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ORIGINAL PAPER

Global warming could shorten the seed lifespan of pioneer tree species and thus natural regeneration window of damaged areas

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Abstract
Prolonged periods without precipitation in spring prevent timely and rapid germination of pioneer tree seeds and could lead to an accelerated loss of germination capacity (reduced lifespan). To get knowledge about the shortening of seed lifespan and, thus, the shortening of natural regeneration windows under climate change, an experiment was conducted. Seeds of *Alnus glutinosa*, *Betula pendula*, *Populus tremula*, *Salix caprea*, *Larix decidua*, *Pinus sylvestris,* and *Picea abies* were exposed to temperatures of 15 °C, 25 °C (past or present climate), and 40 °C (future climate) with low or high humidity for a period of 3 months. Regardless of air humidity, the initial germination percentage of *Alnus glutinosa*, *Betula pendula*, *Larix decidua,* and *Pinus sylvestris* seeds decreased only slightly by 5–15% over the 91-day period when stored at 15 °C and 25 °C. For *Populus tremula* and *Salix caprea*, time windows of maximum 14–49 days and 42–91 days were identified, respectively. However, as climate change progresses with rising temperatures and increasing absolute air humidity values, the window of opportunity for successful germination will shorten for all studied tree species. In the moist air humidity variant of 40 °C, the germination percentage dropped to 0% after 42 days for *Alnus glutinosa*, *Betula pendula,* and *Larix decidua*. The natural regeneration window will be reduced by half from more than three months to about three weeks under climate change. The lifespan of *Populus tremula* and *Salix caprea* seeds will be shortened to 1 week. For *Picea abies*, the time window will shorten to a maximum of 28 days.

Keywords Climate change · Seed storage · Regeneration · Disturbed forest · Norway spruce · *Picea abies*

Introduction

In the last few years, new disturbed areas in Europe's forests have been created almost every year by storms, drought, erosion (flooding), forest fires, and insect calamities (Keenan 2015; Gregow et al. 2017; IPCC 2021). The disturbed areas should no longer be completely artificially reforested (König et al. 2022; Axer et al. 2023; Tiebel et al. 2023), but should be left to succession in Germany if possible. In the successional cycle, ecologically beneficial pioneer tree species, in the bionomic strategy also called ruderals (R-group) (Brzeziecki and Kienast 1994), such as *Alnus glutinosa* (L.) Gaertn. (common alder), *Betula pendula* Roth (silver birch), *Populus tremula* L. (aspen) and *Salix caprea* L. (goat willow) as well as species with pioneer-like behavior such as *Larix decidua* Mill. (European larch) and *Pinus sylvestris* L. (Scots pine), classified in bionomical strategy as competitors-ruderals-stress-tolerant (C-R-S-group) (Brzeziecki and Kienast 1994) are the first arriving tree species on disturbed areas and thus act as nurse crops for subsequent shade tolerant tree species (Burschel and Huss 2003; Stark et al. 2015; Bartsch et al. 2020). In the past, single-layered Norway spruce forests (*Picea abies* L.) were established, which are inherently unstable and no longer considered suitable for many forest sites (Löf et al. 2010). The non-site-appropriate Norway spruce regenerates very well on damaged areas.

Reforestation of disturbed areas by tree species only occurs in the window of the retention period of seed vigor (= lifespan). It is known that germination and

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establishment of some pioneer tree species requires persistently wet conditions in the 1st year of growth, which will lead to establishment difficulties in climate change (McLeod and McPherson 1973; Worrell 1995; Horton and Clark 2001; Dickmann and Kuzovkina 2014; Weisberger 2014; Tiebel et al. 2023). Prolonged periods without precipitation in spring, as evidenced by recent observations in Central Europe (IPCC 2021), prevent timely and rapid germination of tree seeds and could perhaps lead to an accelerated loss of germination capacity (reduced lifespan) of the seeds. The already extreme microclimatic conditions on open areas (high temperatures, all-day radiation, prolonged drought) (Renaud et al. 2011) will intensify under climate change. In the future, this could result in a shortening of the time window for a possible, successful natural regeneration of a disturbed area.

Seed morphology and seed lifespan are species specific (Schönborn 1964). Silver birch and common alder form winged nuts released from catkins (McVean 1956; Perala and Alm 1990). Goat willow and aspen have seeds with pappus, released from capsules of catkins and Scots pine, European larch and Norway spruce have winged seeds, released from cones (Simak 1980; Worrell 1995; Geburek and Stimm 2002; Schmidt 2002; Schütt and Stimm 2006). The seeds of the above-mentioned tree species do not exhibit dormancy (McVean 1953; Atkinson 1992; Lautenschlager-Fleur and Lautenschlager 1994; Worrell 1995; Geburek and Stimm 2002; Bärtels 2008; Burkart 2018). It is known that seeds of goat willow and aspen lose their ability to germinate after ripening. After a few weeks, the seeds have completely lost their vitality (Schönborn 1964; Junttila 1976; Worrell 1995; Tiebel et al. 2018). Silver birch, on the other hand, can establish a persistent soil seed bank where only minor germination losses occur in the 1st year (Granström 1987; Skoglund and Verwijst 1989; Tiebel et al. 2018, 2021). Seed survival times of 2 to 3 years are found for common alder (Winkler 1955; McVean 1956; Schönborn 1964; Granström 1987; Decocq et al. 2004). For Scots pine and European larch, Winkler (1955) and Schütt and Stimm (2006) refer to a natural seed vitality limit of 4 to 10 years. The lifespan of Norway spruce seeds can be 3 to 4 years (Schmidt 2002).

Further, the lifespan of seeds depends significantly on external conditions (Schönborn 1964; Harrington 1972; Walck et al. 2011; Farhana et al. 2022). According to Harrington (1972), Mac Carthaigh and Spethmann (2000), and De Vitis et al. (2020), humidity, warm conditions, and sufficient available oxygen lead to a significant reduction in germination rates. Walck et al. (2011) emphasized that global warming changes the environmental conditions (temperature and water supply), which may prevent, delay, or enhance the germination vigor of species. However, not only germination start and success but also seed aging and seed longevity are affected by the changing conditions.

