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► To cite this version:

Arun K Bose, Barbara Moser, Andreas Rigling, Marco Lehmann, Alexandru Milcu, et al.. Memory of environmental conditions across generations affects the acclimation potential of scots pine. *Plant, Cell and Environment*, 2020, *Trees*, 43 (5), pp.1288-1299. 10.1111/pce.13729 . hal-03101978

HAL Id: hal-03101978

<https://hal.science/hal-03101978v1>

Submitted on 29 Jan 2025



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Memory of environmental conditions across generations affects the acclimation potential of scots pine

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Funding information

FP7 People: Marie-Curie Actions, Grant/Award Number: 749051-REFOREST

Abstract

Long generation times have been suggested to hamper rapid genetic adaptation of organisms to changing environmental conditions. We examined if environmental memory of the parental Scots pines (*Pinus sylvestris* L.) drive offspring survival and growth. We used seeds from trees growing under naturally dry conditions (control), irrigated trees (irrigated from 2003 to 2016), and formerly irrigated trees ("irrigation stop"; irrigated from 2003–2013; control condition since 2014). We performed two experiments, one under controlled greenhouse conditions and one at the experimental field site. In the greenhouse, the offspring from control trees exposed regularly to drought were more tolerant to hot-drought conditions than the offspring from irrigated trees and showed lower mortality even though there was no genetic difference. However, under optimal conditions (high water supply and full sunlight), these offspring showed lower growth and were outperformed by the offspring of the irrigated trees. This different offspring growth, with the offspring of the "irrigation-stop" trees showing intermediate responses, points to the important role of transgenerational memory for the long-term acclimation of trees. Such memory effects, however, may be overridden by climatic extremes during germination and early growth stages such as the European 2018 mega-drought that impacted our field experiment.

KEYWORDS

climate change, drought, maternal environment, transgenerational acclimation, trees

1 | INTRODUCTION

Droughts that are known to chronically alter resource availability in terrestrial ecosystems (Ledger, Brown, Edwards, Milner, & Woodward, 2012) are expected to increase in frequency and severity in the future (Dai, 2012). Increasing water scarcity challenges tree functioning (Blackman, Brodribb, & Jordan, 2010; Sperry, Hacke, Oren, & Comstock, 2002) as well as the productivity of forest ecosystems (Ciais

et al., 2005; Ma et al., 2012). The long generation times of trees hamper trees' adaptation to fast climatic changes, and, thus, the acclimation potential of trees is important to cope with climate change (Hoffmann & Sgrò, 2011; Valladares et al., 2014). However, the gaps in our understanding of the mechanisms that drive the acclimation of trees to altered water availability at different timescales limit our ability to make long-term projections of tree and ecosystem functioning (Nicotra et al., 2010; Watkinson et al., 2003).

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Especially younger stages of a tree's life cycle are more sensitive to climate variations and extremes than the adult stage (Poorter, Bongers, Sterck, & Wöll, 2005), but the potential of seedlings to acclimate to the prevailing environmental conditions determines the future of a forest ecosystem. Seedling growth performance and plasticity is generally assumed to be determined by its genetic makeup and the initial resources provided by the seed and modified by the environmental conditions (light, water, and nutrients; Castro, 1999; Moles & Westoby, 2004; Moser, Walthert, Metslaid, Wasem, & Wohlgemuth, 2017). Energy storage in seeds is driven by the seed mass, which is genetically controlled by the seed bearing (i.e., mother) and by the pollinating tree (i.e., father) through the embryo (Berger & Chaudhury, 2009; Ingram, 2010). In addition to parental genetics, the parental environment might have significant control on seed and seedling performance (Li, Nie, Tan, & Berger, 2013; Moles et al., 2005). The parental environmental effect is assumed to occur through two mechanisms, that is, through maternal and/or epigenetic effects (Holeski, Jander, & Agrawal, 2012). For maternal effects, the interaction of environment and maternal genotype influences the fitness and plasticity of the progeny irrespective of the genotype of the latter (Mousseau & Fox, 1998; Yin, Zhou, Lin, Li, & Zhang, 2019). For example, the seed mass and thus energy storage in seeds can be driven by the environmental influences on maternal fitness irrespective of the seed genotype, and these maternal resources can be "inherited" by the following generation through seeds (Roach & Wulff, 1987). In addition to maternal effects for transgenerational acclimation, recent research showed evidence that the environmental conditions experienced by organisms over the long term can induce changes in gene expression through different epigenetic mechanisms (e.g., Bossdorf, Richards, & Pigliucci, 2008; Holeski et al., 2012; Verhoeven, vonHoldt, & Sork, 2016). In trees, epigenetic changes have been shown to occur through DNA methylation (e.g., Gugger, Fitz-Gibbon, PellEgrini, & Sork, 2016; Hrivnák, Krajmerová, Frýdl, & Gömöry, 2017) and/or through regulatory processes mediated by small RNA molecules (Yakovlev, Asante, Fossdal, Junntila, & Johnsen, 2011; Yakovlev, Fossdal, & Johnsen, 2010). These processes can alter gene expression and consequently influence cell functions (Verhoeven et al., 2016). Recent evidence suggests that the changes in gene expression induced by changes in the growing environment can be inherited by the following generation (Richard, 2006; Yakovlev et al., 2011). If such epigenetic mechanisms affect the performance and functioning of trees in the following generation(s) is, however, not known (Bossdorf et al., 2008; Bräutigam et al., 2013).

Long-term environmental manipulation experiments provide opportunities to understand whether an environmental change experimentally maintained over a long period of time (>10 years) induces changes in trees' reproductive potential (i.e., seed production) and whether transgenerational memory of the growing conditions of the parents affect the offspring acclimation potential. Results from a 15-year long-term irrigation experiment in Switzerland (Pfywald, Valais) showed that irrigation has significantly prolonged the growing season (Eilmann, Zweifel, Buchmann, Graf Pannatier, & Rigling, 2011) and improved growth and biomass of Scots pine (*Pinus sylvestris* L.)

trees (Brunner et al., 2009; Dobbertin et al., 2010; Eilmann et al., 2010; Timofeeva et al., 2017). Based on these findings, in the current study, we anticipate that the long-term irrigation (since 2003) as well as irrigation stop (since 2014) will influence the reproductive potential of *P. sylvestris* trees compared with the nonirrigated naturally xeric control and will modulate the acclimation strategies of the following generation either via maternal mechanism affecting seed resources or via the memory of the long-term environmental conditions transferred from the parents to the offspring (Raj et al., 2011; Richard, 2006). We considered the following research questions: (a) Do the different environmental conditions the trees were subjected to during seed production affect seed mass and subsequently drive offspring growth and mortality (i.e., maternal effects)? (b) If there is no such difference in initial resource availability (i.e., seed mass) and if there are no genetic differences among seed bearing trees, is there still an effect on offspring growth and mortality (i.e., via transgenerational memory)? and (c) Are such memory effects detectable mainly in a controlled environment (water, temperature, and light) under greenhouse conditions or also visible in the field where a multitude of additional factors interact?

