constraints limit height growth in
655 trees at high altitude. *New Phytologist* 189(1): 241-252.
- 656 **Rathgeber CBK, Cuny HE, Fonti P. 2016.** Biological basis of tree-ring formation: a crash course.
657 *Frontiers in Plant Science* 7(734): 1-7.
- 658 **Richardson AD, Carbone MS, Huggett BA, Furze ME, Czimczik CI, Walker JC, Xu XM, Schaberg**
659 **PG, Murakami P. 2015.** Distribution and mixing of old and new nonstructural carbon in two
660 temperate trees. *New Phytologist* 206(2): 590-597.
- 661 **Rigling A, Bigler C, Eilmann B, Feldmeyer-Christe E, Gimmi U, Ginzler C, Graf U, Mayer P,**
662 **Vacchiano G, Weber P, et al. 2013.** Driving factors of a vegetation shift from Scots pine to
663 pubescent oak in dry Alpine forests. *Global Change Biology* 19(1): 229-240.
- 664 **Schönbeck L, Gessler A, Hoch G, McDowell NG, Rigling A, Schaub M, Li MH. 2018.** Homeostatic
665 levels of nonstructural carbohydrates after 13 yr of drought and irrigation in *Pinus sylvestris*. *New*
666 *Phytologist* 219(4): 1314-1324.
- 667 **Shinozaki K, Yoda K, Hozumi K, Kira T. 1964.** A quantitative analysis of plant form - the pipe model
668 theory I. Basic analysis. *Japanese Journal of Ecology* 14: 97-105.
- 669 **Steppe K, Saveyn A, Vermeulen K, Lemeur R. 2006.** A comprehensive model for simulating stem
670 diameter fluctuations and radial stem growth. *Acta Hort.* 718: 35-42.
- 671 **Sterck F, Zweifel R. 2016.** Trees maintain a similar conductance per leaf area through integrated responses
672 in growth, allocation, architecture and anatomy. *Tree Physiology* 36(11): 1307-1309.

- 673 **Szejner P, Belmecheri S, Ehleringer JR, Monson RK. 2019.** Recent increases in drought frequency
674 cause observed multi-year drought legacies in the tree rings of semi-arid forests. *Oecologia* **192**:
675 241-259.
- 676 **Team RC 2019.** R: A language and environment for statistical computing. Vienna, Austria: R Foundation
677 for Statistical Computing.
- 678 **Vester F. 2007.** *The Art of interconnected thinking: Tools and concepts for a new approach to tackling*
679 *complexity*. Berlin: MC.B Verlag.
- 680 **von Arx G, Arzac A, Fonti P, Frank D, Zweifel R, Rigling A, Galiano L, Gessler A, Olano JM. 2017.**
681 Responses of sapwood ray parenchyma and non-structural carbohydrates of *Pinus sylvestris* to
682 drought and long-term irrigation. *Functional Ecology* **31**(7): 1371-1382.
- 683 **Weber P, Bugmann H, Rigling A. 2007.** Radial growth responses to drought of *Pinus sylvestris* and
684 *Quercus pubescens* in an inner-Alpine dry valley. *Journal of Vegetation Science* **18**(6): 777-792.
- 685 **Wehren B, Weingartner R, Schadler B, Viviroli D 2010.** General Characteristics of Alpine Waters. In:
686 Bundi U ed. *Alpine Waters*. Switzerland: Springer Nature, 17-58.
- 687 **Zweifel R, Bangerter S, Rigling A, Sterck FJ. 2012.** Pine and mistletoes: how to live with a leak in the
688 water flow and storage system? *Journal of Experimental Botany* **63**(7): 2565-2578.
- 689 **Zweifel R, Item H, Häsler R. 2000.** Stem radius changes and their relation to stored water in stems of
690 young Norway spruce trees. *Trees* **15**: 50-57.
- 691 **Zweifel R, Rigling A, Dobbertin M. 2009.** Species-specific stomatal response of trees to drought – a link
692 to vegetation dynamics. *Journal of Vegetation Science* **20**: 442-454.
- 693 **Zweifel R, Steppe K, Sterck FJ. 2007.** Stomatal regulation by microclimate and tree water relations:
694 interpreting ecophysiological field data with a hydraulic plant model. *Journal of Experimental*
695 *Botany* **58**(8): 2113-2131.
- 696 **Zweifel R, Sterck F. 2018.** A conceptual tree model explaining legacy effects on stem growth. *Frontiers in*
697 *Plant Sciences* **1**(9): 1-9.
- 698 **Zweifel R, Zeugin F, Zimmermann L, Newbery DM. 2006.** Intra-annual radial growth and water
699 relations of trees – implications towards a growth mechanism. *Journal of Experimental Botany*
700 **57**(6): 1445-1459.