There is little information on how higher temperature and moisture conditions affect the lifespan and germination of pioneer tree species and species with pioneer-like behavior. In contrast, there are many studies and reviews on how seeds of tree species, as well as pioneers, can be artificially stored for years with little loss of germination capacity (Schönborn 1964; Harrington 1972; Rohmeder 1972; Simak 1980; Löffler 1985; Schubert 1998; Mac Carthaigh and Spethmann 2000; Bärtels 2008).

In order to get knowledge about a possible shortening of the natural regeneration window of pioneer tree species, species with pioneer-like behavior and Norway spruce under climate change, an experiment was conducted with *Alnus glutinosa*, *Betula pendula*, *Populus tremula*, *Salix caprea*, *Larix decidua, Pinus sylvestris,* and *Picea abies*. The seeds of the tree species were exposed to different temperature and humidity conditions over a period of 3 months. Of interest was the intensity and speed of germination loss.

The following hypotheses were formulated. (1) High air humidity has a negative effect on the survival rate of germinable seeds of all tree species, regardless of the storage temperature. (2) Higher storage temperatures have a negative influence on the survival rate of germinable seeds of the tree species. (3) Seeds of goat willow and aspen lose their germination capacity the fastest of all tree species because the seeds are generally described as very short-lived (Junttila 1976; Simak 1980; Schütt and Stimm 2014; Tamm 2014). (4) Silver birch seeds show the best storage ability of all tree species because the seeds are able to build up a soil seed bank (Skoglund and Verwijst 1989; Tiebel et al. 2021).

Materials and methods

Seed material

In the study, the pioneer tree species *Alnus glutinosa*, *Betula pendula, Populus tremula*, and *Salix caprea* which colonize open areas in Germany were taken into account. The C-R-S strategic *Larix decidua* and *Pinus sylvestris* were also considered in the study, although they are not classical pioneer tree species according to Brzeziecki and Kienast (1994). *Larix decidua* and *Pinus sylvestris* are very similar to classical pioneer tree species due to their pioneer-like character in the phase of germination and establishment (mineral soil germinators, high light requirement, wide range of soils, and fast juvenile growth) and can make an important contribution as initial colonizers of open areas (Carlisle and Brown 1968; Brzeziecki and Kienast 1994; Geburek and Stimm 2002; Schütt and Stimm 2006). Furthermore, the shade tolerant tree species *Picea abies* was included in the study, because it is one of the most important and stand-forming coniferous tree species in Europe (Schmidt 2002). We received the seeds of *Alnus glutinosa*, *Larix decidua*, *Pinus sylvestris,* and *Picea abies* from the seed kiln of the state forest enterprises of Saxony in Flöhe, Germany. In hilly locations in Saxony, Germany, seed collection was conducted in 2019 for *Alnus glutinosa*, *Larix decidua*, and *Pinus sylvestris*, while *Picea abies* seeds were collected in 2009. The age of spruce seeds had no effect on the study results because long-term stored spruce seeds of more than 20 years show comparably high germination percentages and germination behavior as freshly harvested seeds (Suszka et al. 2005; Simpson et al. 2008). The *Betula pendula* seeds were purchased from the seed kiln in Annaburg, Germany, and were harvested in West and South German Hill Country in 2019.

The seeds of *Salix caprea* were collected from seed trees on 5–6 May 2022 and the seeds of *Populus tremula* on 11 May 2021 in Tharandter forest, Germany. The catkins were collected as soon as the capsules began to open and stored at room temperature for a few days to allow all capsules seed release. The seeds were cleaned from hairs, dried in an excavator for 3 to 4 days, and then packed airtight and frozen at −18 °C.

The pioneer tree species and species with pioneer-like behavior considered in the experiment could be divided into three subgroups by differences in seed morphology: (1) silver birch and common alder, (2) aspen and goat willow as well as (3) Scots pine and European larch. It is assumed that the tree species with morphologically similar seeds have similar storage behavior (Simak 1980; Tiebel et al. 2018).

Experimental design

The seed storage experiment was started on October 5, 2022. The seed lots of the seven tree species were divided among six storage variants. The six variants consisted of three fixed storage temperatures (15 °C, 25 °C, and 40 °C) and two air humidity variants in dry and moist ranges (Fig. 1). Since climate change is expected to alter previously typical seasonal climatic conditions, this experiment was designed to create a broader range of spring and early summer scenarios for seeds resting on the ground. Storage temperatures of 15 °C, 25 °C, and 40 °C indicate past, current, and anticipated future climate conditions, respectively. In temperate forest zone, the air humidity usually varies between 40% and 80% (Hauck et al. 2019; Rüger 2023). Depending on the temperature variants, the dry and moist air humidity variants in the study ranged from 24 to 46%, and 42 to 91% air humidity, respectively (Fig. 1). We selected these humidity variants to attain comparable absolute water contents (g/m^3) across temperature variants, accounting for the temperature-dependent water absorption characteristics of the air (Schönborn 1964; Rüger 2023). Therefore, we had chosen very high humidity values at 15°, and comparatively low humidity values at 40 °C for the moist air humidity variants and vice versa for the variant with low air humidity. The humidity deviations during the storage period of 91 days were 3–24% (Fig. 1). The temperature deviations during the storage were 0.2–1.2 °C.

