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A decade-long study on mortality in European larch (*Larix decidua* Mill.), Japanese larch (*Larix kaempferi* (Lamb.) Car.) and their hybrid

Naincy Sagar[1], Luc E. Pâques[1*] and Stéphane Chantepie[1]

Abstract

Key Message This study, based on a clonal larch experiment under contrasting soil water conditions, showed that Japanese larch exhibited the highest drought-induced mortality, followed by the hybrid and European larch. Mortality was driven by low soil water availability, high temperature, and vapor pressure deficit in late spring, and was negatively correlated with growth, indicating potential for selecting genotypes that combine high growth with greater survival.

Context Mortality induced by climate extremes, particularly by drought, has been of growing concern due to the increasing frequency, intensity, and duration of drought episodes. Predicting tree mortality is a complex and multifaceted issue that involves not only tree-specific traits but also the environment, making it more challenging.

Aim We aimed to identify species-specific mortality induced by the interaction between drought and other environmental factors, as well as the relationship between mortality and growth performance.

Method We estimated the variation in the probability of mortality of *Larix decidua* Mill., *Larix kaempfer* (Lamb.) Car. and their hybrid over ten years in two plots with contrasting soil water availability. Using logistic regression, we identified the environmental variables and time windows that best explained this variation under two watering treatments. Finally, we tested the association between radial growth and mortality.

Results Mortality was negligible for all three taxa in the irrigated plot. In the non-irrigated plot, Japanese larch exhibited the highest mortality, European larch the lowest, and the hybrid an intermediate level. Maximum temperature and vapor pressure deficit in late spring explained the temporal dynamics of mortality. Mortality was associated with reduced radial growth and was negatively correlated with mean long-term growth performance.

Conclusion The differential mortality response of the two species and their hybrid to drought can provide insights for breeding programs. Selection for combined growth and enhanced survival seems possible.

Keywords Climate change, Mortality, Growth, Drought, *Larix*

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*Correspondence:
Luc E. Pâques
luc.paques@inrae.fr
[1] INRAe, BioForA, UMR0588, Orléans 45075, France

1 Introduction

A growing body of scientific literature highlights the large negative impact of climate change across all forested biomes, particularly due to more severe and recurrent drought episodes (Solomon et al. 2007; Cook et al.

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2018), irregular precipitation (Donat et al. 2013), fire hazards (Halofsky et al. 2020), and increased impacts of pests and diseases (Sturrock et al. 2011). Tree mortality due to drought events has been measured worldwide (Hammond et al. 2022), and the effect of drought on mortality is often amplified by an increase in air temperature (Van Mantgem et al. 2009; Peng et al. 2011; Wolf and Paul-Limoges 2023).

Predicting tree mortality is a complex and multifaceted issue. The reasons behind mortality risk are multiple (abiotic, biotic, human) and often interact with each other (Will et al. 2013). This is particularly true for drought-induced mortality. As highlighted in a review by Teskey et al. (2015), the impact of drought on mortality is highly dependent on the characteristics of the event itself (timing, duration, intensity, frequency). In addition, intrinsic tree factors such as size and age, along with the local environment (e.g. soil, stand density), can affect the vulnerability of trees and stands (Dobbertin 2005; Trugman et al. 2021). Moreover, drought often occurs with other stressors, creating interplay effects that can exacerbate tree mortality. High temperatures, for example, can increase drought severity by enhancing evapotranspiration rates, further stressing water resources, and causing physiological stress, leading to increased mortality (Allen et al. 2010; Hartmann et al. 2018; Matusick et al. 2018). This complexity means that a better understanding of the processes driving tree mortality, as well as the impact of drought intensity and duration, is required in order to improve predictions of tree responses to climate change.

Under drought conditions, trees often undergo changes in the foliage (discoloration, leaf shedding) (Vollenweider et al. 2016; Rosner et al. 2016) and experience stem structure alterations, often accompanied by top dieback and cracks (Cameron et al. 2017). These modifications, combined with a marked reduction in both apical and radial growth, with a decrease in the size and number of meristematic cells, are commonly associated with mortality induction or can cause death directly (Orwig and Abrams 1997; Gil-Pelegrín et al. 2004).

The timing, duration, and frequency of drought have an effect on tree responses. An early-season drought episode decreases effective apical and radial expansion that usually occurs during the spring-early summer period, while a late drought depletes carbohydrate reserve, which is necessary for winter survival (McDowell et al. 2008). Drought can lead to immediate tree death within the year (Wolf and Paul-Limoges 2023), but can also cause damage that extends to the following or subsequent years (Bigler et al. 2007). With prolonged or consecutive droughts, radial growth in Douglas fir exhibited more severe decreases in resistance and recovery than during single episodes of a similar intensity (Guisset et al. 2024).

The mortality risk caused by drought also depends on tree size (Mueller et al. 2005) and growth rate (Dobbertin 2005), which means that it is critical to understand the differential response of individual trees. The pace of growth can serve as an early indicator of drought susceptibility, as reduced growth is commonly observed closer to mortality events (Reich 2014). Variation in growth rate is influenced by how trees distribute their carbon resources and how resilient they are to environmental stress and thus to mortality (Wang et al. 2012). Whilst faster-growing trees have a lower resistance to drought stress, they usually exhibit higher recovery (Tao et al. 2024). Overall, faster-growing clones (and taller trees) can achieve higher survival, as shown by some authors (Giovannelli et al. 2007; Kaczmarek et al. 2013). However, the ability to allocate carbon resources is species- and genotype-specific, indicating that while fast-growing trees often show higher survival (McLaughlin et al. 2003; Bennett et al. 2015), their resilience to drought may depend not only on growth rate but also on their hydraulic traits (Trugman et al. 2021).

Different tree species exhibit varying levels of susceptibility to climate-induced stress and, thereby, to mortality. Overall, angiosperm trees seem less affected by drought-related mortality than conifers (Klein 2019; Lloret et al. 2022) due to their higher stomatal sensitivity, leading to early closure of stomata to conserve water. Nevertheless, this stomatal strategy can lead to carbon deprivation when extreme conditions persist (McDowell et al. 2008).

Like a few other gymnosperms, the larch genus (*Larix*) uniquely combines the needle-like leaves of conifers with the seasonal leaf shedding of deciduous trees. Larches are highly valued by foresters and industry for their rapid juvenile growth and the exceptional quality of their wood. In Europe, three main taxa are cultivated (Pâques 2013): European larch (*Larix decidua* Mill.), Japanese larch (*Larix kaempferi* (Lamb.) Car.), and their hybrids. Compared to some evergreen conifers, European larch seems poorly adapted to dry conditions (Eilmann and Rigling 2012; Lévesque et al. 2013; Oberhuber et al. 2014, 2015). Japanese larch, native to the high-elevation volcanoes of Hondo Island, with their very humid environments even during summer, is highly sensitive to summer drought (Masson 2005), and its planting is restricted to oceanic climates. Compared to its parent species, hybrid larch exhibits greater growth (known as heterosis) and plasticity to water availability (Marchal et al. 2019) and more effectively buffers environmental conditions overall (Pâques 2013). Although the physiological, anatomical, and growth responses to drought of the three larch taxa have been compared in studies with seedlings grown in nurseries or greenhouses (Haasemann 1986; Sasani et al. 2021), drought-induced mortality and growth have

not been studied in plantations. Growth rate (and size) can be a source of vulnerability (Dobbertin 2005), so the faster growth of the hybrid compared to European and Japanese larches (Marchal et al. 2017), which is favored by breeding, may be inappropriate at water resource-limited sites.

Our study takes advantage of a unique experiment, involving the three larch taxa planted under two contrasting watering treatments, to address the pressing need to examine the responses of the different taxa, the impact of climate factors, and time variations on tree mortality. Based on logistic regressions, we estimated the probability of mortality across the watering treatments and years for the three taxa and answered the following questions: (1) Do the three larch taxa exhibit different susceptibilities to mortality? (2) Which climatic parameter(s) and time window best predict mortality variation over time, and are they similar for the three taxa? (3) Does high vigor affect the vulnerability of trees to mortality when subjected to water constraints?