2 | MATERIALS AND METHODS

2.1 | Irrigation experiment

A 100-year-old xeric Scots pine (*P. sylvestris* L.) forest has been subjected to long-term irrigation since June 2003. The experiment is located at Pfywald in the canton Valais of Switzerland (46°18'N, 7°3'E, 615 m above sea level). The forest is characterized as even aged with 730 stems per hectare (Dobbertin et al., 2010). The area is one of the driest inner alpine valleys of the European Alps, with a mean annual temperature of 10.1°C (19.1°C for June–August) and mean annual precipitation of 603.2 mm (169 mm for June–August) for the period 1981–2010 (Data from the MeteoSwiss station Sion). The soil, a Rendzic Leptosol, is shallow and characterized by low water retention (Brunner et al., 2009).

The 1.2-ha experimental area was initially divided into eight plots of 1,000 m² each. Four plots were randomly selected for irrigation, and the four remaining plots serve as nonirrigated naturally dry controls. The irrigation has been running every night from first April to 30th September since June 2003. The irrigation water is taken from a water channel next to the experimental area. The amount of irrigation water was set to double the annual precipitation compared with the nonirrigated plots (see yearly amount of irrigated water in Figure S1). In 2014, each irrigated plot was divided into two plots for an additional "irrigation-stop" treatment. Trees in the irrigation-stop treatment have not been receiving any irrigation since the first October 2013.

2.2 | Offspring experiment

In order to disentangle drought-induced parental legacy effects, legacy effects of irrigation on soil properties, and direct environmental

drivers on seed and seedling performance, we carried out two offspring establishment experiments, one at the experimental site in Pfywald (referred to as “field”) and another under controlled environmental conditions in the greenhouse at the Swiss Federal Research Institute WSL (“greenhouse”).

2.2.1 | Cone sampling and seed preparation

For the experiments, a total of 57 trees (23, 18, and 16 in “irrigated,” “irrigation stop,” and “control,” respectively) were selected randomly for cone sampling. The sampling was performed in February 2017 when cones were ripe. All cones were harvested from each sampled tree. The sampled cones were heated in an oven at 45°C for 48 hr to fully open the scales. Seeds were extracted from the opened cones; the filled seeds were separated from the empty ones by a blower and then stored at 2°C (He et al., 2018).

For the two experiments (field and greenhouse), we considered all seeds from all mother trees, meaning that trees with higher seed production in a treatment contributed more seeds to our experiment than trees with lower amounts of seeds. The total number of seeds selected from a tree represents the percentage of seeds produced by that tree to the total number of seeds produced by all trees of a treatment. We selected 7,200 seeds for the field experiment (2,400 for each treatment [control, irrigated, and irrigation stop]) and 5,400 seeds (1,800 for each treatment) for the greenhouse experiment. Therefore, we needed 4,200 seeds (2,400 for field experiment and 1,800 for greenhouse experiment) from each treatment. From 4,200 seeds, we randomly picked seeds for different seed beds of the field and the greenhouse experiment.

2.2.2 | Greenhouse experiment

In the greenhouse, three temperature-controlled chambers were installed for ambient, ambient +2°C, and ambient +4°C temperature, and the temperature was adjusted to four different periods of the day (i.e., 0.01–6.00, 6.01–12.00, 12.01–18.00, and 18.01–24.00 hr) from 24th April to 30th September 2018. We have two replications of each temperature chamber. Ambient temperature of the four different periods of the day represents the average temperature for that period of the past 30 years of the Swiss climate station Sion (Table S1), which is located at 4.8-km distance from the field site Pfywald. In each temperature chamber, two shading treatments (full light and shading) were installed. Shaded pots received five times less sunlight than pots in full light condition.

For each shading treatment within each temperature chamber, three pots (i.e., one for each treatment the mother tree was subjected to) were used for watering treatment, and three other pots were used for a drought treatment. Each pot sized 735 cm². There were 15 quadrats (each sized 49 cm²) in each pot. We sowed five seeds in each quadrat, which makes 75 (15 × 5) seeds in each pot. The watering/drought treatment was applied only for seedling growth and not for seed germination. The seed germination was monitored for the first

8 weeks since seed sowing (see below), and all pots were equally watered during these 8 weeks to avoid early death. The two watering treatments represent (a) watered: watered to 45% of soil water holding capacity two times in a week and (b) drought: watered to 10% of soil water holding capacity once in a week (see Table S2). Watering was performed by hand with a watering can. For soil water holding capacity, we first watered the pot to its 100% water holding capacity. We then measured the weight of the 100% saturated pot. We then determined the volume of water needed for 45% and 10% saturation, and those volume of water were applied for 45% and 10% water holding capacity. In the greenhouse, the experimental design can be described as follows: 5 seeds × 3 levels of mother tree × 15 quadrats × 2 levels of watering × 2 levels of shading × 3 levels of temperature × 2 replications = 5,400 seeds.

2.2.3 | Field experiment

In each of the four replicated plots of the irrigation experiment (12 plots in total), 10 seed beds were prepared by removing the vegetation. In each of the control and irrigation-stop plots, five of 10 seed beds were weekly watered by hand with a watering can from 12th April to 25th September of 2018, and five other seed beds were kept as unwatered. In irrigated plots, all seed beds were watered each night by the permanent irrigation system (Dobbertin et al., 2010). In each seed bed (400 cm²), six quadrats (each sized 100 cm²) were created, two of which were sowed with the same seed type. In each quadrat, 10 seeds were sown on 11–12th April 2018, which makes 20 seeds for each seed type within each seed bed and a total 60 seeds/bed (i.e., 10 seeds × 2 quadrats × 3 seed types = 60 seeds per bed). In the field experiment, the experimental design can be described as follows: 20 seeds × 3 levels of mother tree × 10 seed beds × 3 levels of irrigation treated plots × 4 replications = 7,200 seeds (see Table S2).

2.2.4 | Genotyping of seeds

The original irrigation experiment with the mother trees consisted of a randomized block design within a homogeneous forest stand. This design makes it highly unlikely that groups of seeds that derive from a specific mother treatment represent different genetic groups. To support this assumption, that these seed groups do not differ genetically, we randomly selected individual seeds from all mother trees of the three treatments and performed seed genotyping and characterized genetic structure and differentiation among the seed groups (see details of the analysis in the Table S3 and Figure S2).