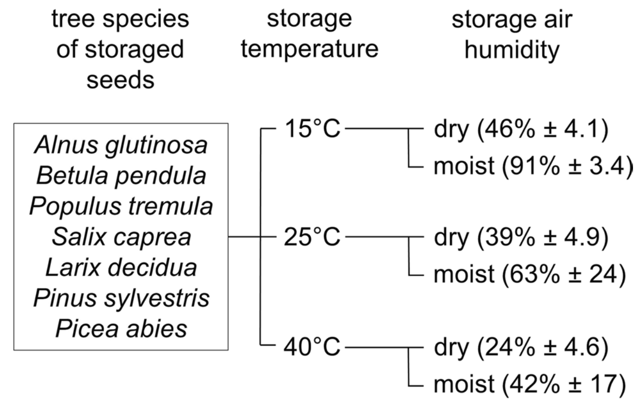

Fig. 1 Experimental design of seed storage study at different temperatures and humidity levels

The seeds were stored in paper bags in closed, two-chambered vessels. The two-chambered vessels were used to provide the humidity of the air by adding humidifying water or dehumidifying silica gel in the lowest chamber. One dry and one moist humidity vessel was placed in each of the two drying cabinets and one refrigerator, which were used to maintain the temperatures during the storage period.

Each week 100 seeds of each tree species were taken from all storage variants. Subsequently, the seed weight was recorded and a germination test started (Santagapita et al. 2014). Seed weight was measured to determine the effect of humidity on seed water content. The germination test was used to control the remaining germination percentage and the effect of storage conditions. The seeds were sown on moist filter paper in 6 cm Jacobsen seed germination kits with domes and set to germinate at 25 °C for 21 days with 16 h light and 8 h darkness (ISTA 2012). The germination tests were checked for successful germination weekly according to ISTA (2012).

Data analysis

To evaluate differences in seed weights among tree species and the two humidity variants, the Mann–Whitney U test was employed due to the non-normal distribution of seed weights. To analyze the correlation between air humidity and seed weight of the tree species, the Spearman correlation coefficient (rho) was used (Zar 2010).

The study was a nested experiment with fixed and random effects. The depending variable, germination capacity, exhibited a binomial distribution since each seed was counted as a single observation (alive or dead) (Tiebel et al.

2021, 2023). Therefore, generalized linear mixed models (GLMM) were used to analyze the effects of temperature (categorical variable, $n=3$), air humidity (categorical variable, $n=2$), and storage period (continuous variable) as fixed effects on germination capacity (seed vigor retention) (Zuur et al. 2009). Seed weights were strongly correlated with humidity (p-value < 0.007, cor > 0.33). Due to the collinearity between the two variables, only humidity was considered in the models (Zuur et al. 2009; Axer 2022). We decided to use humidity as the variable also affects seed weight. Cabinet ($n=3$), vessel ($n=6$), and paper bag ($n=42$) were included as random effects in the models.

We assumed that the storage behavior and influencing effects would be different due to seed morphological differences, so we calculated separate models for each tree species. A manually stepwise backward approach, based on AIC values, was applied to find the best model fit (Wallraf and Wagner 2019; Tiebel 2021; Tiebel et al. 2023). For modeling, the R software version 4.2.2 and the "glmmTMB" package version 1.1.5 were used (Brooks et al. 2017; R Core Team 2022).

Table 1 Results of the correlation analysis between air humidity [%] and seed weight of 100 seeds of *Alnus glutinosa, Betula pendula, Populus tremula, Salix caprea, Larix decidua, Pinus sylvestris,* and *Picea a bies*

Tree species	Thousand-seed weight [g]	Humidity & weight		
		rho	p-value	
Alnus glutinosa	1.26	0.496	0.000	***
Betula pendula	0.12	0.336	0.007	**
Populus tremula	0.12	0.432	0.001	***
Salix caprea	0.10	0.173	0.378	N.s
Larix decidua	4.15	0.599	0.000	***
Pinus sylvestris	5.61	0.574	0.000	***
Picea abies	7.52	0.774	0.000	***

The thousand-seed weight after drying at 105 °C for 2 days is also shown

(N.s. not significant; * significant; ** very significant; *** highly significant)

Results

Seed weight

The seed weight of 100 seeds per tree species correlated significantly with the measured air humidity values for all tree species, except for *Salix caprea* (Table 1). Seed weights increased with increase in humidity. However, for *Salix caprea,* the seed weights differ not significantly between the storage variants dry and high humidity (Fig. 2). The mean thousand-seed weight after drying at 105 °C for 2 days of each tree species is also shown in Table 1. *Betula pendula, Populus tremula,* and *Salix caprea* showed the lightest seed weights, which were comparable with 0.1 g. *Picea abies* had the highest thousand-seed weight, followed by *Pinus sylvestris* and *Larix decidua*.

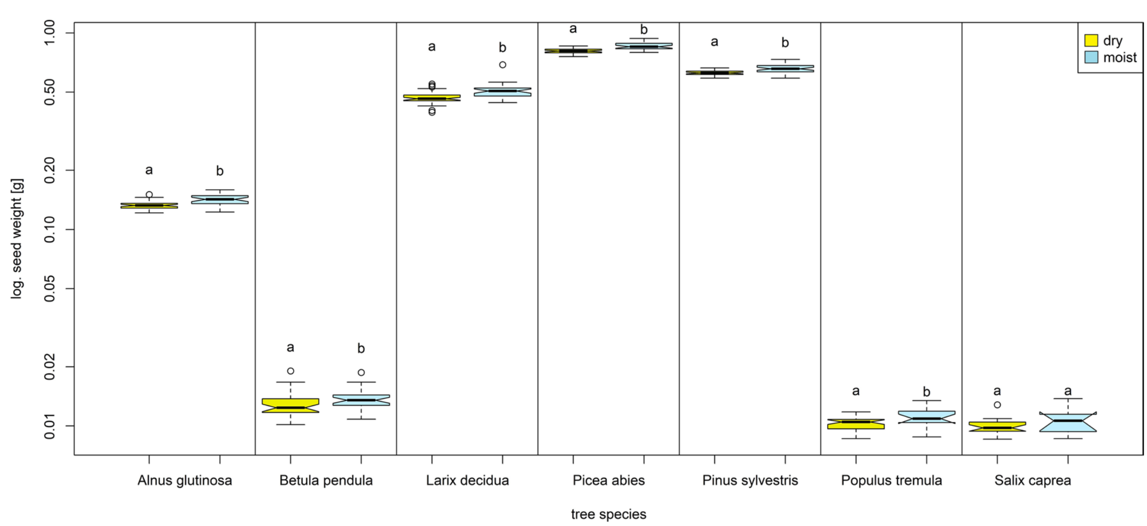

Fig. 2 Seed weight [g] of 100 *Alnus glutinosa*, *Betula pendula*, *Populus tremula, Salix caprea, Larix decidua*, *Pinus sylvestris,* and *Picea abies* seeds stored at dry and moist air humidity conditions. The letters indicate significant differences between dry and moist stored seeds of one tree species (Mann–Whitney U test: $p < 0.05$)