2 Materials and methods

2.1 Experimental site and genetic material

The material monitored in this study is a subset of an inter-/intra-specific diallel mating design involving nine European larches (EL) and nine Japanese larches (JL) (Marchal et al. 2017). The European larches were from the Sudetan Mountains population (*sudetica*) and the Japanese larches were from different populations on Hondo Island. This subset includes 12 full-sib families of EL, 12 of JL, and 12 full-sib hybrid larch (HL) families, all sharing the same EL and JL parents. Each family includes 12 individuals (clones), each represented by a variable number of ramets produced by grafting in the spring of 2011. In order to reduce a possible impact of the rootstock on tree development, seedlings from a unique seed source (FH201-Lavercantière-PF hybridization seed orchard) were used. Progenies from this orchard recombining one EL clone as mother and around 30 full-sib clones of JL as father are characterized by a narrow genetic basis (Philippe and Pâques 2003). A total of 1900 trees were included in the analyses.

Grafted plants were established when they were 2 years old at the nursery of INRAe-Orléans (latitude: 47.83 N, longitude: 1.91 E, elevation: about 108 m) during winter 2013. The experimental site is on a flat area characterized by a poor sandy soil with heavy gravel loads and a poor water retention capacity (around 35 mm). Combined with a low annual rainfall (less than 700 mm), conditions are far from ideal for reforestation with larch but highly suitable for testing its susceptibility to soil water deficit. To this end, the trial was divided into two plots to study the behavior of the three taxa of larch (EL, JL, HL) with two different irrigation treatments (hereafter "Treatments"): irrigated (IRR) and non-irrigated (NIRR). The irrigated plot has been drip irrigated daily (since 2015) during the whole growing season (April to September), and the other (NIRR) has not received any irrigation except during the first 2 years following planting. Monthly differences in water supply (rain + irrigation) can be seen in Fig. 1 together with the soil water potential. In the context of our experiment, drought is characterized by lower soil water potential in summer compared to other seasons and is amplified in the NIRR plot. Within each plot, a split-plot design is used with taxa planted in bands replicated three times and four incomplete randomized blocks within bands with complete randomization of clones. This design was selected to reduce competition between taxa. Trees were planted at a spacing of 2.5 × 3 m. Regular mowing is the only cultivation treatment used to reduce grass competition.

2.2 Meteorological, edaphic variables, and mortality assessment

The meteorological data from 2013 to 2023 originate from a Meteo-France meteorological station located within the nursery of INRAe-Orléans (Lat: 47.83 N, Long: 1.91 E). The daily data included temperatures (average, maximum, and minimum) in degrees Celsius, relative humidity (%), rain (mm), and global radiation (W/cm^{-2}). Based on these data, the Vapor Pressure Deficit (VPD, KPa) was calculated following Brice and Hall (2020), using relative humidity and average air temperatures. In 2015, the site was equipped with six soil humidity probes (TDR model CS616 and WM model 257L) installed at depths of around 24 cm (TDR24; WM24) and 60 cm (TDR60, WM60) in both IRR and NIRR plots to record the soil water content and potential. In addition, BILJOU, a water balance model (Granier et al. 1999; https://appgeodb.nancy.inra.fr/biljou/fr/), was used to estimate the soil relative extractable soil–water (REW). Due to the difficulty in monitoring Leaf Area Index (LAI, a major parameter in the model) across years and with canopy gaps, we fixed it at a stable value of 5. REW was thus used as an index to compare years and to characterize the variation in soil water availability within and over the years.

Data on tree mortality were collected yearly from 2013 to 2023 (Pâques 2025a). Each tree observed during the following spring with persistent height elongation was considered alive, and a tree with a dried or dead stem was considered dead. A year after the tree was considered dead, it was excluded from the analysis. Absence or presence of stem top dieback was also included in the study and recorded annually. Data can be found at https://doi.org/10.57745/RRUYLW.

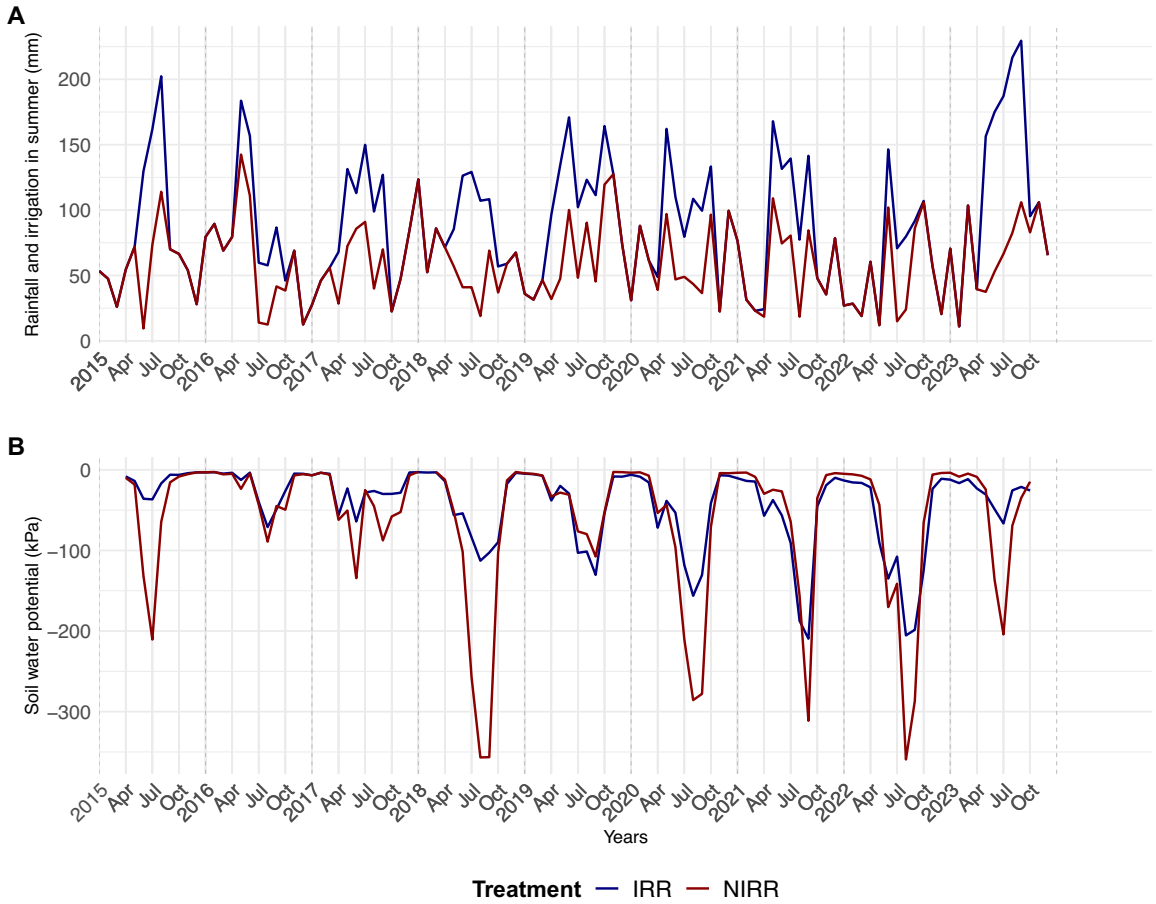


Fig. 1 **A** Available water, i.e., monthly cumulated water supply (rain and irrigation) for trees in the two treatments over the years 2015 to 2023, and **B** soil water potential (kPa) over the years (at 24 cm soil depth) measured by means of watermark soil probes at the experimental site. The blue line refers to the irrigated treatment (IRR), and the red line corresponds to the non-irrigated treatment (NIRR)

2.3 Statistical analysis

2.3.1 Effect of treatment, year, and taxa on mortality

The effect of soil water availability, year, and taxa on the probability of mortality of trees was assessed by modeling the live/dead outcomes with logistic regressions (i.e., a generalized linear model with a binomial distribution for outcome and logit link function). All possible combinations of the factors (year, taxa, and treatment) and their interactions were tested to comprehensively evaluate their effects on tree mortality. The models were evaluated using the Akaike Information Criterion corrected for small sample size (AICc, Hurvich and Tsai 1995), with the smallest AICc identifying the model that best fits the data, and where a difference of at least 2 units from other candidate models is taken as substantial support (Burnham and Anderson 2004).

The analysis used the "glm" function from the R programming language (R Core Team, 2024). In logistic regression, when the predictor variables perfectly predict the outcome variable, their coefficient estimates tend toward infinity (called separation) and may prevent the model from converging. To address this issue, we fitted the logistic regressions using penalized likelihood methods implemented in the "brglm2" package (Kosmidis 2022), providing finite and well-behaved likelihood estimates even in complete or quasi-complete separation cases (Firth 1993).

2.3.2 Best environmental predictor of mortality and relevant window periods

Before testing for the best environmental predictor of mortality, we selected uncorrelated meteorological and edaphic variables.