2.3 | Seed and offspring measurements

For individual seed weight, three replicates of 100 seeds per tree were randomly selected and weighed to calculate average seed weight (He et al., 2018).

2.3.1 | Seed germination and offspring mortality

For seed germination, we counted the number of new emerging offspring every week over the 8 weeks since the sowing. For offspring mortality, we monitored the survival and death of germinated offspring every 2 weeks from 15th May to 28th September 2018.

2.3.2 | Offspring growth

For offspring growth, we measured total leaf area (cm²), shoot length (cm), leaf biomass (g), shoot biomass (g), and root biomass (g). However, we were not successful with the whole root sample collection from the field; hence, below-ground biomass were not analysed for the field experiment. The field samplings for offspring total leaf area and biomass were conducted by the end of the 16th and 25th week since sowing, whereas the greenhouse samplings were conducted by the end of the 14th and 23rd week since sowing. The total leaf area was measured by using the software WinFolia image analyser (Regent, Quebec, Canada). For offspring dry biomass, offspring samples were dried in an oven for at least 3 days at a constant temperature of 60°C.

2.4 | Response and predictor variables

We considered seed germination success (i.e., number of emergences relative to the total number of sown seeds), offspring mortality (i.e., number of dead offspring relative to the total number of germinated offspring), total leaf area, above-ground biomass (i.e., leaf and shoot weight), below-ground biomass (i.e., root weight), and root to shoot ratio as response variables.

For predictor variables, mother tree treatments (i.e., irrigation legacy of the mother trees the seeds are originating from) and the current watering regimes were considered for both experiments (field and greenhouse). The soil legacy type (i.e., irrigation legacy in soil) was considered only for the field experiment, whereas temperature and shading were considered only for the greenhouse experiment.

2.5 | Data analysis

2.5.1 | Seed weight

The weight of an individual seed was modelled as a function of mother tree treatments (three levels: irrigated, irrigation stop, and control). Because the weight of an individual seed varies across trees and the tree that produced higher number of seeds usually has a higher number of offspring in the forest, we also converted the tree-level individual seed weight to weighted tree-level individual seed weight. For this, the average seed weight of an individual tree was weighted by the total number of seeds produced by that tree.

2.5.2 | Seed germination and seedling performances

Greenhouse experiment

The seed germination success rate was modelled as a function of mother tree treatments, temperature (three levels: ambient, ambient +2°C, and ambient+4°C), light (two levels: full light and shade), and two-way interactions between treatments and temperature and between treatments and light. Light was measured in terms of photosynthetically active radiation using Digital Plant Canopy Imager CI 110/120. The offspring-related response variables were modelled as a function of mother tree treatments, temperature, light, watering, and two-way interactions between treatments and temperature, between treatments and light, and between treatments and watering.

For testing the effect of time since sowing on germination success under greenhouse condition, the germination success was modelled as a function of mother tree treatments, time since sowing (four levels: 14, 28, 42, and 56 days), light, temperature, and interaction between light and time since sowing, between temperature and time since sowing, and between mother tree treatment and time since sowing.

Field experiment

For the irrigated plot where all seed beds were equally watered, the response variables were modelled as a function of mother tree treatments only. For control and irrigation-stop plots, the response variables were modelled as a function of mother tree treatments, soil legacy type (two levels: control and irrigation stop), current watering regimes (two levels: not irrigated and weekly irrigated), and two way interactions between treatments and soil legacy type and between treatments and current watering regimes. However, since most of the offspring died in the control and in the irrigation-stop plots during the first 16 weeks since sowing, the response variables were not analysed there by the end of the 25th week since sowing. In addition, offspring growth (i.e., total leaf area and above-ground biomass) was analysed only for weekly irrigated seedbeds because only 11 offspring were alive in nonirrigated seed beds by the end of the 16th week since sowing in control and irrigation-stop plots.

For testing the effect of time since sowing on germination success at control and irrigation-stop plots in field condition, the germination success was modelled as a function of mother tree treatments, time since sowing (three levels: 42, 49, and 56 days), watering, interaction between time since sowing and watering, and interaction between mother tree treatment and time since sowing.

2.6 | Statistical analysis

We used a mixed effect modelling approach (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), in which our variables of interest were considered as fixed effects, whereas hierarchical designs of the experiments were incorporated as random effects (i.e., seedlings beds nested within plots in the context of the field experiment, seedling

quadrats nested within pots, and pots nested within climate chambers in the context of the greenhouse experiment). For the analysis of individual seed weight and number of seeds produced by a tree, mother tree treatments were considered as fixed effects, whereas seed-bearing trees nested within plots were considered as random effects. We used log transformation for the weighted individual seed weight and number of seeds produced by a tree. Effects of predictor variables on seed germination and offspring mortality (i.e., percentage data) were assessed by generalized linear mixed effect models using the function *glmer* in the lme4 package in R with negative binomial distribution (Bates, Maechler, Bolker, & Walker, 2017), whereas the effects of predictor variables on seed weight, number of seeds produced by a tree, and offspring growth (leaf area, biomass, and root to shoot ratio) were assessed by linear mixed effect models using the function *lme* in the nlme package in R (Pinheiro, Bates, DebRoy, & Sarkar, 2014). The post hoc Tukey multiple comparison test was performed to detect the statistical differences (Hothorn, Bretz, & Westfall, 2008). We visually verified the assumptions of normality and variance homogeneity of the residuals. We used square root and log transformation for above-ground biomass and leaf area index, respectively. All analysis was performed in programming language R version 3.5.3 (R Development Core Team, 2018).

3 | RESULTS

3.1 | Genetic characterization

We found no significant genetic differentiation among the seed groups of the three mother treatments (irrigated, irrigation stop, and controls). Analysis of molecular variance of seeds showed that only 1% of the genetic variation was found among mother treatments and 99% within them ($p = .001$; Table 1). Analysis of genetic structure showed that all seeds represent one genetic cluster (Figure S3).

3.2 | Seeds

The individual seed weight, weighted-individual seed weight, and total number of seeds produced by an individual tree were similar ($p \geq .12$) across the three treatments the mother trees were subjected to (Figure 1). The mean of individual seed weight from trees located in control, irrigation-stop, and irrigated plots varied between 3.5–6.8, 3.4–6.7, 3.6–7.4 mg, respectively.