Storage

Alnus glutinosa and *Betula pendula*

The germination capacity of the *Alnus glutinosa* and *Betula pendula* seeds was 80% ± 5.6 and 17% ± 2.4 before storage, respectively (Fig. 3). During the storage period of 91 days at 15 °C and 25 °C as well as dry and moist air humidity, the germination capacity of *Alnus glutinosa* and *Betula pendula* seeds showed a variation of higher and lower germination percentages. Nevertheless, the germination capacity at the end of the study was as high as at the beginning. During storage at 40 °C and high air humidity, the seeds of *Alnus glutinosa* and *Betula pendula* continuously lost their ability to germinate, until after 42 days all seeds were dead.

As a significant influencing effect on the survival rate of *Alnus glutinosa* seeds, storage at 40 °C was shown to have a positive effect (Table 2, Fig. 4). However, the combination of storage period and 40 °C had a negative effect on the survival rate. The interactions between the storage temperatures of 25 °C and 40 °C and high humidity showed a significant reduction in the germination capacity. For *Betula pendula*,

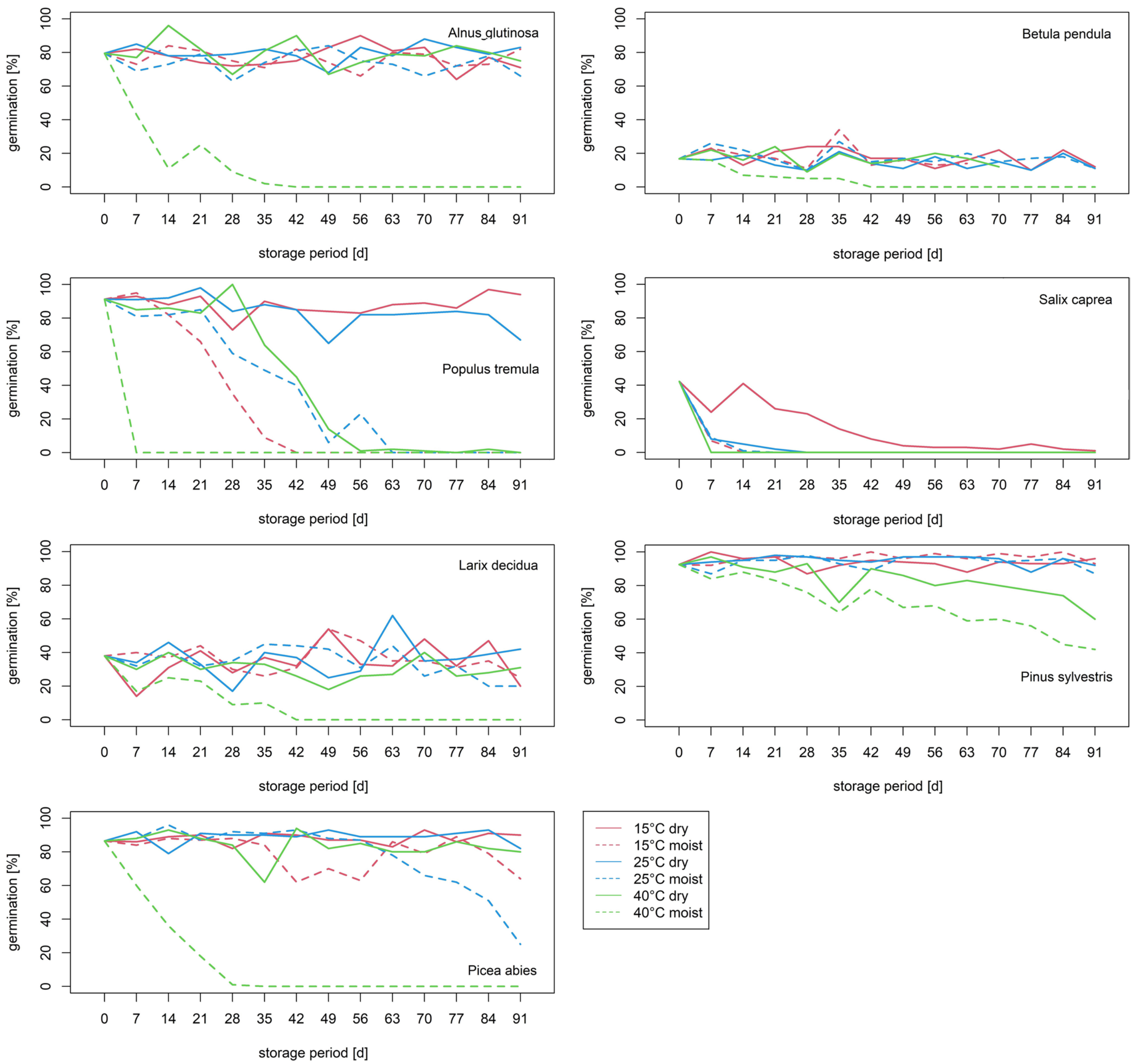

Fig. 3 Change in germination capacity [%] of *Alnus glutinosa*, *Betula pendula, Populus tremula, Salix caprea, Larix decidua*, *Pinus sylvestris,* and *Picea abies* seeds over storage period [d] at different temperature conditions (15 °C, 25 °C, and 40 °C) and air humidity conditions (dry and moist)