701
702

703 The following Supporting Information is available for this article:

704

705 **Fig. S1** Distribution of annual precipitation over Switzerland and the location of the research site
706 Pfywald.

707 **Fig. S2** Frequency distribution of sapwood rings per tree and sapwood widths.

708 **Fig. S3** Sensitivity of model output to changes in the turnover rates of needles, sapwood, and carbon
709 reserves.

710 **Table S1** Diameter at breast height and tree height for the pine (*Pinus sylvestris*) trees equipped with
711 dendrometer and sap flow sensors and group into subplots with treatment.

712 **Table S2** Model parameters and their values for the three different treatments and the two
713 scenarios.

714 **Table S3** Sensitivity analyses of model output to changes of the turnover rates of needles, sapwood,
715 and carbon reserves.

716 **Methods S1** Model equations.

717 **Methods S2** Calculation of environmental index.

718

719

720

721 **Tables and Figures**

722 **Table 1.** Explanatory power of model simulations for measured variables stem growth (GRO),
 723 needle length (NL), and shoot length (SL) of Scots pine.

Explanatory power of model for measurements									
	Trees in control plot			Trees in irrigation-stop plot			Trees in irrigated plot		
	R ² _NoMemo	R ² _Memo	Δ	R ² _NoMemo	R ² _Memo	Δ	R ² _NoMemo	R ² _Memo	Δ
GRO	19.2%	68.8%	49.6%	83.3%	97.1%	13.8%	na	na	na
NL	5.9%	5.9%	0.0%	79.2%	79.2%	0.0%	67.6%	67.6%	0.0%
SL	1.4%	16.2%	14.8%	34.7%	86.6%	52.0%	52.5%	87.5%	35.0%
Explanatory power of ENV for modelled variable GRO									
GRO	92.4%	19.8%	-72.7%	88.7%	56.9%	-31.8%	93.0%	63.1%	-29.9%

724 Listed are the determination coefficients of a linear regression (R^2) between the measured and
 725 modelled annual values for control, irrigation-stop, and permanently irrigated trees. Additionally,
 726 R^2 was calculated for the environmental index ENV and the modelled GRO. Δ is the difference
 727 between the two simulation scenarios ‘Memo’ and ‘NoMemo’. A positive value indicates an
 728 improvement of the explanatory power of the scenario ‘Memo’. na = not available.

729

730 **Table 2.** Responsiveness of annual means of Scots pine responses after stopping the irrigation.

	SAP	TWD	NL	SL	CT	GRO
First strong response [yrs]	1	1	1	2	gradual	gradual
Matching control level [yrs]	> 4	4	1	>4	4	4
Legacy type	negative (but see intra-seasonal responses)	negative (but see intra-seasonal responses)	negative	negative with 1 year delay	positive	positive

731 Listed are the number of years after the irrigation-stop in 2013 when the measured variables
732 returned to the level of the control trees. Measurements refer to sap flow (SAP), tree water deficit
733 (TWD), needle length (NL), shoot length (SL), crown transparency (CT), and radial stem growth
734 (GRO). CT and GRO did not show a strong response but were more of a gradual nature. The
735 legacy type refers to the scheme in Fig. 1.

736

737

738 **Fig. 1.** Alternative physiological or morphological responses of irrigated trees to a stop of the
739 treatment in comparison to non-irrigated control trees. A positive legacy effect suggests that a
740 response variable remains above the level of the control for several years. A tree without a legacy
741 effect returns to the level of the control trees without delay. A negative legacy effect leads to a
742 response variable below the level of the control before returning to the control level.

743

744 **Fig. 2.** System-analytical tree model to quantify legacy effects according to (Zweifel & Sterck,
745 2018). The model consists of four elements that describe the tree status at the beginning of the
746 year (crown, bud, carbon reserve and sapwood). The model further takes up the key processes of
747 radial stem growth, crown growth, needle length growth (NL), shoot length growth (SL), and
748 carbon reserve growth. The elements are linked to a network with positive linear functions
749 (indicated as arrows with numbers) weighted by a weighting factor (WF). Additionally, the
750 turnover (TO) rates for the crown (needles), the sapwood, and the carbon reserves quantify the
751 time that is needed to renew the respective organ or reserve. With this network of functions, the
752 new status of crown, bud, carbon reserve and sapwood are calculated. The model is run by an
753 index for environmental conditions (Supporting Information Methods S2). Functions and
754 additional explanations for the numbered arrows are given in Methods S1.