We applied logistic regression to determine the meteorological and edaphic variables, along with their most relevant window periods, that best predict tree mortality. We focused exclusively on the non-irrigated area of the experimental site, as almost no mortality was observed in the irrigated (IRR) area. The analysis was conducted separately for the three larch taxa. To explore

different window periods, we utilized the package "climwin" which systematically tests a range of possible windows to determine those that best explain the variation in mortality between years (Van De Pol et al. 2016). For each meteorological and edaphic variable, weekly means were tested over the period from mid-April to October 30 th. We determined the meteorological and edaphic variables that provided the most explanation of the data, along with the optimal climate window, by comparing the ΔAICc of each model with a model without weather data included (i.e., a constant model). Two strategies were used to ensure the environmental signal's robustness. First, to decrease the risk of overfitting, the mean ΔAICc of each model was estimated using repeated *K*-fold cross-validation with $k = 5$ (Van De Pol et al. 2016), repeated 200 times, resulting in 1000 evaluations for each mean. Then, we used the mean ΔAICc to find the models with the best support ($\Delta AICc_{best}$). The *K*-fold implementation from the "climwin" package was slightly modified to measure the predictive accuracy of logistic regressions using a logarithmic loss function. Second, to ensure that the environmental signal identified by the best candidate models did not result from chance, the "environmental" variables were randomized, and a new search for window periods was initiated. This procedure was repeated 1000 times, and the best candidate model from each randomized dataset was used to build a distribution of $\Delta AICc_{rand}$ (Van De Pol et al. 2016). The probability of observing $\Delta AICc_{best}$ by chance (termed pΔAICc) was estimated as the percentile of $\Delta AICc_{rand}$ that exceeded the value of $\Delta AICc_{best}$ (Bailey et al. 2016). The amount of deviance explained by the best "environmental" variables on mortality and the significance of the relationship were assessed through an analysis of deviance (ANODEV, Skalski 1996).

2.3.3 Link between tree growth and probability of mortality at individual and clonal level

We first investigated the relationship between individual live/dead status and the annual diameter increments, measured the year preceding mortality. The analysis was conducted only in the non-irrigated plot, in which the highest loss of individual trees was detected. We fitted a logistic regression with the taxa effect interacting with both the annual diameter increment (hereafter diameter growth) and year as categorical fixed effects to account for potential year-to-year variation. To facilitate comparability across taxa, the diameter growth was centered-reduced before analysis. As no diameter growth was estimated for 2014, the period included in the analyses ranged from 2015 to 2023. The study used the "glm" function with a penalized likelihood (see above for details) from the R programming language (R Core Team, 2024). The significance of the interaction between taxa and diameter growth was assessed using the Wald test implemented in the 'lmtest' R package (Zeileis and Hothorn 2002). The probability of mortality was predicted using the 'marginal effect' R package (Arel-Bundock et al. 2024).

The covariation between the diameter growth increment and the probability of mortality was explored at the clonal level using trivariate mixed linear regressions. The models were built to test for the covariation between the mortality of clones in the non-irrigated plot (trait 1), the diameter growth measured on identical clones located in the non-irrigated plot (trait 2), and the diameter growth of their respective clones in the irrigated plot (trait 3). We accounted for the average yearly effect (confounded with age) on diameter growth (IRR and NIRR) and mortality by fitting years as a fixed effect for all three traits. The variances and covariances between both diameter growth and probability of mortality among clones were modeled as a multivariate clone random effect. This allowed us to estimate a variance–covariance matrix among traits at the clone level and predict the merit of each clone for each trait. The correlations between the three traits (COR_{trait}) were estimated by dividing the covariance estimates by the product of the squared variances of the traits.

Trivariate mixed models were fitted under a Bayesian framework with the MCMCglmm package (Hadfield 2010), which allows setting different distributions for each trait of a multivariate model (here gaussian for both diameter growth and binomial for live/dead trait). We used a weakly informative Gelman prior for fixed effects of the mortality trait where $D = (\pi^2/3) + \sigma^2$ (with σ^2, the total variance due to the random effect). For the random effect, we used a parameter expanded prior with a scale of 10e4 (Hadfield 2010). As the residual variance is not identifiable in the likelihood of the binary trait, the residual variance for the mortality trait was set to one (Hadfield 2014). Models were run on 11e6 iterations with a burning phase of 1e6 iterations and a thinning of 5e3. Then, the posterior distribution of each parameter consists of 2e3 posterior samples. Convergence was checked through visual inspection and measure of autocorrelation of the posterior samples (we ensured that autocorrelation was lower than 0.05). To estimate the statistical differences in COR_{trait} between taxa, we first calculated the difference in posterior samples between taxa for each COR_{trait}. We then estimated the 95% credible interval on these differences and considered the difference statistically significant at a *p*-value of 0.05 if the credible interval did not include 0.

3 Results

Tree mortality and reduced growth were observed across all taxa in the non-irrigated (NIRR) compared to the irrigated (IRR) treatment (Figs. 2, 3, and 4). Under almost all conditions, hybrid larch exhibited the highest growth performance, either matching or exceeding that of European and Japanese larch species (Fig. 2). Japanese larch appeared to be the most vulnerable, exhibiting the highest loss in the number of trees in both treatments (Fig. 4), with more than 45% of dead trees in 2023 in the NIRR plot. European larch (EL) followed, with a mortality rate of around 35%, while hybrid larch (HL) showed slightly lower mortality, reaching just over 30% in the NIRR treatment, approximately 15% less than Japanese larch. In parallel, the top dieback symptoms were nearly absent in the irrigated plot but were more frequently severe in the non-irrigated plot. Japanese larch was the most affected taxon, with almost 50% of trees with symptoms, European larch the least (25%), and hybrid larch intermediate (around 35%) in 2023. The incidence of top dieback in 2015 was highest in the case of Japanese larch (almost 50%), but for 2018, the highest increase in top dieback was for European larch (15% in 2017 to around 25% in 2018), while

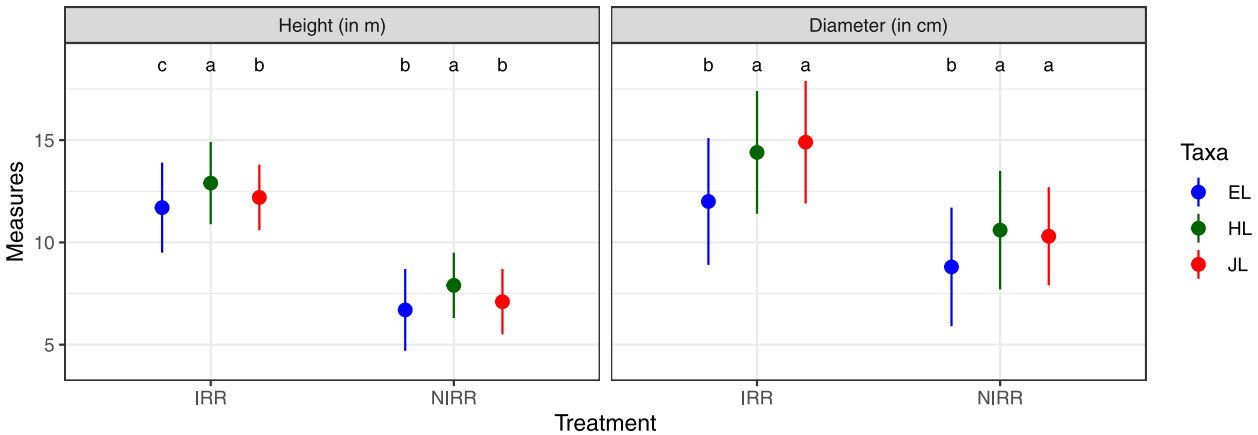


Fig. 2 Average growth in irrigated (IRR) and non-irrigated (NIRR) plots at age 10 for European larch (IRR: 317; NIRR: 180), Japanese larch (IRR: 320; NIRR: 140), and hybrid larch (IRR: 308; NIRR: 178). Bars correspond to the standard deviation. Significant differences in means between taxa were tested using Tukey's test for each treatment and each trait separately. Different letters indicate significant differences