Table 2 GLMM results of the survival probability [%] of *Alnus glutinosa*, *Betula pendula, Populus tremula, Salix caprea, Larix decidua*, *Pinus sylvestris,* and *Picea abies* seeds depending on storage period, different temperature conditions (15 °C, 25 °C, and 40 °C) and air humidity conditions (dry and moist)

Tree species	Fixed effects	Estimate	Std. error	*p*-value	
Alnus glutinosa	(Intercept)	1.313	0.097	0.000	***
	period	−0.002	0.002	0.238	
	moist	−0.044	0.090	0.622	
	25 °C	0.096	1.389	0.491	
	40 °C	1.293	0.168	0.000	***
	period:25 °C	0.002	0.002	0.495	
	period:40 °C	−0.023	0.003	0.000	***
	moist:25 °C	−0.316	0.127	0.013	*
	moist:40 °C	−3.595	0.149	0.000	***
Betula pendula	(Intercept)	−1.367	0.129	0.000	***
	period	−0.004	0.002	0.137	
	moist	0.010	0.197	0.960	
	25 °C	−0.274	0.190	0.151	
	40 °C	−0.084	0.195	0.666	
	period:moist	−0.002	0.005	0.650	
	period:25 °C	0.001	0.004	0.769	
	period:40 °C	−0.000	0.004	0.955	
	moist:25 °C	0.276	0.274	0.314	
	moist:40 °C	0.064	0.311	0.837	
	period:moist:25 °C	0.000	0.006	0.935	
	period:moist:40 °C	−0.065	0.012	0.000	***
Populus tremula	(Intercept)	2.648	0.976	0.007	**
	period	−0.004	0.003	0.152	
	moist	−0.477	0.979	0.626	
	25 °C	0.568	1.195	0.635	
	40 °C	−0.132	1.198	0.912	
	period:moist	−0.112	0.005	0.000	***
	period:25 °C	−0.004	0.004	0.247	
	period:40 °C	−0.109	0.006	0.000	***
Salix caprea	(Intercept)	−0.323	0.330	0.323	
	period	−0.066	0.004	0.000	***
	moist	0.666	0.342	0.051	
	25 °C	–0.809	0.405	0.046	*
	40 °C	−1.149	0.408	0.005	**
	period:moist	−0.309	0.035	0.000	***
Larix decidua	(Intercept)	−0.766	0.108	0.000	***
	period	0.003	0.002	0.131	
	moist	0.345	0.150	0.022	*
	25 °C	0.088	0.152	0.562	
	40 °C	0.098	0.153	0.521	
	period:moist	−0.006	0.003	0.029	*
	period:25 °C	−0.000	0.003	0.957	
	period:40 °C	−0.006	0.003	0.024	*
	moist:25 °C	−0.014	0.212	0.947	
	moist:40 °C	−0.083	0.236	0.724	
	period:moist:25 °C	−0.003	0.004	0.388	
	period:moist:40 °C	−0.062	0.008	0.000	***

Table 2 (continued)

Tree species	Fixed effects	Estimate	Std. error	*p*-value	
Pinus sylvestris	(Intercept)	2.862	0.217	0.000	***
	period	−0.004	0.004	0.326	
	moist	−0.013	0.327	0.968	
	25 °C	0.219	0.323	0.498	
	40 °C	−0.227	0.275	0.408	
	period:moist	0.015	0.007	0.023	*
	period:25 °C	0.000	0.006	0.944	
	period:40 °C	−0.017	0.005	0.000	***
	moist:25 °C	−0.446	0.454	0.327	
	moist:40 °C	−0.579	0.392	0.140	
	period:moist:25 °C	−0.010	0.009	0.278	
	period:moist:40 °C	−0.020	0.007	0.008	**
Picea abies	(Intercept)	1.877	0.152	0.000	***
	period	0.003	0.003	0.389	
	moist	−0.115	0.204	0.571	
	25 °C	0.135	0.220	0.539	
	40 °C	0.003	0.210	0.987	
	period:moist	−0.011	0.004	0.002	**
	period:25 °C	−0.001	0.004	0.781	
	period:40 °C	−0.008	0.004	0.043	*
	moist:25 °C	1.647	0.319	0.000	***
	moist:40 °C	0.104	0.321	0.747	
	period:moist:25 °C	−0.028	0.006	0.000	***
	period:moist:40 °C	−0.166	0.015	0.000	***

The intercept represents the storage variant at 15 °C and dry air humidity
(N.s. not significant; * significant; ** very significant; *** highly significant)

the analysis of all individual effects or interactions of tested effects revealed only one detectable influence. With increase in storage period during moist storage at 40 °C, *Betula pendula* seeds lost their viability.

Populus tremula* and *Salix caprea

Populus tremula and *Salix caprea* seeds had an initial germination capacity of 91% ± 4.0 and 42% ± 3.8, respectively (Fig. 3). In general, the seeds of *Populus tremula* and *Salix caprea* stored at high air humidity continuously lost their germination capacity. *Salix caprea* seeds were no longer viable after 7 days (40 °C moist) and 14 days (15 °C and 25 °C moist). In the case of *Populus tremula*, complete loss of seed viability lasted 7 days (40 °C moist), 42 days (15 °C moist), and 63 days (25 °C moist). In the storage variant of 40 °C and low air humidity, *Salix caprea* seeds also lost their viability after 7 days. In the variant 15 °C and dry humidity, the seeds showed decreasing germination capacity, but complete loss of germination capacity took 91 days. The *Populus tremula* seeds retained their viability in dry storage at 15 °C and 25 °C for the longest time and reached germination capacity of 94% and 67% after 91 days of storage, respectively.

The preservation of the viability of *Populus tremula* seeds depended on the interactions between the storage period, humidity, and temperature. The interactions of storage period and high air humidity as well as storage period and 40 °C had a negative effect (Table 2, Fig. 4). For *Salix caprea*, the model expresses also a negative interaction between the storage period and moist air humidity. Further, the survival rate of *Salix caprea* seeds was significantly reduced by the storage temperatures 25 °C and 40 °C as well as the storage period.