755

756 **Fig. 3.** Mean daily time courses of soil volumetric water content (10-80 cm) in control plots (no
757 irrigation, red), irrigated plots (blue) and plots where irrigation was stopped at the end of 2013
758 after 11 years of treatment (orange). The irrigation was active during the non-freezing period of
759 the year. Periods of missing irrigation during the irrigation period indicate outages of the irrigation
760 system (blue horizontal line). Data resolution: 1 hour.

761

762

763 **Fig. 4.** Time courses of tree water deficit (TWD) of irrigation-stop (orange lines) and control trees
764 (red lines) of Scots pine over 7 years. At the end of 2013, the irrigation treatment (blue horizontal
765 bars) was stopped. A TWD of zero means a fully hydrated tree. Increased TWD indicates stem
766 shrinkage and thus an increased lack of water in the stem, meaning increased drought stress. Bold
767 lines show the mean of three trees; the thin lines indicate the standard error of the mean. Data
768 resolution: 10 minutes.

769

770 **Fig. 5.** Running means of sap flow rates over 24 hrs of trees ($n=3$) of the irrigation-stop (orange)
771 and the control (red) trees for the years 2011 to 2017 (Scots pine). Bold lines show the mean, the
772 thin lines indicate the standard error of the mean. Irrigation (blue vertical line) was stopped at the
773 end of 2013. The lower panel of each year shows the difference in sap flow rates between treated
774 and control trees. Areas coloured in orange indicate higher sap flow rates of the treated trees,
775 whereas areas coloured in red indicate higher sap flow rates of the control trees. Data resolution:
776 10 minutes.

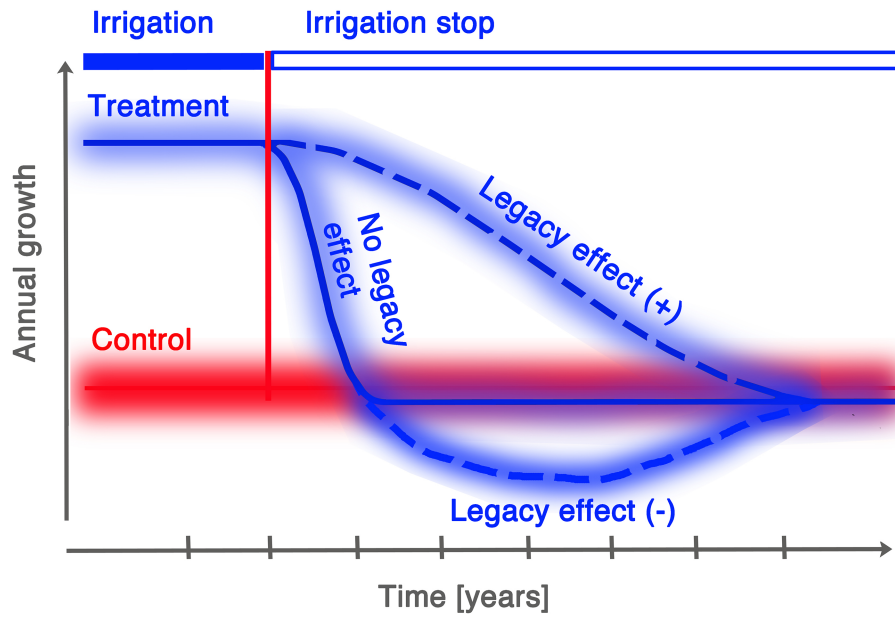
777

778 **Fig. 6.** Mean radial stem increments (GRO) of wood and bark of Scots pine trees in control (no
779 irrigation, red) and irrigation-stop (orange) plots. Bold lines show the mean of three trees, the thin
780 lines indicate the standard error of the mean. The irrigation (blue horizontal bars) was stopped at
781 the end of 2013. The red line in 2016 ends prematurely because of a logger failure.