Source of variation	df	SS	MS	Est. Var.	% Var.	p value
Among treatments	2	9.650	4.825	0.028	1	.001
Within treatments	269	609.386	2.265	2.265	99	

Abbreviation: MS, mean square; SS, sum of squares.

3.3 | Seed germination

We detected no statistically significant effect ($p > .25$) neither of the mother tree nor of the temperature (ambient, ambient+2°C, and ambient +4°C) on seed germination success under controlled greenhouse conditions (Table S4). However, shaded pots had a higher emergence numbers than pots in the full light condition by the end of the 14 days since sowing. However, this initial effect of shade on emergence numbers disappears by the end of the 28 days since sowing (Figure S4). The effect of mother tree on seed germination success in the field was driven only by current watering regimes, where daily (irrigation treatment) as well as weekly watering (performed by hand in the irrigation-stop and control treatments) significantly ($p < .001$) increased the germination success (Table S5 and Figure S5). Watering treatments were not applied for seed germination assessments under controlled greenhouse condition.

3.4 | Offspring mortality

After seedling establishment, mortality and growth were assessed by the end of the 14th and 23rd week since sowing under controlled greenhouse condition. We detected no mortality of germinated seedling by the end of the 14th week since sowing. However, by the end of the 23rd week since sowing, increased temperatures (+2 and +4°C) increased mortality, whereas the watering treatment led to reduced mortality rates of seedlings. The hot-drought treatment (i.e., ambient +4°C in combination with drought) resulted in the highest mortality (Figure 2) of 24% of germinated seedlings irrespective of mother tree origin. Offspring originating from irrigated and irrigation-stop trees had higher mortality under hot-drought conditions relative to offspring originating from control trees (Table S6 and Figure 2).

Under field conditions, offspring mortality and growth were assessed by the end of the 16th and 25th week since sowing. The mortality was primarily driven by the current watering regimes. Offspring growing in the irrigation treatment (which were watered automatically every night) had lowest mortality (Table S7 and Figure 3c). Mortality was >90% by the end of the 16th week since sowing in the control and irrigation-stop treatment. If watered once per week, mortality decreased <80% in these two treatments (Figure 3a,b). In none of the treatments (control, irrigation stop, and irrigation), the origin of the seedlings, that is, if they were offspring from mother trees exposed to different irrigation treatments, affected mortality rates. The offspring mortality in the daily irrigated seed beds (i.e., in the irrigation treatment) primarily resulted from fungi and insect defoliation, whereas offspring mortality in the control and irrigation-stop plots

TABLE 1 Partitioning of genetic variation (analysis of molecular variance analysis) among and within seed populations. Populations were defined according to the treatment of mother trees

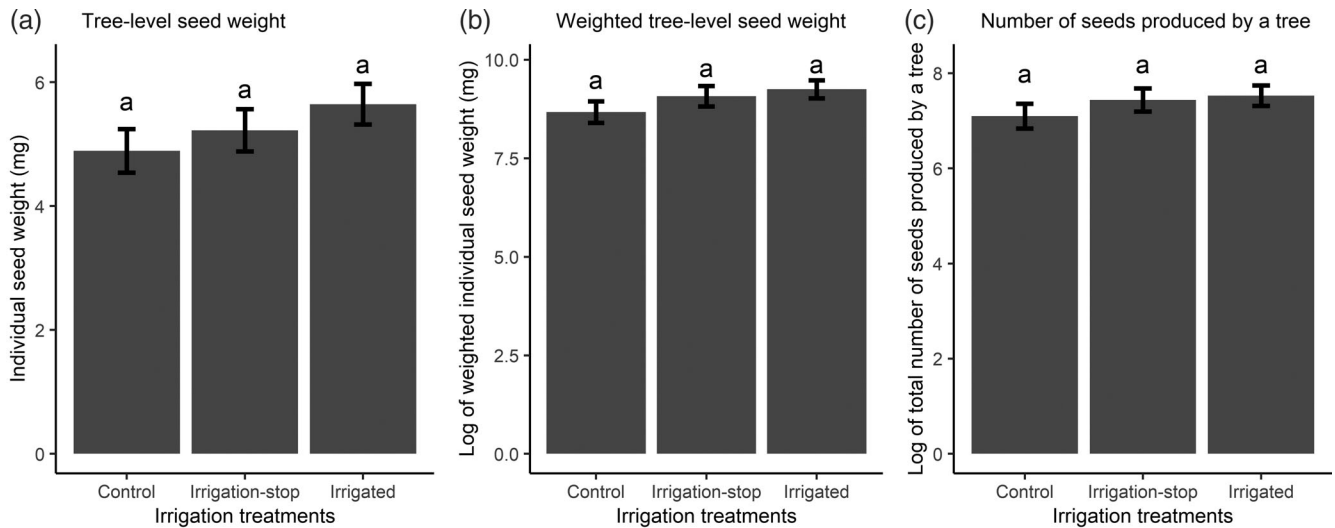


FIGURE 1 Linear mixed effect model-driven (a) tree-level individual seed weight, (b) tree-level weighted individual seed weight, and (c) number of seeds produced by a tree across the three irrigation treatments. The error bar represents mean \pm SE. Three replications of 100 seeds were selected from each tree. Total of 57 trees were nested within nine independent treatment units. The weighted tree-level individual seed weight was quantified by multiplying individual seed weight with the total number of seeds produced by a tree. The letters on top of the bars show the results of the post hoc Tukey multiple comparison test