Larix decidua* and *Pinus sylvestris

The initial germination capacity of *Larix decidua* was 38% ± 5.3, compared to 92% ± 3.4 of *Pinus sylvestris* (Fig. 3). The germination percentages of *Larix decidua*

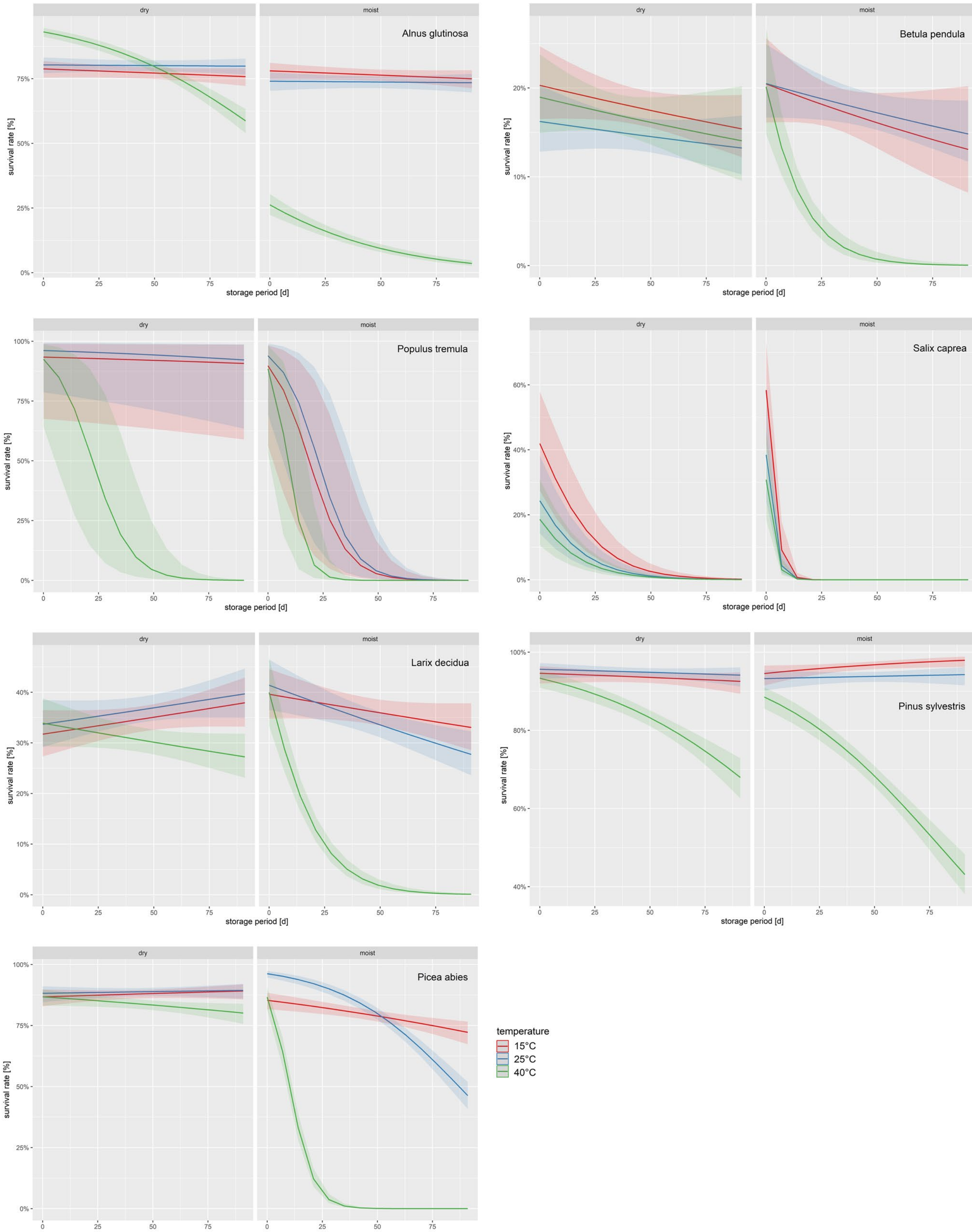

Fig. 4 GLMM predictions of the survival and germination probability [%] of 1 *Alnus glutinosa*, *Betula pendula*, *Populus tremula*, *Salix caprea*, *Larix decidua*, *Pinus sylvestris*, and *Picea abies* seed after storage [d] at different temperature conditions (15 °C, 25 °C, and 40 °C) and air humidity conditions (dry and moist). Note the different *y*-axis scales

showed high variations over the storage period for all storage conditions, except the variant 40 °C and moist humidity. After 42 storage days at 40 °C and moist humidity, all seeds were dead. Low germination losses were observed under storage conditions at 15 °C (moist and dry) and 25 °C (moist) for *Larix decidua*, whereas comparable germination rates were recorded at 25 °C and dry storage to the initial germination percentage. For *Pinus sylvestris* seeds, the storage variants of 40 °C had only influence on viability. Germination rates decreased over the storage period and reached 42% (moist humidity) and 60% (dry humidity) at the end of the study.

The analyses with the GLMM showed for both tree species a significant negative influence of the interaction between storage period and 40 °C as well as storage period, 40 °C, and moist humidity (Table 2, Fig. 4). In contrast, the combination of moist air humidity and storage period had a negative effect on maintaining the germination capacity of *Larix decidua* and a positive effect on that of *Pinus sylvestris*.

Picea abies

The germination capacity of the *Picea abies* seeds was 87% ± 5.7 before storage. At the end of the storage period, all dry storage variants showed comparable germination rates to the initial germination capacity (Fig. 3). In all moist air storage variants, the germination rates decreased over time and reached 0% in the 40 °C variant after 28 days.

The GLMM results indicated that the tested individual effects did not influence the survival rate of *Picea abies* seeds; however, the interactions between these effects did have a significant impact (Table 2, Fig. 4). In general, high humidity in interaction with the storage period negatively affected the germination capacity. The interaction of the 40 °C storage temperature in combination with the storage period had a negative influence, as well as high humidity in combination with the storage period and the temperature variants 25 °C and 40 °C. Storage at 25 °C and high humidity showed significantly better survival rates than storage at 15 °C.