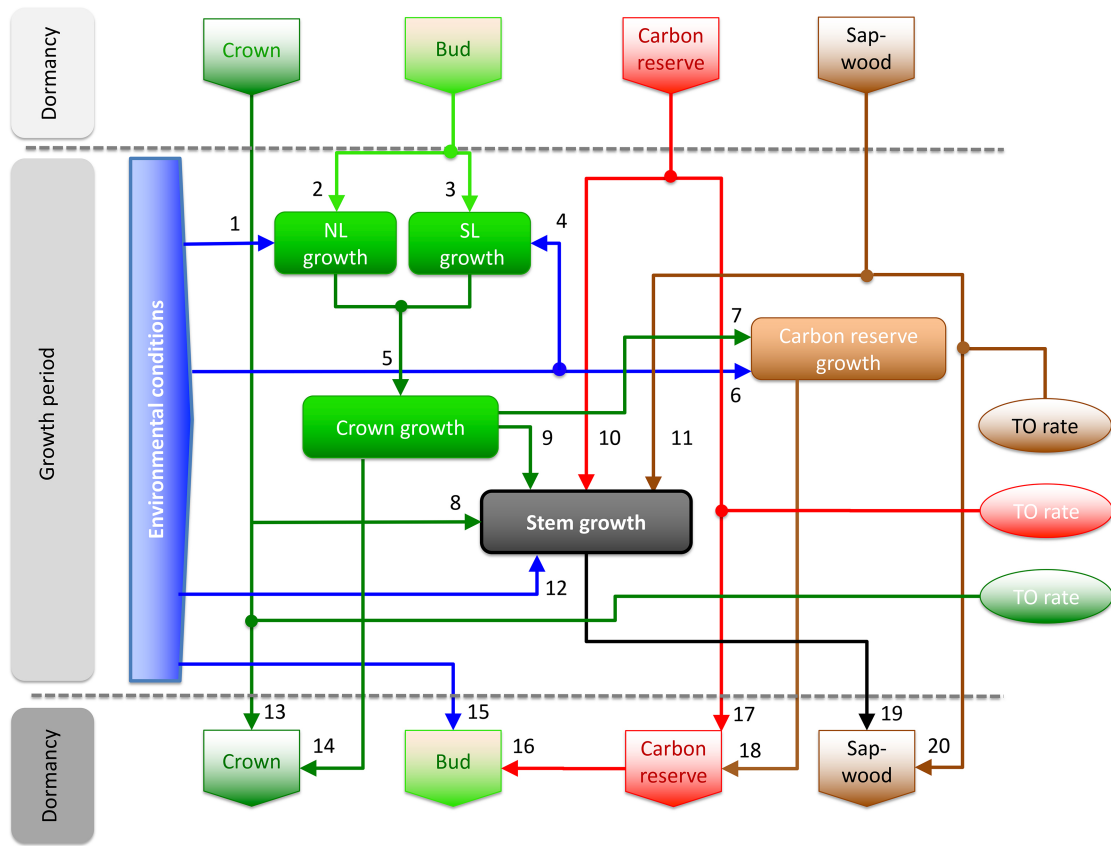
782

783

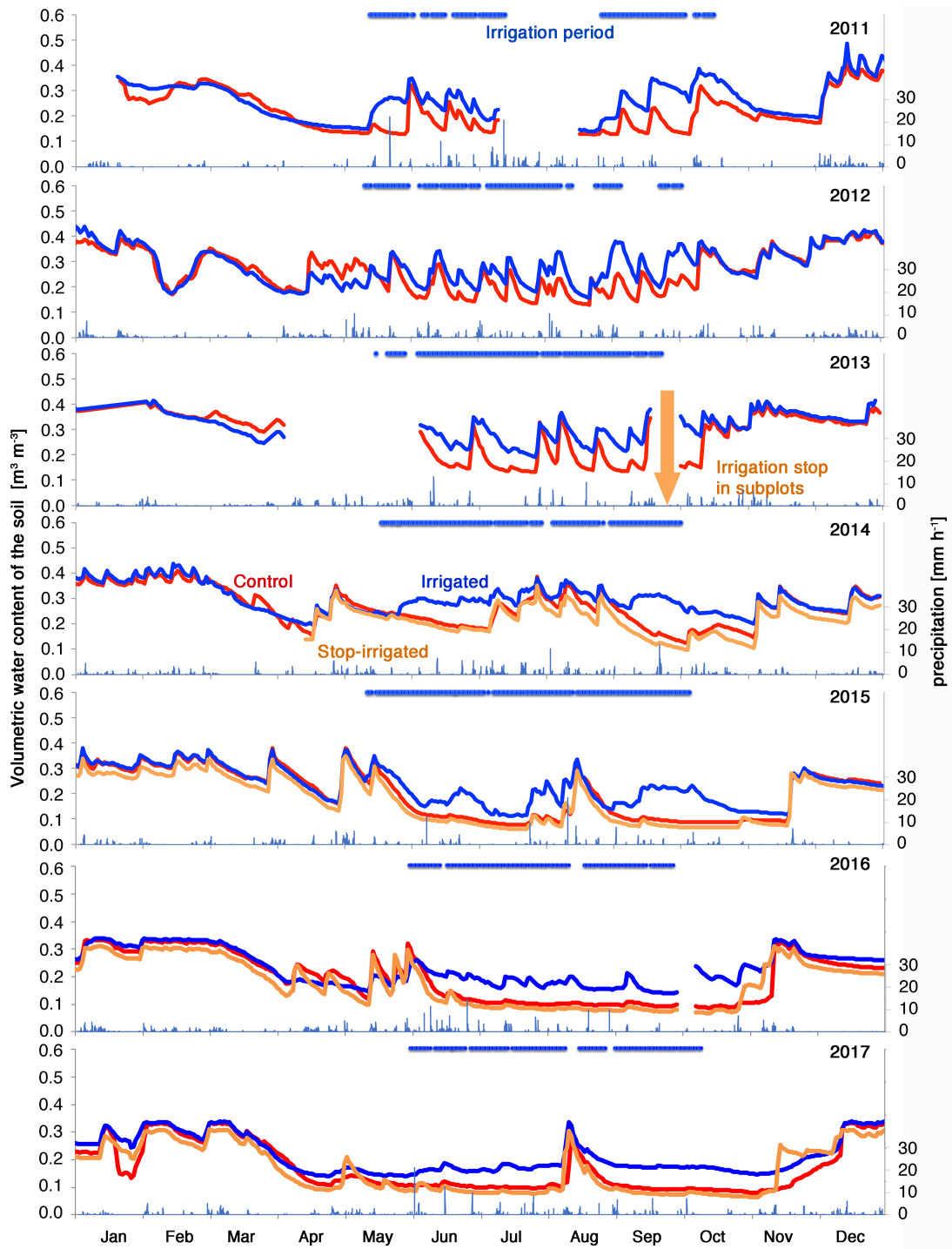
784 **Fig. 7.** Measurements (full lines) vs model results (broken lines) of two scenarios ‘NoMemo’
785 (crossed squares) and ‘Memo’ (circles) of Scots pine. ‘NoMemo’ excluded any type of memory
786 effects by setting the turnover rates of needles, sapwood and carbon reserves to 1 year. Scenario
787 ‘Memo’ set the turnover rates to more realistic values, i.e., 5 years (needles), 50 years (sapwood)
788 and 10 years (carbon reserves). **a)** Environmental index (Supporting Information Methods S2)
789 calculated for the control (red symbols), the irrigation-stop (orange symbols) and the irrigated
790 plots (blue symbols). Positive values indicate favorable growth conditions above the average,
791 negative values indicate poor growth conditions below the average. **b)** Measured and modelled
792 needle lengths. **c)** Measured and modelled shoot lengths. **d)** Mean measured crown transparency
793 and modelled crown status (proxy for leaf area). **e)** Measured and modelled mean annual growth
794 increments (GRO). Note: Missing measurements or scenarios in some panels indicate not
795 available data.