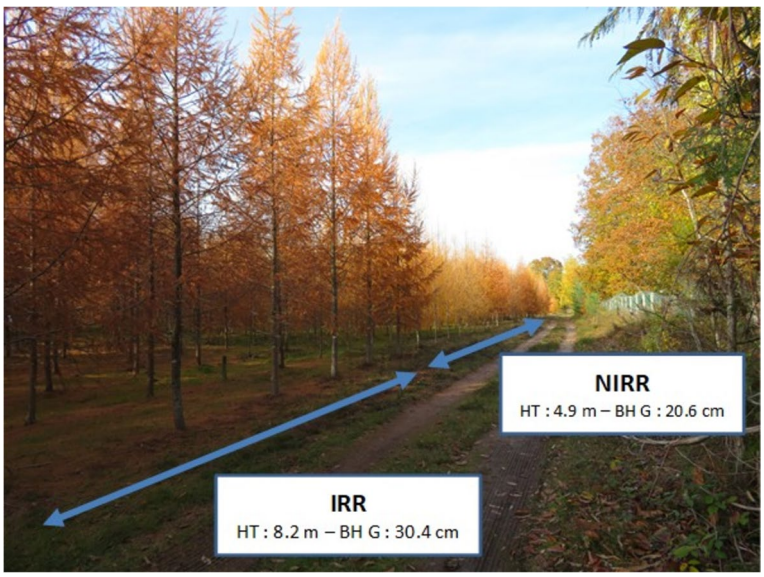


Fig. 3 General view of the experiment at INRAE Orléans nursery in Autumn 2019, with irrigated (IRR) and non-irrigated (NIRR) plots. Average height (HT) and breast height girth (BH G) in Fall 2019 are presented

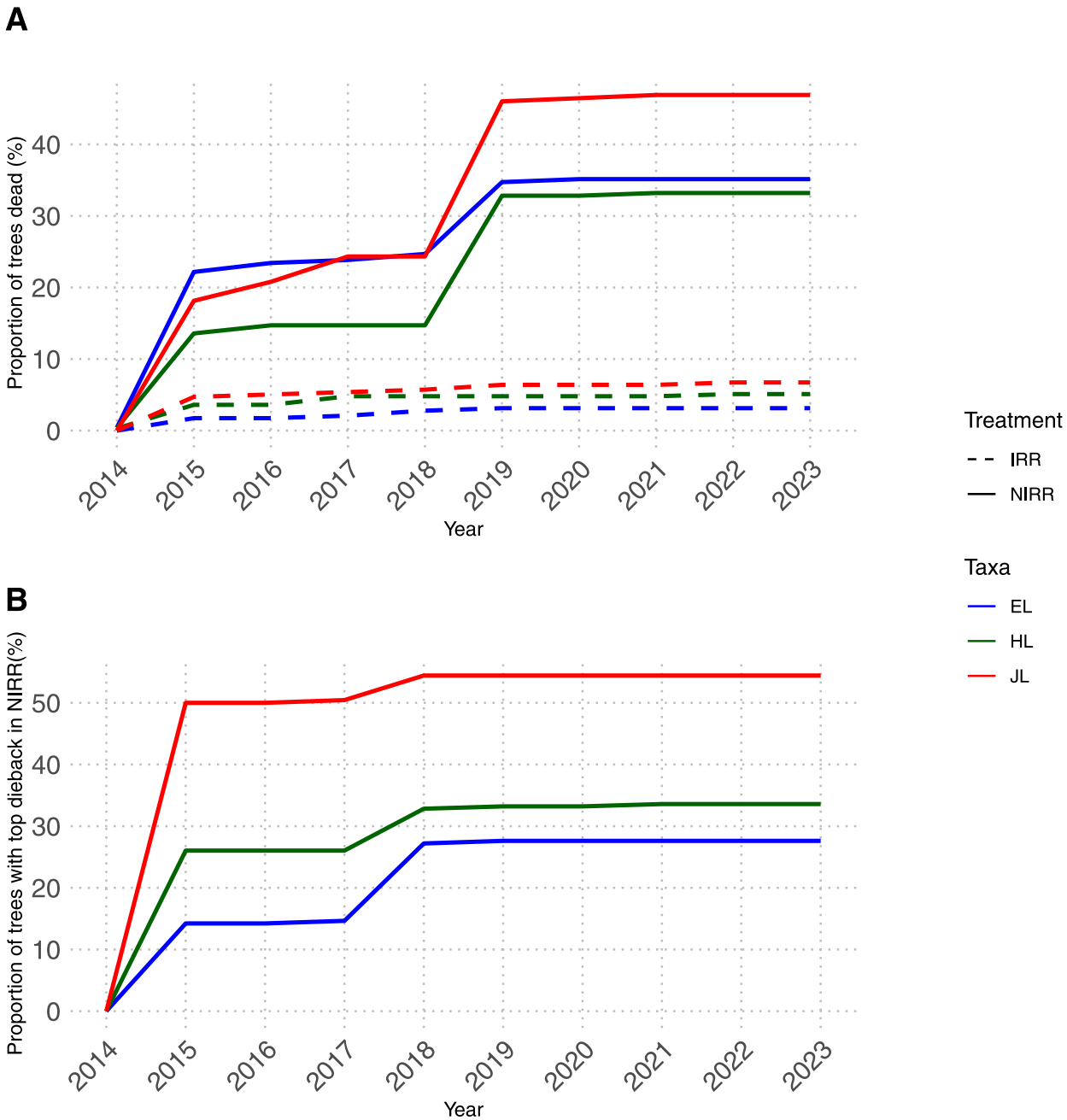


Fig. 4 **A** Cumulative percentage of trees lost from 2014 to 2023 for the two treatments (IRR and NIRR) and the three taxa, EL (blue), JL (red), and HL (dark green). **B** Cumulative percentage of top dieback in the non-irrigated (NIRR) plot

hybrid larch showed a gradual increase, reaching 35% in the same year.

3.1 Effect of treatment, year, and taxa on mortality

Among all logistic regressions that tested the impact of treatment, year, and taxa on mortality, the AICc comparison provided substantial statistical support for the model with an additive effect of taxa and interaction between treatment and year (ΔAICc = 7.951 when compared with the second-best model Treatment × Year) (Table 1).

According to this best model, Japanese larch mortality was higher than that of hybrid and European larch. The probability of mortality increased in the non-irrigated plot compared to the irrigated plot. A significant variation in the probability of mortality was estimated among years, with a higher probability of mortality in 2015 and

Table 1 Result of the model selection based on AICc (corrected Akaike information criterion). Models are ranked from lowest to highest AICc. Taxa refers to the European, Japanese, and Hybrid larches. Treatment corresponds to the two water treatments: irrigated and non-irrigated and the years are from 2014 to 2023. ΔAICc is estimated relative to the most parametrized model (Taxa × Treatment × Year)

Code	Model	AICc	ΔAICc
1	Taxa + Treatment × Year	2099.752	− 78.649
2	Treatment × Year	2107.703	− 70.698
3	Taxa + Treatment + Year	2128.803	− 49.598
4	Taxa × Treatment + Year	2130.673	− 47.728
5	Treatment + Year	2136.552	− 41.849
6	Taxa × Treatment × Year	2178.401	0
7	Taxa + Year	2421.401	243
8	Year	2426.181	247.8
9	Taxa × Year	2437.666	259.3
10	Taxa + Treatment	2781.751	603.4
11	Taxa × Treatment	2783.617	605.2
12	Treatment	2791.124	612.7
13	Taxa	3091.297	912.9
14	Constant	3096.847	918.4

2019 for the non-irrigated plot. In the irrigated plot, the greatest probability of mortality was detected in 2015, but it was below 0.3 (Fig. 5).