Discussion

General influence of humidity and temperature on seed lifespan

The presented study could show that increasing air humidity resulted in significantly increased seed weights in the case of all species, except of *Salix caprea*. The seed moisture adapted to the surrounding humidity. This is not surprising, since this correlation has already been proved and confirmed by Schönborn (1964), Harrington (1972), Löffler (1985), and De Vitis et al. (2020). The rapid dying of the goat willow seeds might be the reason that the goat willow seeds of the dry and moist humidity variants did not differ, but the morphologically similar aspen seeds did (Brouwer and Stählin 1975; Simak 1980). The seeds of these two species had approximately 0.1 g thousand-seed weight at 0% seed moisture and, thus, comparable seed sizes. However, there were significantly fewer measurements of seed weights of goat willow than aspen because we only used seed weights of germinable seeds.

The results of the storage tests showed that high air humidity conditions over the storage period had a negative effect on the persistence of seed germination compared to dry air humidity (hypothesis 1, Fig. 4). However, high humidity in interaction with temperature did not generally have a significant negative effect on seed lifespan of the tested tree species. Humidity had a negative effect on seed vigor retention only in interaction with 40 °C. The missing negative effect of high humidity in interaction with the temperatures of 25 °C and 15 °C on seed lifespan might have been due to the reducing absolute humidity (g/m^3) with decrease in air temperature. For example, air at 40 °C can absorb up to 51.15 g/m^2 of water, while air at 25 °C and 15 °C can only absorb up to 23.05 g/m^2 and 12.85 g/m^2 of water, respectively (Schönborn 1964; Rüger 2023). It appears that only absolute moisture levels above 12 to 15 g/m^2 of water in the air, as exhibited by the dry 40 °C and moist 25 °C variants in the study, had a significant negative effect on seed survival.

In the literature, high humidity is often described as a disadvantage for maintaining seed viability during storage (Schönborn 1964; Simak 1980; Mac Carthaigh and Spethmann 2000; Fenner and Thompson 2005; De Vitis et al. 2020). Because of high humidity and thus increasing seed moisture weights, metabolic processes of the seeds are stimulated and as a result, seed reserves are depleted (Schönborn 1964; Mac Carthaigh and Spethmann 2000). This leads to gradual degeneration of the embryo and loss of germination capacity (Fenner and Thompson 2005; Tammela et al. 2005; Kranner 2013; De Vitis et al. 2020). In addition, mold occurred during seed storage under high humidity conditions in the seeds of goat willow, aspen, Norway spruce, and Scots pine, which also contributed to the reduction of germinable seeds over time. According to Harrington (1959, cited in Schönborn 1964), fungal growth on and in the seed is already stimulated at seed moisture of more than 12–14%.

Hypothesis 2, according to which higher storage temperatures have a negative effect on the survival rate of germinable seeds of tree species, was proved by the study. With the exception of *Betula pendula*, model results showed a significant reduction in seed lifespan at 40 °C and increased storage time. According to Harrington (1972), increasing temperature accelerates the rate of metabolic processes in the seed and thus seed degeneration. The higher absolute humidity values at 40 °C mentioned above could also have been a reason for the accelerated seed mortality rate. Löffler (1985) noted that seeds with lower seed moisture at seed release from cone or catkins, such as Scots pine, European larch, silver birch, common alder, and Norway spruce, are less sensitive to temperature fluctuations and heat. This could be the reason why the seeds showed best survival at the storage temperatures of 15 °C and 25 °C, with the exception of *Salix caprea*.

Tree species-specific differences in seed vigor retention

As Harrington (1972) and Fenner and Thompson (2005) noted, seed aging is tree species specific. Contrary to our expectations, differences in storability did not always occur between the morphologically different tree seeds. Only two different groups could be detected: (1) *Populus tremula* and *Salix caprea* and (2) *Alnus glutinosa*, *Betula pendula, Larix decidua*, *Pinus sylvestris,* and *Picea abies*.

Consistent with hypothesis 3, goat willow and aspen were most sensitive to the tested storage variants. Goat willow seeds showed a rapid viability loss across all variants. Especially with increase in temperature and humidity, the germination rates reduced considerably. The results of the present study were comparable to those of Junttila (1976). After 23 days, the viability of goat willow seeds had reduced by 50% in the 18 °C storage variant. At 27 °C, it was only 6 days to the 50% reduction in germination success (Junttila 1976). The reason for the rapid loss of germination may be the already high moisture content of the seeds when they are released from the capsule (Schubert 1998), the short time it takes for the small seeds to saturate with water compared to larger seeds, and the absence of seed reserve (Simak 1980; Fenner and Thompson 2005; Argus 2006). The fact that aspen seeds showed "longer" lifespans at low humidity and storage temperatures up to 25 °C in comparison with goat willow may be due to the different seed coats (testa). While the testa of the goat willow looks transparent and the embryo already appears green, the aspen has a white shimmering testa (Fig. 5). This testa may provide better protection against environmental influences. Wettstein (1936, cited in Simak 1980) and Reim (1930, cited in Simak 1980) also found germination percentages of 70% and 73% after 12 days and 79 days of storage of aspen seeds at room temperature, respectively. The storage conditions at Moss (1938) corresponded to our variant of 25 °C and low humidity. After four weeks, the aspen seeds showed a germination percentage of 100%. However, under humid and hot conditions, the protection of the aspen seeds by the testa failed. The germination window for *Populus tremula* and *Salix caprea* will be shortened to 1 week in the future. Therefore, in climate change, even very short dry periods can lead to a complete loss of germination capacity of goat willow and aspen seeds.