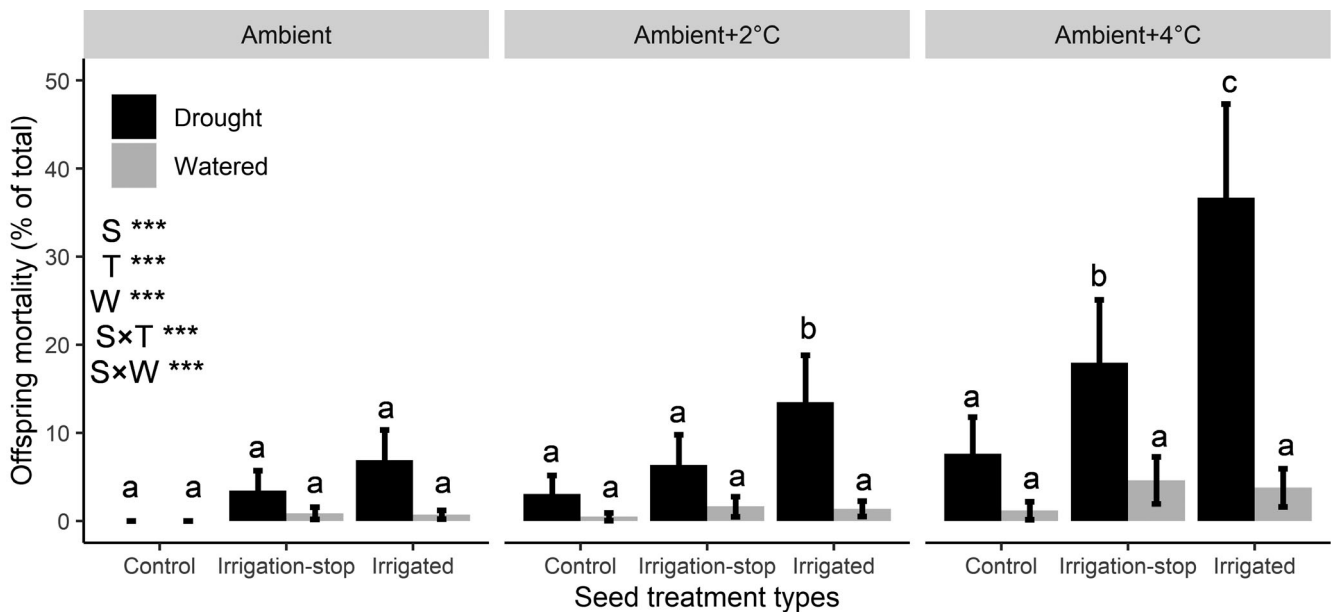


FIGURE 2 Generalized linear mixed effect model-driven mortality of germinated seedlings by the end of the 23rd week since seed sowing under controlled greenhouse condition. The error bars represent mean \pm SE. A total of 1,080 quadrats were nested within six independent treatment units. S indicates the seed treatment effect; T the temperature effect; W the watering effect; S \times T the seed treatment and temperature interaction term; and S \times W the seed treatment and watering interaction term ($*p < .05$, $**p < .01$, $***p < .001$). The letters on top of the bars show the results of the post hoc Tukey multiple comparison test (see also Table S6)

resulted from drought-induced desiccation (independent if they were watered once per week by hand or not at all).

3.5 | Offspring growth

Under controlled greenhouse condition, by the end of the 14th week since sowing, total leaf area, above-ground biomass, below-ground

biomass, and root to shoot ratio were higher in full light than in shaded condition (Table S8). By the end of the 23rd week since sowing, we detected statistically significant effects of the treatments the mother trees experienced on offspring growth variables but depended upon temperature, water, and light (i.e., interactions were significant; Table 2 and Figure 4). Offspring from irrigated trees had a higher above-ground biomass relative to offspring from control trees when they received full light and water (i.e., watering to 45% of water

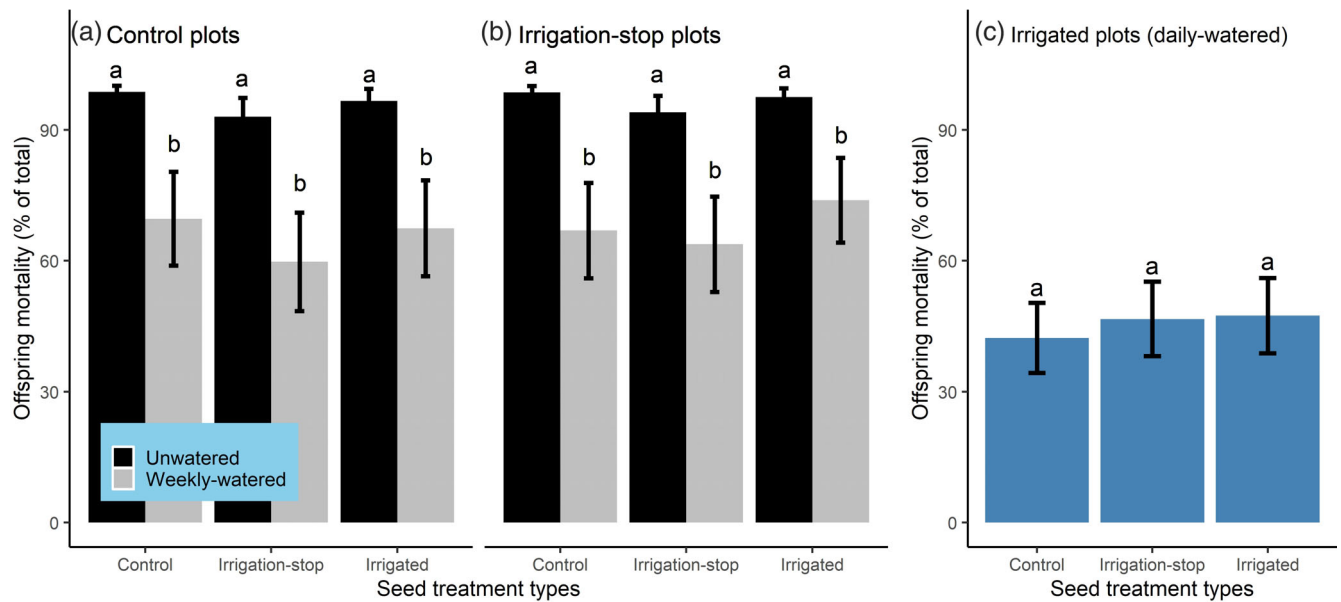


FIGURE 3 Generalized linear mixed effect model-driven mortality of germinated seedlings by the end of the 16th week since seed sowing in the field condition. The samples from control and irrigation-stop plots were analysed together, whereas samples from irrigated plots were analysed separately because all seed beds of irrigated plots were daily watered. The error bar represents mean \pm SE: 480 quadrats were nested within eight independent treatment units in control and irrigation-stop plots, whereas 240 quadrats were nested within four independent treatment units in irrigated plots. The letters on top of the bars show the results of the post hoc Tukey multiple comparison test

holding capacity twice a week). However, offspring from irrigated trees had a lower below-ground biomass as well as a lower root to shoot ratio when they experienced the hottest temperature (i.e., ambient $+4^{\circ}\text{C}$) and drought (i.e., watering to 10% of water holding capacity once a week) treatment in combination (Table 2 and Figure 4).

Under field condition, by the end of the 16th week since seed sowing, total leaf area and above-ground biomass were higher in offspring from all three origins in control plots relative to irrigation-stop plots when they were weekly watered by hand (Table S9). In the irrigated plots, total leaf area, and above-ground biomass were also similar across offspring from mother trees subjected to the three different treatments both at the end of the 16th and 25th week since seed sowing (Table S9).