3.2 Predictor of mortality with the explicative environmental variable, climate window, and influence of years

3.2.1 Environmental variable selection and extreme years

Strong correlations were found between several of the climatic variables (Table 2). We removed T_avg and T_min from the climatic analyses to avoid redundancy, as they correlated with T_max (0.99 for T_avg, 0.93 for T_min). VPD and R_hum were negatively correlated (−0.89); R_hum was excluded from further analysis, and VPD, which combines temperature and humidity, was a preferred variable because it provides a more comprehensive measure of plant physiological stress linked to air drought. TDR24 and TDR60 provide a direct measure of volumetric water content at 24 cm and 60 cm depth and are highly correlated with REW (0.91 between REW and TDR24 and 0.89 between REW and TDR60). Soil water mark, which measures the pressure needed for the roots to draw up water (WM24 and WM60), was also found to be correlated with REW (−0.73, WM24 and −0.704,

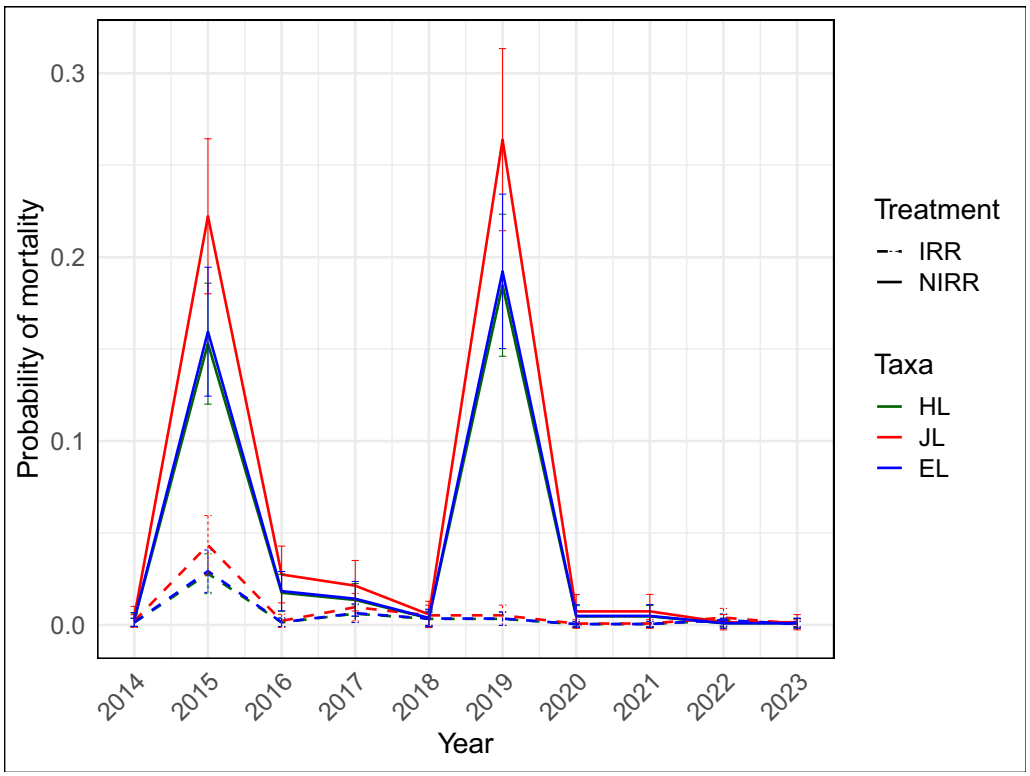


Fig. 5 Estimates of mortality probabilities from 2014 to 2023 for the two treatments among the three taxa of Larch according to the best mortality model (model 1, Table 2). EL, JL, and HL are European, Japanese, and Hybrid larches, respectively; IRR and NIRR are irrigated and non-irrigated plots. Bars around estimates represent the 95% confidence interval

Table 2 Pearson correlations between environmental variables recorded at INRAe Orléans meteorological station. T_avg is the average temperature, T_min is minimum temperature, T_max is maximum temperature, R_hum is relative humidity, G_rad is global radiation. REW is relative extractable water, VPD is vapor pressure deficit, TDR is Time domain reflectometry at 24 and 60 cm soil depth, and WM is Watermark soil probe measurement (soil water potential) at 24 and 60 cm depth. The values are bold when significant ($p < 0.05$)

	WM24	WM60	TDR24	TDR60	Rain	T_avg	R_hum	G_rad	T_min	T_max	VPD	REW
WM24	1	0.97	− 0.81	− 0.80	− 0.11	0.64	− 0.49	0.49	0.61	0.66	0.65	− 0.73
WM60		1	− 0.77	− 0.78	− 0.11	0.63	− 0.45	0.44	0.61	0.64	0.62	− 0.70
TDR24			1	0.95	0.18	− 0.84	0.67	− 0.76	− 0.77	− 0.87	− 0.81	0.91
TDR60				1	0.08	− 0.84	0.58	− 0.70	− 0.79	− 0.85	− 0.76	0.89
Rain					1	0.11	0.18	− 0.05	0.22	0.03	− 0.08	0.10
T_avg						1	− 0.71	0.85	0.97	0.99	0.89	− 0.91
R_hum							1	− 0.89	− 0.55	− 0.76	− 0.89	0.69
G_rad								1	0.73	0.88	0.89	− 0.80
T_min									1	0.93	0.80	− 0.86
T_max										1	0.90	− 0.90
VPD											1	− 0.88
REW												1

WM60). REW was preferred because it is a more integrative variable to reflect soil water availability. Thus, the climate variables selected for further analysis were maximum temperature (T_max), vapor pressure deficit (VPD), rain (Rain), relative extractable water (REW), and global radiation (G_rad).

3.2.2 Explicative environmental parameter and window for each taxon

For European Larch, T_max was the most explicative climate variable (based on AICc, Table 3), and the climate windows with the strongest correlations to mortality were concentrated in June and July. Specifically, the most

Table 3 Output from the "climwin" analysis for each European (EL), Japanese (JL), and hybrid (HL) larches. Models are ranked based on the ΔAICc (constant model − climatic model). For each taxon, only the first six models are presented. Model with substantial support are displayed in bold along with the result of the analysis of deviance (*F* statistics, *p*-value significance level, R^2). R^2 corresponds to the annual variation in mortality explained by the variation in the climatic variable

	Variable	ΔAICc	Window period	pΔAICc	*F* statistics	*p*-value	R^2 (%)
European larch	T_max	− 106.547	June 21 to July 8	< 0.001	47.29	< 0.001	85.53%
	T_max	− 101.55	June 21 to July 4	< 0.001			
	T_max	− 99.82	June 21 to July 6	< 0.001			
	T_max	− 98.782	September 3 to September 9	< 0.001			
	T_max	− 98.07	June 25 to July 1	< 0.001			
	T_max	− 98.07	September 3 to October 31	< 0.001			
Japanese larch	VPD	− 75.27	June 14 to July 4	< 0.001	20.46	0.002	71.89%
	VPD	− 74.56	June 21 to July 4	< 0.001	20.29	0.0019	71.72%
	T_max	− 73.83	June 21 to July 4	< 0.001	21.84	0.002	73.19%
	T_max	− 71.77	June 14 to July 8	< 0.001			
	T_max	− 71.12	June 21 to June 28	< 0.001			
	VPD	− 70.49	July 4 to July 6	< 0.001			
Hybrid larch	VPD	− 128.97	June 21 to July 4	< 0.001	6.958	0.029	46.51%
	T_max	− 127.07	June 21 to June 27	< 0.001	7.31	0.026	47.75%
	T_max	− 119.74	June 21 to July 4	< 0.001			
	VPD	− 116.47	June 14 to July 4	< 0.001			
	VPD	− 114.51	June 21 to July 1	< 0.001			
	T_max	− 110.73	June 21 to July 8	< 0.001			

significant climate window opened and closed between June 21 and July 8. The model with T_max explained more than 85% of the annual variation in probability of mortality ($p < 0.05$) (Table 3). As the mean weekly T_max increased, the probability of European Larch mortality increased sharply, particularly at temperatures above 28 °C. This trend was driven by extreme years like 2015 and 2019, which had the highest probabilities of mortality (Fig. 6A).

In hybrid Larch, VPD and T_max explained the annual variation in mortality with the same support (ΔAICc between best VPD and best T_max models equal −1.90, Table 3). The climate window for VPD that best explained mortality spanned June and July (June 21 to July 4). The mortality was positively correlated with VPD in this window, with a steep increase in mortality observed for values over 1–1.25 kPa. VPD explained 47% of the annual variation in the probability of mortality ($p < 0.05$) (Table 3) (Fig. 6C). The climate window for T_max that best explained mortality was from June 21 to June 27. An increase in T_max during this window was related to an increase in mortality and explained 48% of the yearly variation in mortality.

For Japanese Larch, VPD and T_max explained the most annual variation in mortality (Table 3). Although two models showed similar and close AICc values for VPD, the best-fitting model was selected. For VPD, the climate windows ranged from June 14 to July 4, and the model explained 71.9% of the total variance. The probability of mortality increased with an increase in VPD: 2019 had the highest probability of mortality for VPD above 0.8 kPa (Fig. 6E). T_max had the same statistical support as VPD and explained 73.2% of variation in mortality with the best climate window from June 21 to July 4.

3.3 Tree growth and probability of mortality at the individual annual diameter growth and clonal level

Analyzing the link between the probability of mortality and diameter growth (Fig. 7) at the individual ring level, considering the ring growth in the preceding year, revealed a significant relationship between reduced diameter growth and increased probability of mortality among the three larch taxa in the non-irrigated plot. All three taxa had increased mortality when there was lower diameter growth (0% to approx. 20%), with a significant difference between species (Wald test on interaction term: $p = 0.026$). European Larch exhibited higher mortality trends, with mortality probabilities rapidly decreasing as diameter growth increased.