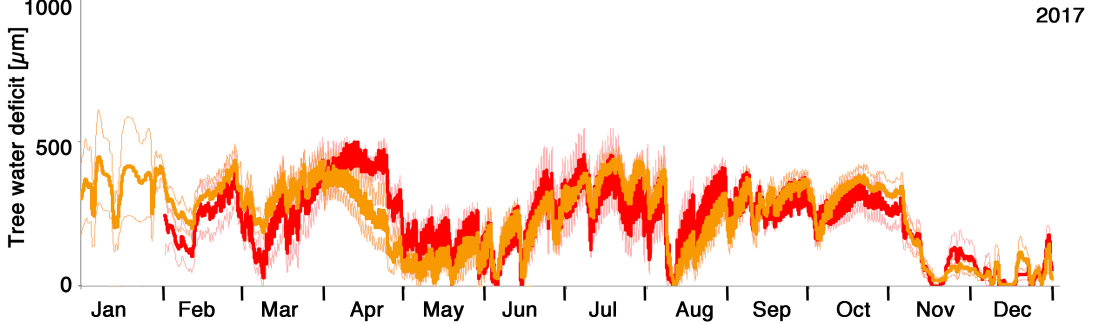
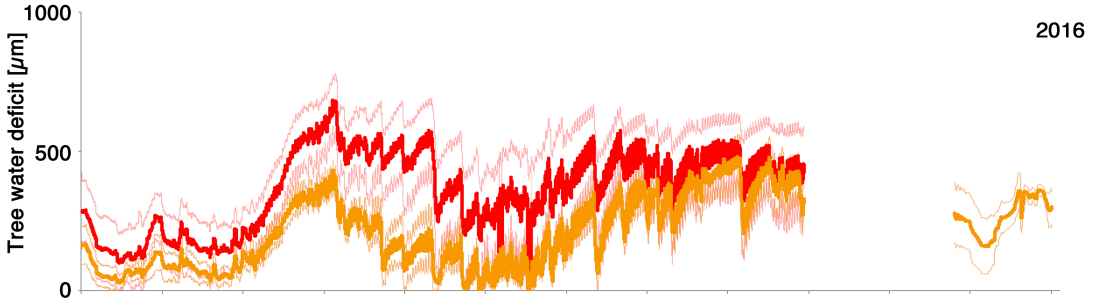
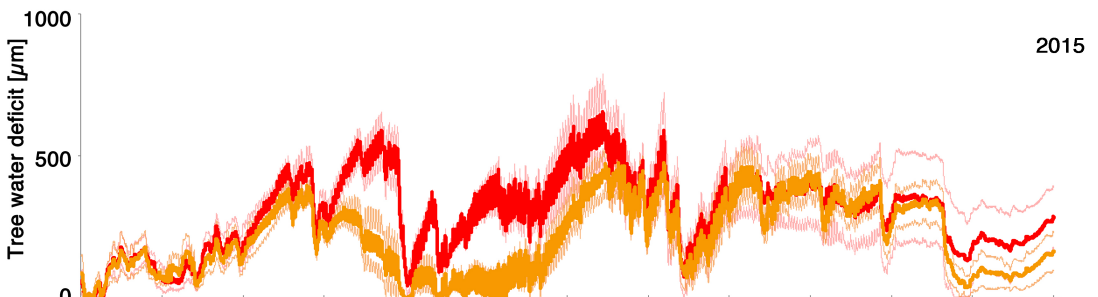
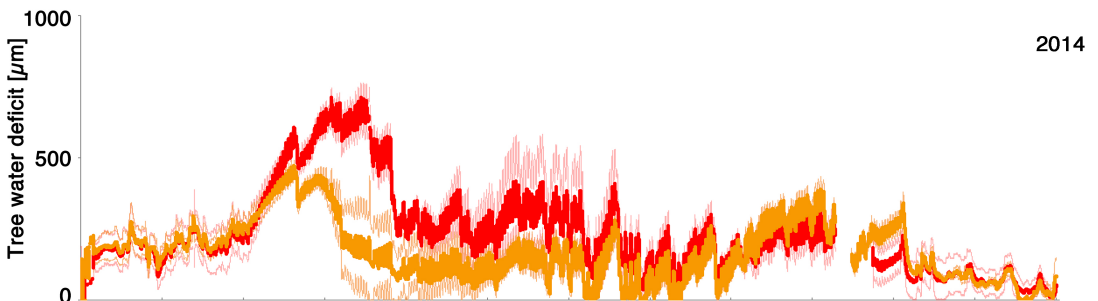