4 | DISCUSSIONS

The long-term water availability treatments of the mother trees had no effect on seed weight, seed germination, offspring growth, and offspring mortality shortly after germination (until 14th week since sowing of the seeds). However, when exposed to warm and drought conditions for a longer period (i.e., by the end of the 23rd week after sowing) under controlled conditions, offspring from mothers that experienced different long-term water regimes displayed large differences in growth strategies (Figure 4). Under increased temperatures combined with drought in the greenhouse, offspring from irrigated and irrigation-stop trees had a higher mortality than offspring from control trees. However, offspring from irrigated trees had a higher

above-ground biomass when they were adequately watered and provided with full light than offspring from control trees. These results of lower growth in moist condition but lower mortality in dry condition of offspring originating from regularly drought-exposed control trees compared with offspring from irrigated trees indicated the strong influence of the parental environmental memory (Raj et al., 2011). Thus, the memory of the parental environment passed on from the parents to the offspring might be an important mechanism for the acclimation potential of trees to rapid environmental changes (Crisp, Ganguly, Eichten, Borevitz, & Pogson, 2016).

Trees from the irrigation-stop treatment received irrigation from 2003 to 2013 but have not received any irrigation during the last 3 years prior to seed sampling. Offspring of these trees displayed mortality patterns and biomass allocation strategies (i.e., root to shoot ratio) similar to offspring of irrigated trees but total leaf area and above-ground biomass growth strategies similar to offspring of non-irrigated control trees. This may be a result of the parental environmental memories of both irrigation (2003–2013) and non-irrigation (2014–2016) conditions and points to the fact that a full readjustment to changed environmental conditions takes more than 3 years.

The plant–environment interaction is traditionally based on an idea that environment does not induce any changes in the DNA sequence but may induce changes in the phenotype, that is, in the range of its genetically determined plasticity leading to changes in health and fitness of the individuals. Improved health and fitness as a consequence of acclimation to a set of environmental conditions may result, for example, in heavier seeds, and seed mass in Scots pine is known to be positively correlated with seed germination success (Castro, 1999; Reich, Oleksyn, & Tjoelker, 1994). However, our results

TABLE 2 Total leaf area (cm²), above-ground biomass (g), below-ground biomass (g), and root to shoot ratio of germinated seedlings under controlled greenhouse condition by the end of the 23rd week since sowing of the seeds

Fixed effects	Total leaf area (cm ²)			Above-ground biomass (g)			Below-ground biomass (g)			Root to shoot ratio		
	Coefficients (mean ± SEM)	t	p	Coefficients (mean ± SEM)	t	p	Coefficients (mean ± SEM)	t	p	Coefficients (mean ± SEM)	t	p
Intercept	1.91 ± 0.10	18.26	<.001	0.23 ± 0.01	26.58	<.001	0.13 ± 0.01	23.47	<.001	1.38 ± 0.06	24.27	<.001
C vs. I	0.09 ± 0.12	0.73	.467	0.004 ± 0.01	0.31	.753	-0.002 ± 0.01	-0.30	.764	-0.35 ± 0.05	-0.83	.407
C vs. IS	-0.27 ± 0.12	-2.18	.030	-0.03 ± 0.01	-2.76	.006	-0.01 ± 0.01	-1.56	.120	-0.07 ± 0.08	0.29	.773
Full light vs. shade	-0.97 ± 0.08	-12.22	<.001	-0.10 ± 0.01	-12.68	<.001	-0.06 ± 0.004	-12.12	<.001	-0.35 ± 0.05	-6.93	<.001
Ambient vs. ambient +2°C	0.13 ± 0.10	1.30	.194	0.01 ± 0.01	1.44	.150	0.01 ± 0.01	1.98	.048	0.09 ± 0.06	1.54	.125
Ambient vs. ambient +4°C	-0.08 ± 0.10	-0.87	.387	-0.01 ± 0.01	-1.79	.075	-0.01 ± 0.01	-1.01	.315	0.03 ± 0.06	0.51	.613
Drought vs. watered	0.25 ± 0.08	3.10	.002	0.01 ± 0.01	1.75	.081	-0.01 ± 0.004	-2.07	.039	-0.20 ± 0.05	-3.89	<.001
C vs. I when full light relative to shade	-0.21 ± 0.11	-1.091	.057	-0.02 ± 0.01	-2.34	.020	-0.001 ± 0.01	-0.19	.853	0.06 ± 0.07	0.84	.404
C vs. IS when full light relative to shade	0.05 ± 0.11	0.40	.686	-0.001 ± 0.01	-0.10	.921	-0.01 ± 0.01	-1.25	.212	-0.11 ± 0.07	-1.54	.124
C vs. I when ambient +2°C relative to ambient	-0.001 ± 0.14	-0.001	.999	-0.01 ± 0.01	-0.86	.391	-0.01 ± 0.01	-1.16	.246	-0.07 ± 0.09	-0.77	.444
C vs. IS when ambient +4°C relative to ambient	-0.02 ± 0.14	-0.17	.865	-0.003 ± 0.01	-0.20	.841	-0.03 ± 0.01	-3.52	<.001	-0.33 ± 0.09	-3.81	<.001
C vs. I when ambient +2°C relative to ambient	0.10 ± 0.14	0.73	.466	0.01 ± 0.01	0.41	.681	0.001 ± 0.01	0.10	.920	-0.07 ± 0.09	-0.76	.448
C vs. IS when ambient +4°C relative to ambient	0.08 ± 0.14	0.56	.576	0.02 ± 0.01	1.21	.226	0.001 ± 0.01	0.07	.943	-0.15 ± 0.09	-1.71	.087
C vs. I when drought relative to watered	0.05 ± 0.11	0.44	.663	-0.01 ± 0.01	3.14	.002	0.01 ± 0.01	1.82	.070	0.01 ± 0.07	0.08	.934
C vs. IS when drought relative to watered	0.07 ± 0.11	0.63	.531	0.01 ± 0.01	2.20	.059	0.01 ± 0.01	1.59	.114	0.03 ± 0.07	0.41	.479

Note. C, I, and IS refer to mother trees that were subjected to three different irrigation treatments: three levels of temperature: (a) ambient (average temperature of past 30 years of Pfynwald, Valais, Switzerland where the seed-bearing trees are growing), (b) ambient +2°C, and (c) ambient +4°C; two levels of light: (a) full light and (b) shade (i.e., five times lower light availability relative to full light condition); and two levels of watering: (a) watered (watering to 45% of soil water holding capacity applied twice in week) and (b) drought (watering to 10% of soil water holding capacity applied once in week). Three hundred sixty seedlings were nested within six independent treatment units.