At the clonal level, we also found a significant negative correlation between the probability of mortality and diameter growth in the non-irrigated plot for all three taxa (Table 4). While the correlation was higher for Japanese larch, no significant differences could be detected between the species (Table 5). For hybrid larch, the variance in probability of mortality was small compared to the other taxa, and the correlation with diameter growth in NIRR was only marginally significant when considering the 95% Credible Interval (CI) (Table 4, Fig. 8). The probability of mortality of clones in the non-irrigated plot was not correlated with the diameter growth of their respective copies (ramets) in the irrigated plot (Table 4, Fig. 8) for any of the taxa, even though the diameter growth at clonal level was significantly correlated between the non-irrigated and the irrigated plots (Table 4).

4 Discussion

Predicting tree mortality induced by the combined effects of drought and heat is highly challenging, whether using physiological approaches or analyzing experimental setups on a large spatial scale. Indeed, although some studies have attempted to predict tree mortality based on physiological characteristics, such as water potential and hydraulic safety limits, these methods have proven relatively ineffective (Anderegg et al. 2016; Li et al. 2022). In large-scale mortality studies conducted across multiple geographic sites in natural forests or plantations, the exact causes of mortality are often unknown and most probably multifactorial. In addition, the high variability in factors such as soil, stand structure, age, and genetic origin affecting susceptibility and vulnerability to mortality makes it difficult to disentangle how these diverse influences interact across different temporal and spatial scales (Anderegg et al. 2016; Trugman et al. 2021). In our study, we were able to make use of observations on the same cloned trees from the three *Larix* taxa, established

(See figure on next page.)

Fig. 6 The probability of mortality in European (EL), hybrid (HL), and Japanese (JL) larch taxa as related to the key climatic variables. **A** European larch: probability of mortality related to mean weekly maximum temperature. **B** Hybrid larch: probability of mortality based on mean weekly maximum temperature. **C** Hybrid larch: probability of mortality based on mean weekly vapor pressure deficit. **D** Japanese larch: probability of mortality based on mean weekly maximum temperature. **E** Japanese larch: probability of mortality based on mean weekly vapor pressure deficit. The sites illustrate the relationship between mortality and climatic factors (climate windows are displayed at the top), with shaded areas representing 95% confidence intervals. The red points represent the percentage of mortality in a particular year

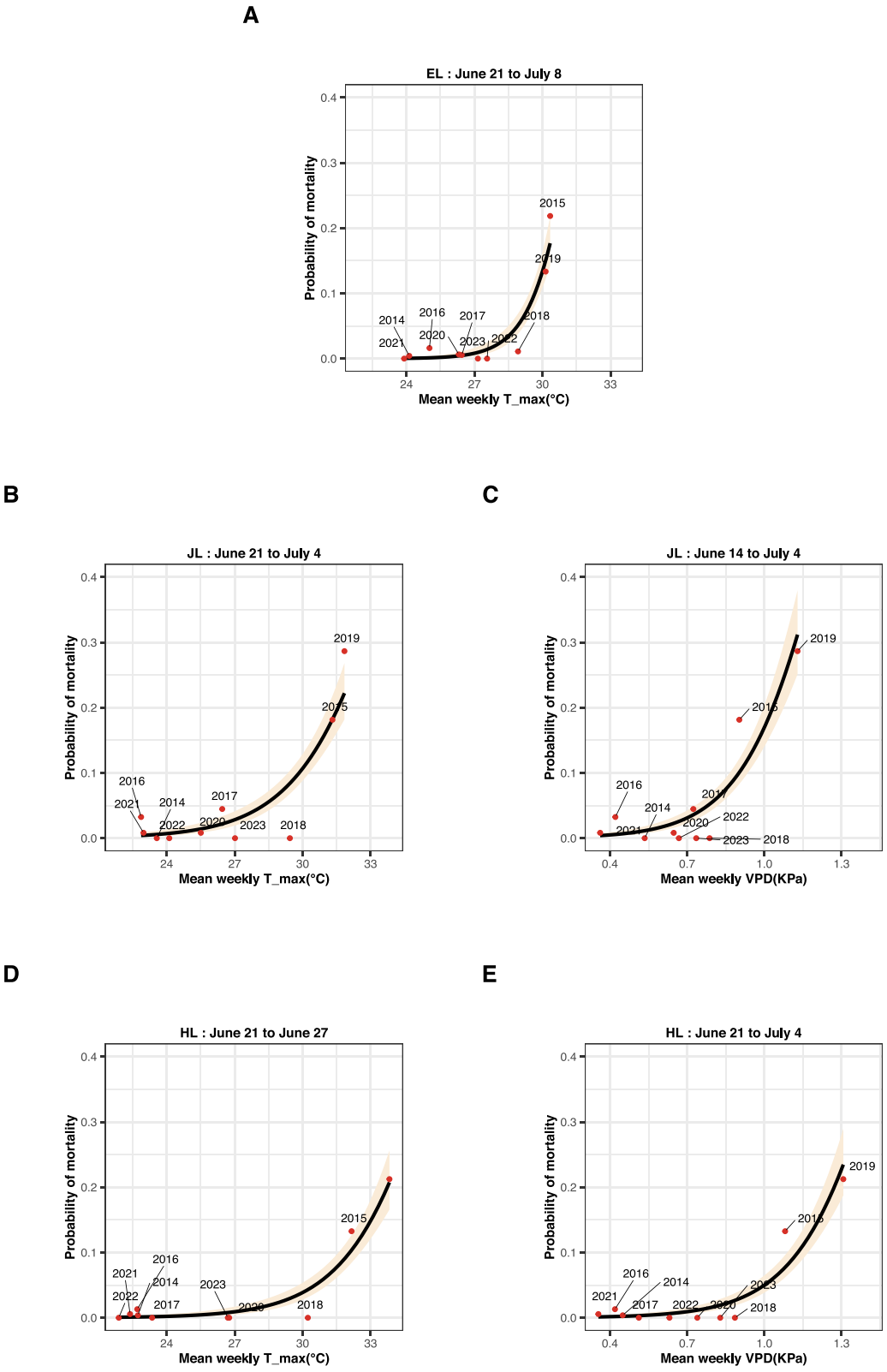


Fig. 6 (See legend on previous page.)

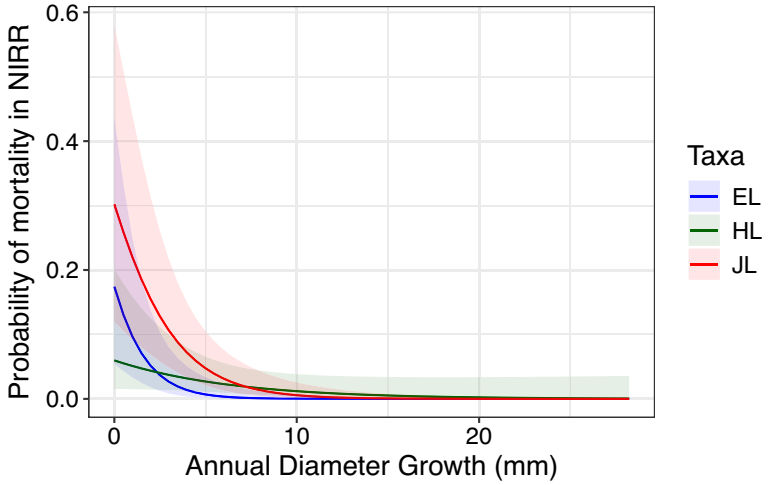


Fig. 7 Predicted probability of mortality for the three taxa (European, hybrid and Japanese) of larch in the non-irrigated plot (NIRR) as a function of annual diameter growth increment measured in the preceding year. The shaded areas represent the 95% confidence intervals

Table 4 Variance estimates of probability of mortality and of diameter growth in irrigated and non-irrigated plots at clone level and correlations between these traits. Estimates correspond to the posterior mode and brackets to the 95% credible interval. NIRR and IRR refer, respectively, to the non-irrigated and irrigated plots of the experiment. Significant correlations are in bold