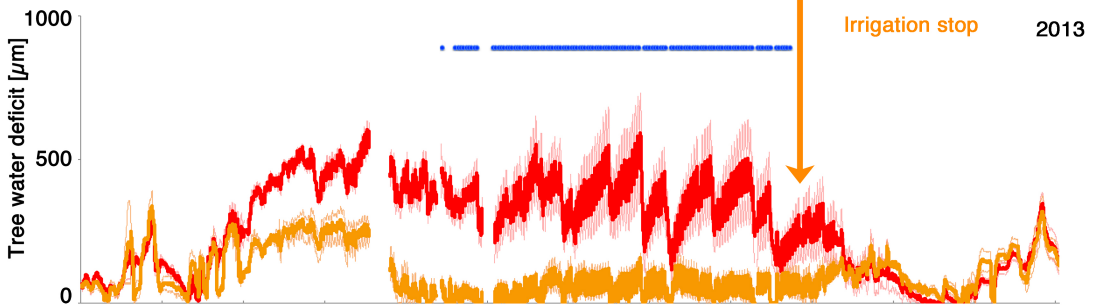
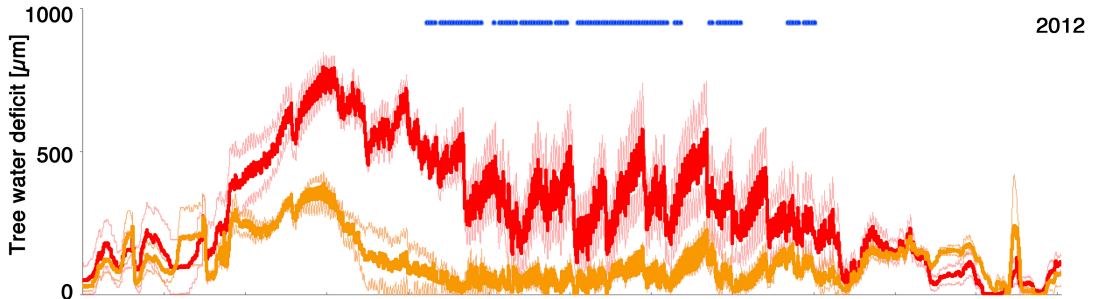
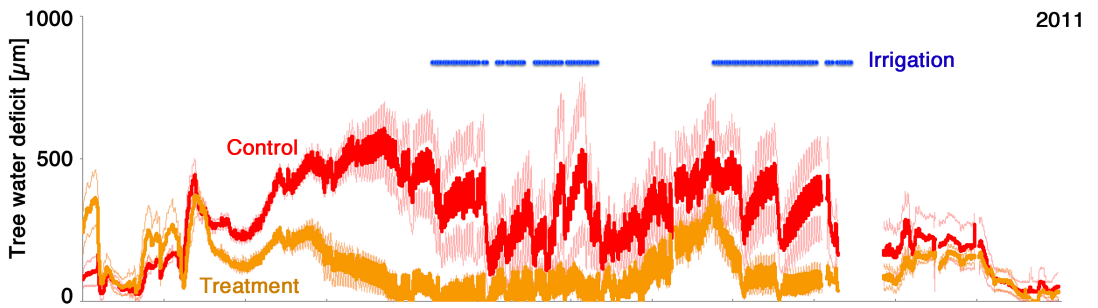
nph_16582_f1.jpg