Abbreviations: C, control; I, irrigated; IS, irrigation stop; SEM, standard error of mean.

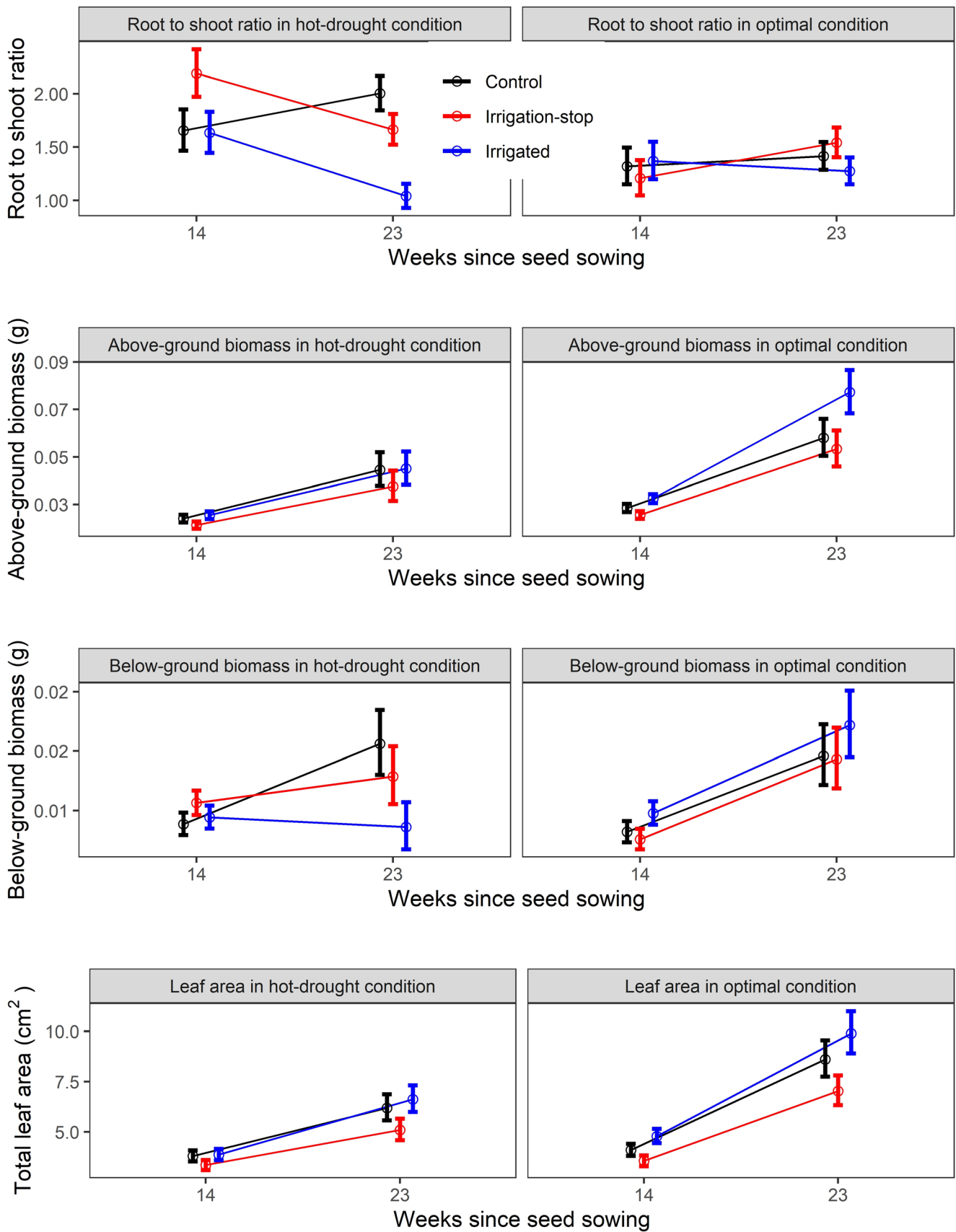


FIGURE 4 Linear mixed effect model-driven offspring root to shoot ratio, above-ground biomass, below-ground biomass, and total leaf area under two controlled greenhouse conditions: (a) optimum: ambient temperature with well-watered and full light condition and (b) hot-drought: ambient +4°C with drought and full light condition. The error bars represent mean \pm SE: 360 seedlings were nested within six independent treatment units

suggest that the effect of the parental environment on seedling performance cannot be always explained by seed mass and thus indicate the role of other transgenerational effects for Scots pine acclimation, which might include epigenetic mechanisms (Bräutigam et al., 2013) or nutrient composition in seeds (Milberg & Lamont, 1997). Moreover, other direct effects of the mother tree environment on the seed and embryo such as changed lipid, protein, or hormone composition might also be possible (Roach & Wulff, 1987). Seed mass as a driver for the difference in seedling performance can be excluded in this study because our analyses showed that trees from all irrigation treatments (including controls) produced large as well as small-sized seeds, and the number of large seeds and the individual seed weights were similar across irrigated, irrigation-stop, and control treatments (Figure 1). These results may suggest that although long-term irrigation improved the growth (biomass and leaf area) and physiological activity (root to shoot ratio) of Scots pine (Brunner et al., 2009; Dobbertin et al., 2010; Timofeeva et al., 2017), the reproductive potential such as production of heavier seeds has not been significantly changed in this study. This is in line with the findings of Bisi et al. (2016) that showed a non-responsive seed production behaviour of Scots pine to climate warming. Given the comparable seed weights among treatments and thus the same starting conditions concerning seed storage supply, seed germination in our study was primarily driven by watering after sowing of seeds and not by any other variables considered in our study (light, temperature, and mother tree treatments; Table S2).