	European larch	**Hybrid larch**	**Japanese larch**
Variance mortality	2.02 [0.47:6.24]	0.55 [0.00:1.99]	1.67 [0.77:4.34]
Variance growth IRR	0.11 [0.08:0.15]	0.13 [0.09:0.17]	0.11 [0.08:0.15]
Variance growth NIRR	0.19 [0.13:0.28]	0.17 [0.12:0.24]	0.23 [0.15:0.33]
Correlation (mortality, growth IRR)	− 0.09 [− 0.32:0.21]	0.12 [− 0.21:0.52]	− 0.17 [− 0.43:0.09]
Correlation (mortality, growth NIRR)	− 0.37 [− 0.78: − 0.03]	− 0.38 [− 0.83: − 0.05]	− 0.76 [− 0.95: − 0.49]
Correlation (growth IRR, growth NIRR)	0.24 [0.02:0.45]	0.28 [0.05:0.41]	0.22 [0.03:0.48]

Table 5 Difference in variance and correlation estimates between taxa for mortality probability and diameter growth in irrigated and non-irrigated plots. Variance and correlation values for each taxon are provided in Table 3. Estimates correspond to the posterior mode and brackets to the 95% credible interval. NIRR and IRR refer, respectively, to the non-irrigated and irrigated plots of the experiment. Significant correlations are in bold

	Difference HL-EL	**Difference HL-JL**	**Difference EL-JL**
Correlation (mortality, growth IRR)	0.18 [− 0.26:0.71]	0.29 [− 0.18:0.77]	0.10 [− 0.25:0.48]
Correlation (mortality, growth NIRR)	− 0.07 [− 0.57:0.54]	0.26 [− 0.20:0.79]	0.44 [− 0.09:0.80]
Correlation (growth IRR, growth NIRR)	0.03 [− 0.27:0.33]	0.04 [− 0.31:0.30]	0.03 [− 0.34:0.29]

on the same site under two contrasting watering treatments, in even-age plots with the same stand density and cultivation management. The grafting strategy used in our study was implemented by ensuring that the source of hybrid larch rootstocks was as genetically homogeneous as possible, in order to limit variable impacts of rootstock on mortality. While vegetative propagation by cutting allows the trees to develop on their own roots, this technique was not possible in this case because of the loss of juvenility of the ortets (age 17 at time of collection). Recently, a heteroplastic grafting experiment on hybrid and Japanese larches rootstocks showed that the scion had a significant effect on mortality but not the rootstock species (Pâques 2025b), suggesting a low or limited impact of grafting on our results.

Vegetative propagation by cutting of the individuals used in this study could have been a better alternative than grafting (i.e., trees development on their own

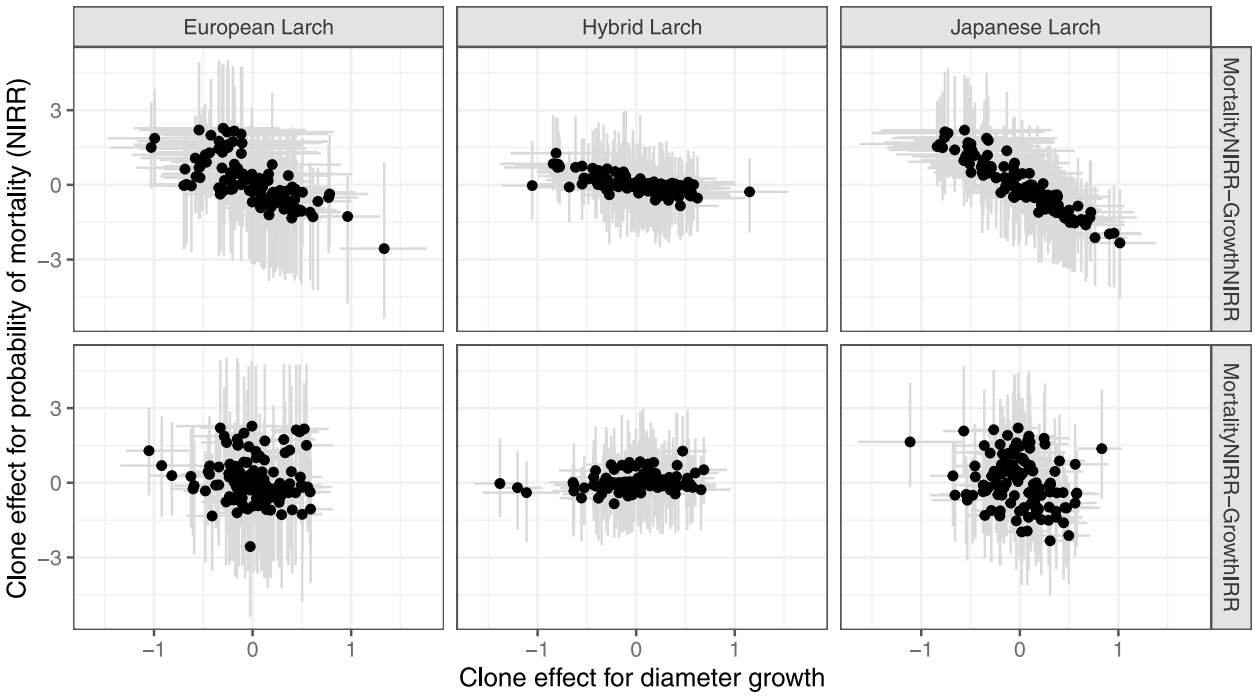


Fig. 8 Clonal effect on probability of mortality and diameter growth for European, hybrid, and Japanese larch. Gray bars represent the 95% credible intervals. The first row represents the covariation between the clonal effect on probability of mortality and diameter growth for trees in the experiment's non-irrigated plot (NIRR). The second row represents the covariation between the clonal effect on probability of mortality for trees in the non-irrigated plot and the diameter growth for trees in the irrigated plot (IRR)

roots) but it was technically not possible because of the loss of juvenility of the ortets (age 17 at time of collection). Grafting was the only possibility left, and we took care to use the most genetically homogeneous source of hybrid larch rootstocks available. Recently, we showed, thanks to a heteroplastic grafting experimentation on either hybrid or Japanese larches, that the scion had a significant effect on mortality but not the rootstock species (Pâques 2025b). This comforts our results.

The significant reduction in diameter and height in the non-irrigated plot compared to the irrigated plot indicates that the environmental conditions at the experimental site, in terms of soil water capacity and annual precipitation, were suboptimal for all larch taxa. In contrast, irrigation allowed growth to be at levels comparable to those of optimal plantation sites in France (corresponding to the best yield class according to Hamilton and Christie 1971; Pauwels and Marenne 1999). Apart from the additional water supply in the irrigated plot, all other environmental factors (climatic variables, soil characteristics, cultivation management (e.g., soil preparation, weeding)) were similar in the two plots. In addition, our experimental approach, which utilized vegetative propagation of the same genotypes, eliminated bias from uncontrolled genetic variability. Notable variations in mortality between the two plots (IRR and NIRR) suggest, therefore, in the absence of any other known causes of mortality, that soil water availability was the crucial factor in determining the survival of trees, whatever the taxa.

During the experiment, almost all dead trees were located in the non-irrigated plot (45% in NIRR compared to 5% in IRR). Most of the mortality occurred between 2015 and 2019, with variable levels in the three taxa. The highest mortality was linked to high maximum temperatures and vapor pressure deficits, particularly at the beginning of the summer, when growth is at its maximum. During these exceptional years and periods, mean maximum temperatures and VPD exceeded 30 °C and 0.9 kPa, respectively, meaning that, at times, maximum daily temperatures could reach over 38 °C (2015) and 42 °C (2019), and VPD 1.9 and 2.4 kPa, respectively. It was also observed in the experiment that these two sources of stress were highly detrimental to trees, with leaf discoloration observed during summer, a high frequency of stems with top dieback in 2015 and 2018, and, finally, mortality. For the non-irrigated trees, neither rain nor REW (Relative Extractable Water) were significant factors, as evidenced by the models tested; however, it should be highlighted that the effects of the watering treatments did significantly affect mortality. As additional water supply was the only difference between irrigated and

non-irrigated plots, water limitation in NIRR should be considered a major cause of mortality. During this period, trees in the irrigated plot were exposed to the same extreme temperature and VPD conditions, but they remained vital with fast growth, green foliage, little top dieback, and less mortality. This highlights the importance of the compensatory effect of water supply in the irrigated plot and of the soil water stress exacerbated by maximum temperature and VPD in the non-irrigated plot.