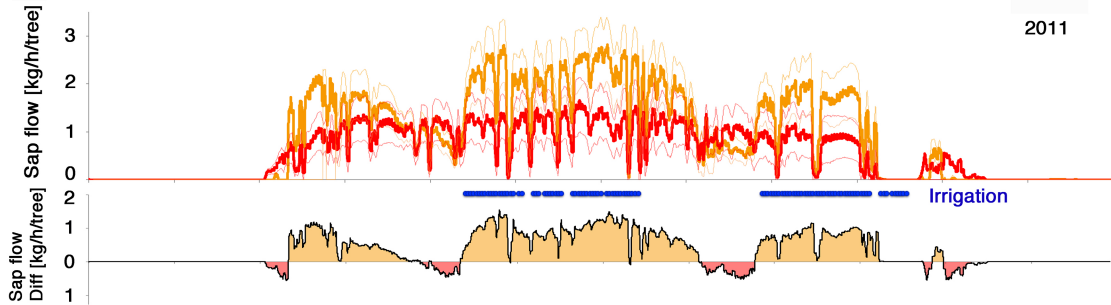
nph_16582_f2.jpg



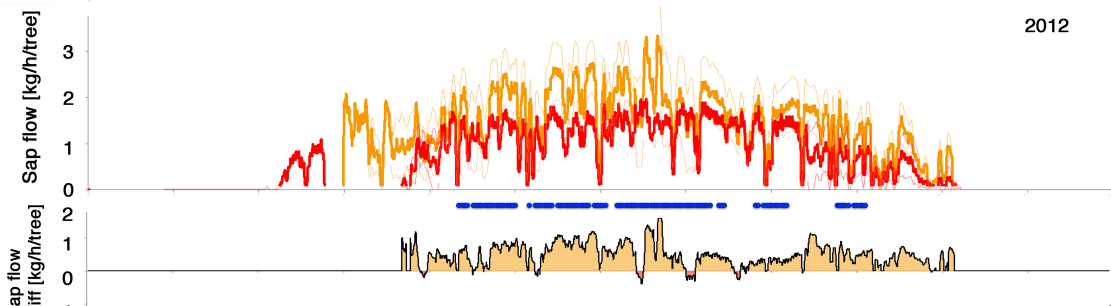
nph_16582_f3.jpg



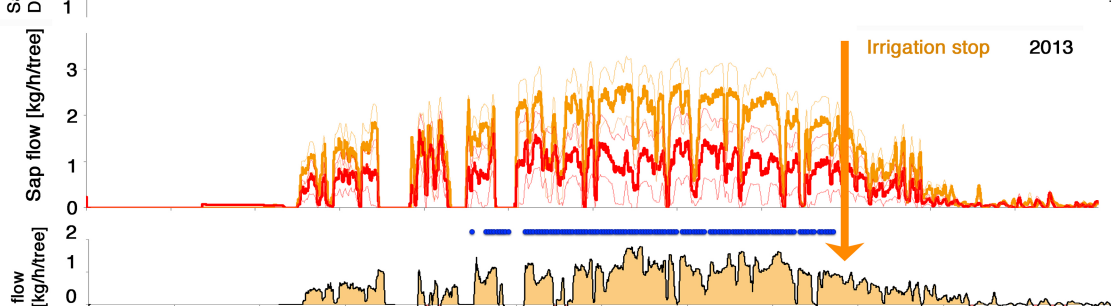
2011



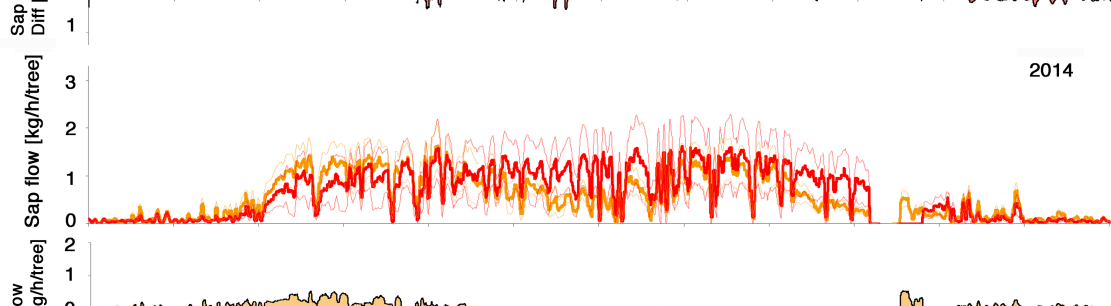
2012



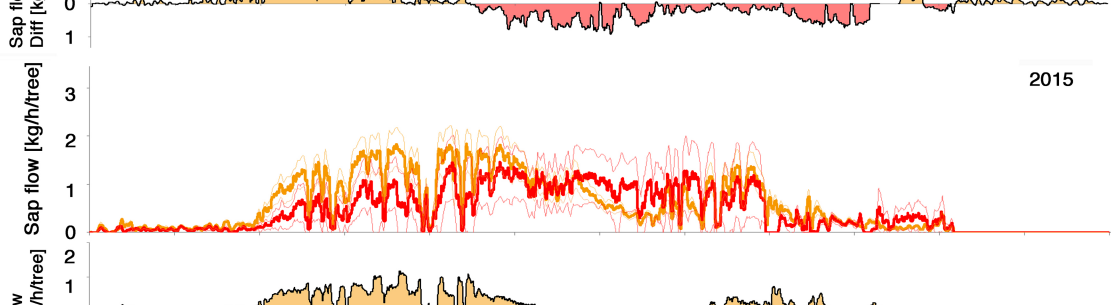
2013



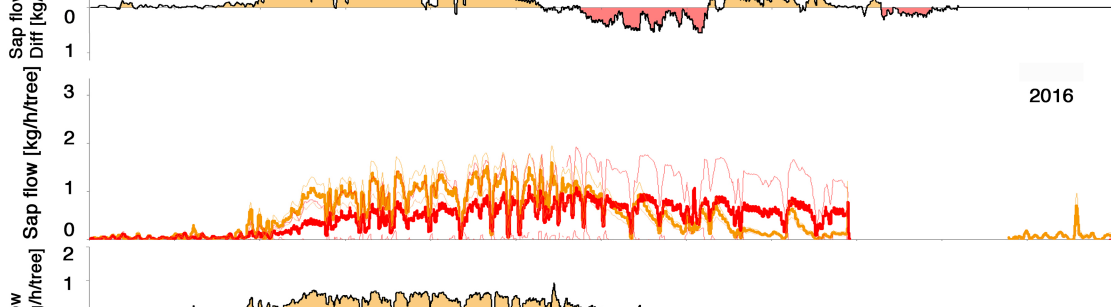
2014



2015



2016



2017