Similar to the results of seed germination success, the offspring growth (leaf area and biomass) and mortality during the initial period (until Week 14 after sowing) was primarily driven by watering. The importance of water supply for Scots pine seed germination and offspring growth or mortality during the initial period has also been reported by other studies (Bachofen, Wohlgemuth, & Moser, 2019; Castro, 1999; Moser et al., 2017). Thus, the environmental legacy to which the mother trees have been exposed to did not influence the early offspring development, which was mainly affected by direct environmental cues. In contrast, the later offspring development showed clear indications for a memory of the parental environment. Under hot-drought condition the offspring were exposed to in the greenhouse, the development of root to shoot ratio from 14th to 23rd week provided valuable insights into biomass allocation strategies utilized by offspring from different irrigation origin. A large root to shoot ratio is considered to be an advantageous strategy to survive in a water-limited environment (Lloret, Casanovas, & Penuelas, 1999; Richter et al., 2012). Below-ground biomass of offspring from non-irrigated control trees increased significantly from the 14th to the 23rd week under hot-drought condition, whereas it either decreased or remained unchanged in offspring with mothers from the irrigation or irrigation-stop treatment (Figure 4). The increase in the root to shoot ratio in offspring originating from control trees indicates their ability to adequately response to harsh environmental conditions within several weeks, whereas the acclimation potential of the offspring from irrigated trees is—with the same genetic makeup—lower, leading to higher mortality. At the same time, the higher above-ground growth in terms of leaf area and biomass of the offspring from

irrigated trees under optimal (well-watered and full light) conditions points to a higher competitive potential under optimal growing conditions. Consequently, transgenerational memory is associated with a trade-off between the ability to acclimate to stressful conditions and to perform competitive under optimal conditions. Such trade-off patterns have also been observed for local (genetic) adaptation, as tree provenances that grow best under good conditions show often the strongest growth decline under suboptimal conditions (Jansen, Sohr, Kohnle, Ensminger, & Gessler, 2013).

The original irrigation experiment with the mother trees used a complete randomized block design with four blocks for each treatment (irrigation, irrigation-stop, and controls) in a homogeneous forest stand. Therefore, it is highly unlikely that the seeds from different mother treatments are genetically different. This was supported by genetic analyses of seeds using six microsatellite markers, which did not show a clustering of seed groups according to the three mother tree treatments and rather indicated that seeds represent one genetic cluster. Moreover, irrigation treatments that were started in the year 2003 did not cause any environmental filtering (i.e., genotype selection) as no increase in tree mortality in this old-growth forest stand occurred after irrigation.

Our results provided a strong indication that there are factors and mechanisms other than pollination, seed mass, and direct environmental drivers (light, water, and temperature) controlling offspring's long-term growth and mortality responses. Recent studies indicated a central role of transgenerational epigenetic effects for the acclimation/adaptation capacity of trees to drought (Raj et al., 2011; Yakovlev et al., 2010). The transgenerational epigenetic memory effect is broadly understood as a type of adaptive phenotypic plasticity that can be inherited by the following generation during the development of the embryo (Bossdorf et al., 2008; Richard, 2006). Trees are long-living organisms with a complex life cycle where they are often exposed to environmental fluctuations, and plasticity is widely recognized as an important mechanism for their survival under changing climate (Nicotra et al., 2010). Recent evidence suggests that long-term morphological and physiological plasticity to climatic stresses may induce epigenetic changes (i.e., changes in gene expression) in trees (Bräutigam et al., 2013; Gugger et al., 2016; Hrivnák et al., 2017; Yakovlev et al., 2010; Yakovlev et al., 2011), which can alter (i.e., silence or activate) gene expression and can thus influence the plant growth and physiological responses to changes in the growing environment (Bossdorf et al., 2008; Verhoeven et al., 2016).

In our study site, the long-term irrigation (from 2003 to 2016 in irrigated plot and from 2003 to 2013 in irrigation-stop plot) might have thus induced changes in gene expression through epigenetic mechanisms as seen in their different acclimation potential to hot-drought as well as optimal conditions. However, we cannot exclude other physiological and molecular mechanisms as there might be also impacts of the environment of the mother tree on nutrient, lipid, protein, or hormone composition in seeds. Independent of the nature of the mechanism, the offspring are displaying a carryover effect of their parental environment on their growth and survival. Epigenetic changes on the molecular level as induced by the parental

environment have recently been reported for Norway spruce (*Picea abies*) and poplar (*Populus* spp) trees. For Norway spruce, Yakovlev et al. (2010) sequenced 16 micro RNAs that showed different transcription levels between offspring from cold environment and from warm environment. For poplar, Raj et al. (2011) collected trees of same genotypes from different geographic locations, grew them under common environmental conditions, and exposed them to drought stress. In this experiment, genome-wide DNA methylation levels and transcriptome composition related to environmental conditions where parental trees were growing were detected. Based on these observations, the inheritance of changes in gene expression is a likely explanation for the differences in functioning observed in our study. Our results are complementing these molecular studies by showing the functional phenotypic consequences of the transgenerational memory for the offspring acclimation potential. However, our studies under field conditions also indicate that very harsh environmental conditions as observed in the extremely hot and dry summer 2018 (Buras, Rammig, & Zang, 2019) can override such effects. In nonwatered seed beds of the field experiment, 90–100% of germinated offspring were dead by the end of the 16th week since sowing of the seeds independent of the treatment of the mother trees. Comparable overriding effects of direct extreme environmental drivers have, however, also been observed for tree genotypes with different (local) adaptation (Moser et al., 2017).

The future climate is expected to be associated with more frequent and longer drought events (Dai, 2012), which will challenge the acclimation potential of forest tree species (Adams et al., 2009). Here, we report on the strong influence of environmental memories that mother trees experienced on offspring's growth and survival. We show that offspring from trees with a given genotype growing in a dry environment are better adapted to survive in dry conditions as indicated by their biomass allocation strategies towards the root development. The impact of parental environmental memory on offspring's performance could have a profound impact on species composition of the terrestrial ecosystems. In the applied forest management context, foresters need to consider the location of seed sources (i.e., where parent trees are growing) prior to selecting their plantation materials (seedlings/saplings) from different seed orchards because a seedling stock may exhibit different phenotypic diversity, which may respond differently to prevailing conditions, despite their genetic identity.

ACKNOWLEDGEMENTS

We are grateful to the following colleagues from WSL who provided help on various aspects of this study: Gabor Reiss and Ulrich Wasem (experiment installations); Lukas Bächli, Marie Dobbertin, Yann Vitasse, and Charlotte Grossiord (data collection); Nikola Vasic and Stephanie Pfister (laboratory measurement); and Benjamin Dauphin (participated in a discussion). We are also grateful to the local forester Konrad Egger for technical support in the field, the Burgen Gemeinde Leuk for long-term permission of the field experiment, and the HYDRO Exploitation SA for supplying irrigation water and electricity.

AUTHOR CONTRIBUTIONS

A.K.B., A.G., A.R., and A.M. conceived the ideas; A.K.B., A.G., A.R., B.M., and T.W. designed methodology; M.P. and C.R. performed seed genotyping; A.K.B. analysed the data and led the writing of the manuscript with the important contributions from all authors.

CONFLICT OF INTEREST

None declared.

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How to cite this article: Bose AK, Moser B, Rigling A, et al. Memory of environmental conditions across generations affects the acclimation potential of scots pine. *Plant Cell Environ*. 2020;43:1288–1299. <https://doi.org/10.1111/pce.13729>