While in 2015 there was a clear association between top dieback and mortality of young trees, this direct link was not observed in 2018 on larger trees. Instead, mortality peaked in 2019, suggesting that trees exposed to stress in 2018, as indicated by top dieback, did not die immediately but succumbed the following year. Top dieback seriously weakens the tree with a reduced green crown and a compromised vascular system (Klesse et al. 2021), making it more susceptible to further damage. This pattern indicates that prior stress events, reflected here by top dieback, can predispose trees to increased mortality in subsequent years, especially under continued or exacerbated adverse conditions (Guisset et al. 2024).

Cavitation and carbon starvation are considered the primary drivers of dieback and tree death under drought conditions (McDowell et al. 2008). Although no formal test is possible based on the 2015 and 2019 years, the high frequency of stems affected by top dieback observed in the same year or the year preceding that with the highest mortality rate suggests that, among the two major factors of mortality due to drought, cavitation can be implicated. Under adverse conditions, elevated transpiration rates lead to the formation of air bubbles in the xylem, causing cavitation, which impairs water transport (Anderegg et al. 2016). Portions of trees not supplied with water may become so dehydrated that they die. Prolonged and severe drought conditions, as experienced by trees in nearly all years, but particularly in 2015 and 2019, could also lead to carbon starvation. However, contrary to common belief, Hajek et al. (2022) found no evidence that carbon starvation—marked by reduced starch and increased soluble sugars—was the leading cause of mortality in temperate species with canopy dieback. Instead, changes in non-structural carbohydrates (NSCs) could be a reaction to stress rather than a direct cause of mortality.

Among the three larch taxa tested, Japanese Larch was found to be the most vulnerable to water limitation. Native to high elevation mountains of Hondo Island in Japan, Japanese larch is well adapted to environments with high rainfall and high air humidity. Our experiment confirms its high sensitivity to high VPD (in addition to T_max). Japanese larch is known by foresters to suffer from summer drought when transferred to a continental climate; there, European larch is preferred for plantations (Masson 2005). For European larch, our results identified T_max (and not VPD) as the main climatic variable affecting its survival. European larch, described in previous studies as an anisohydric taxon (Anfodillo et al. 1998; Swidrak et al. 2013; Klein 2014; Leo et al. 2014) was also shown, at the sapling stage, to exhibit slower growth and a hydraulically safer wood (higher wall/lumen ratio and smaller pit cavity area better equipped to tolerate water stress) than the two other taxa (Sasani et al. 2021): this would predispose it to be more tolerant to drought. These characteristics would, indeed, suggest that it would be less prone to cavitation during severe drought episodes. This is confirmed by the overall reduced proportion of trees with top dieback over the ten years of observation (Fig. 4B), particularly in 2015 but not in 2018. The extreme heat recorded in 2018, a shift in wood hydraulic characteristics with tree aging, or any underlying unknown factor might explain this difference. Together with Japanese larch, hybrid larch was described as isohydric by Sasani et al. (2021). With a higher phenotypic plasticity of growth in relation to soil water availability than its parents, hybrid larch proved to have a high reactivity to soil water deficit with a substantial decline of growth (Marchal et al. 2019). Hybrid larch also proved susceptible to air humidity (VPD) and T_max, like Japanese larch, but to a lower degree and exhibited an overall lower mortality than Japanese and European larches. The well-known fast growth of the hybrid compared to its parent taxa (Greenwood et al. 2015; Marchal et al. 2017) does not seem to adversely affect its survival during drought. Our study relying on progeny sharing common parental clones thus allowed a sound comparison of the three taxa. However, the limited number of genotypes tested for each taxon potentially restricts the generalization of results at the taxon level.

The use of slow-growing species for afforestation purposes is increasingly advocated in the context of global changes. Because of their better resource-saving, more efficient carbon storage (Atkinson et al. 2012; Signori-Müller et al. 2022) and safer hydraulic wood properties (Eller et al. 2018), they would resist climatic stresses better and exhibit better survival (Zhu et al. 2018). However, species-specific behavior in terms of aspects of resilience (resistance and recovery) to climate stresses and possible trade-offs (Tao et al. 2024) complicates the generalization. The link between tree growth and mortality is another important part of predicting tree mortality. We considered it at two levels: at the individual diameter level, approximated by annual diameter increment (ring width), and at the clonal level.

The analysis of the probability of mortality and diameter growth at the individual diameter level showed a

significant relationship, where reduced growth one year was linked to increased mortality the following year across all three larch taxa. This partially aligns with findings summarized by Cailleret et al. (2017), who observed a consistent trend across various sites and species, showing that a general decline in radial growth often precedes mortality.

At the clonal level, mortality and growth in non-irrigated conditions also had a negative correlation for all taxa: the faster-growing clones had a better survival rate than the slow-growing ones. Similar conclusions were reached, for example, for Poplar (Kaczmarek et al. 2013). Giovannelli et al. (2007) observed that the fast-growing clones such as *P. deltoides* Marsh. "Dvina" exhibited lower mortality under drought conditions, suggesting more efficient water use and resource allocation than slower-growing counterparts. Similarly, a strong positive correlation ($r = 0.49$) between growth and survival was found in poplar clones at age 10, as recalculated from Kaczmarek et al. (2013), highlighting the advantage of selecting vigorous clones for areas with water stress. Nevertheless, these results contrast with those of Monclus et al. (2006), who observed that most productive poplar (*Populus*×*euramericana*) genotypes displayed low drought tolerance (meaning they are more prone to mortality). More globally, Bennett et al. (2015) concluded that larger trees suffer more (are more at risk) during water stress events than slow-growing trees. Fast growth appears advantageous in high-resource environments, but excess costs make it disadvantageous in low-resource ones (Grime 1977, 1979 in Reich 2014). Our results, together with the ones cited above on poplar, challenge this view. Faster-growing trees might be associated with rapid root establishment and deeper rooting, which could enhance survival (Kaczmarek et al. 2013). This is supported at the taxon level by a previous study on larch (Pâques et al. 2022): hybrid larch, the most vigorous taxa, not only had greater above-ground biomass but also greater coarse and fine root biomasses than both European and Japanese parents, potentially improving resource acquisition and seedling establishment (Hamberg et al. 2018). The significant positive correlation between survival and growth exhibited at the clonal level suggests that selecting vigorous clones may enhance afforestation in drought-prone areas. For hybrid larch, where this correlation is only marginally significant, selecting vigorous clones is unlikely to negatively affect survival.

These results bring some preliminary answers to breeders' concerns about selecting for fast growth and its consequences on tolerance to stress and, finally, on survival. From this perspective, fast growth does not seem detrimental and supports the use of hybrids in place of parent species and the selection of clones, combining fast growth and low susceptibility to mortality. However, the absence of a link between the growth of clones in the non-limiting water site and their survival in water stress conditions indicates the need to test genotypes and select those that perform best in stressful conditions.

A primary limitation of this study, as in many studies of this type, was our inability to partition the climate variable effects, as could be done in a factorial design testing the separate factors and their interactions at different levels. Another drawback of such a study is the underestimation of ontogenic effects and the progressive genetic erosion of the material over the years through mortality from stress events (once dead, a genotype can no longer be tested at an older age or under other climatic conditions). Temporally disconnected trials could solve this problem by isolating yearly and ontogenic effects.

5 Conclusion

In this study, we were able to establish differential water availability with contrasting water constraints across sites, resulting in distinct responses between the three larch taxa. This experimental approach with a control of potential sources of bias (e.g., soil, age, stand management) allowed us to answer our questions about taxa-specific susceptibility to mortality, key climatic predictors of mortality, and the effect of high vigor under soil water deficit. Under general drought conditions, European larch emerged as the least sensitive taxon and Japanese larch as the most susceptible, with maximum temperature and vapor pressure deficit during the early summer being the most explicative factors influencing mortality.

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Code availability
This work is a part of the thesis that is yet to be defended, which is why we would still use the data to answer other questions. The code developed for this study's analysis will be available upon reasonable request from the corresponding authors.

Authors' contributions
Naincy Sagar: methodology, formal analysis; investigation; visualization; writing—original draft. Luc E. Pâques: conceptualization; writing—review and editing; visualization; supervision; project administration; funding acquisition. Stéphane Chantepie: conceptualization; methodology; investigation; data analysis; writing—review and editing; supervision. The authors read and approved the final manuscript.

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Data availability
The dataset has been deposited at https://doi.org/10.57745/RRUYLW. It will be fully accessible by September 30, 2025. Meanwhile, the data and materials used in this study are available upon reasonable request from the corresponding authors.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
All authors consent to the publication of this manuscript.

Competing interests
The authors declare that they have no competing interests.

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