Common alder, silver birch, Scots pine, and European larch, seeds formed the 2nd group of pioneer trees, respectively, a group of species with pioneer-like behavior. When stored at 15 °C and 25 °C, regardless of air humidity, the initial germination percentage decreased only slightly by 5–15% over the 91 days period. McVean (1955) refers to the fact that *Alnus glutinosa* seeds can remain viable in water for up to 12 months because of their oily testa. The oily testa may explain why common alder seeds showed similar good storage behavior to silver birch seeds in this study (cf. Granström 1987), although McVean (1955) reported that only a few common alder seeds were viable after 1 winter. Silver birch seeds are known to persist in the soil for several years (Skoglund and Verwijst 1989; Mac Carthaigh and Spethmann 2000; Tiebel et al. 2021), which explains their potential to maintain seed viability under a wide range of storage conditions. There were

Fig. 5 Seeds of *Salix caprea* (left) and *Populus tremula* (right)

contradictory statements about Scots pine. While Granström (1987) found a complete loss of germination capacity of *Pinus sylvestris* seeds in the soil after only 1 year, Schönborn (1964) referred to the natural vitality limits of Scots pine and European larch seeds between 7 and 10 years. Schütt and Stimm (2006) also referred to successful germination of Scots pine seeds years after maturation. This showed that Scots pine seeds must be able to survive higher temperatures, what our study was able to show. According to Shearer (2008), *Larix decidua* seeds can also survive 1–2 years in the cone without significant germination loss and can even survive storage periods at 10 °C for more than 14 years. Therefore, even after long dry periods with low or high humidity conditions in the past, sufficient germinable seeds of Scots pine, European larch, common alder, and silver birch remain viable for natural regeneration.

Nevertheless, the initial germination percentage of the *Alnus glutinosa*, *Betula pendula, Larix decidua,* and *Pinus sylvestris* seeds at the storage temperature of 40 °C decreased over the storage period. In the moist air humidity variant of 40 °C, the germination percentage dropped to 0% after 42 days for the tree species, with the exception of Scots pine. In the dry variant of 40 °C, the probability of a seed losing viability over time was 5–6% for European larch and silver birch and 30–35% for Scots pine and common alder. Davies et al. (2020) also noticed a continuous decrease in seed germination of *Alnus glutino*sa and *Betula pendula* seeds at 45 °C and 60% humidity over 30 days, which confirmed our results. Therefore, the natural regeneration window for *Betula pendula*, *Alnus glutinosa* and *Larix decidua* will also be reduced by half from formerly more than 3 months to about six weeks under climate change, with only 50% of seeds germinable after 7 days for *Alnus glutinosa* and 21 days for *Betula pendula* and *Larix decidua*.

In accordance with the 4th hypothesis, this study showed that birch seeds do not have a better persistence ability compared to Scots pine, European larch, and common alder. The tree species are to be assessed as equal in terms of seed vigor retention. The circumstance that Scots pine, European larch, common alder, and silver birch are significantly more able to tolerate dry and warm conditions compared to goat willow and aspen may be related to the thicker seed coat (Schubert 1998) of these tree species and their greater surface-to-volume ratio (Fenner and Thompson 2005). The thicker seed coat makes water uptake more difficult, and due to the greater surface-to-volume ratio, the seeds require more water to reach the species-specific water content (Mac Carthaigh and Spethmann 2000; Fenner and Thompson 2005). Further, the seeds of common alder, silver birch, European larch, and Scots pine have seed reserves (endosperm) (McVean 1955; Turcek 1961; Geburek and Stimm 2002; Schütt and Stimm 2006; Pietzarka and Roloff 2014). Thus, it takes a longer time before the metabolic processes start and until the seed reserves are depleted.

Picea abies, as the only shade tolerant tree species in the study, showed similarly good storage behavior as *Larix decidua*, *Pinus sylvestris*, *Alnus glutinosa,* and *Betula pendula* in the dry variants. Schubert (1998) showed that Norway spruce seeds with 8% seed moisture were still germinable 14 years after storage at 2–12 °C. Schmidt (2002) refers to the germination capacity of Norway spruce seeds up to 3–4 years, Schönborn (1964) up to 7–10 years. However, in the presented study, high air humidity had a negative effect on Norway spruce seed vigor retention across all temperature ranges. This indicates that Norway spruce seeds generally do not survive well at higher air humidity levels. Consequently, dry periods of more than three to four weeks could become a problem in the future. This could counteract the future advance of non-site-appropriate spruce at high densities in damaged areas and the establishment of spruce-dominated target stands.

Conclusion

Natural regeneration of disturbed areas by pioneer tree species and species of pioneer-like behavior only occurs in the window of seed lifespan. Up until now, it was not known how long this time window would be and whether it could be shortened during climate change. This issue was of particular importance, as prolonged periods of no rainfall in the spring will prevent timely and rapid germination of seeds.

The study was able to show that the previous time window for successful germination of *Alnus glutinosa*, *Betula pendula*, *Larix decidua,* and *Pinus sylvestris* seeds was more than 91 days. Long, precipitation-free periods on dry soil could be survived by seeds without significant loss of germination capacity. For *Populus tremula* and *Salix caprea*, it was already known that the seeds remain viable only a few days to weeks after germination (Junttila 1976; Simak 1980; Schütt and Stimm 2014; Tamm 2014). The study identified time windows of maximum 14 to 49 days for goat willow and 42 to 91 days for aspen. Thus, aspen seeds were also able to survive longer dry periods and participate in natural regeneration.

However, as climate change progresses with rising temperatures and increasing absolute air humidity values, the window of opportunity for successful germination will shorten for all studied tree species. Silver birch, common alder, and European larch seeds were able to survive maximum dry periods of six weeks. Regarding the establishment of silvicultural densities of regeneration on damaged areas, it is important to consider that after 7 days, only 50% of common alder seeds and after 21 days only, 50% of silver birch and European larch seeds were still germinable. For

Norway spruce, the time window will shorten to a maximum of 28 days (ten days to 50% seed viability loss). The lifespan window of *Populus tremula* and *Salix caprea* seeds will be shortened to 1 week in the future. Alternatives to generative reproduction via annual seed rain do not exist. *Populus tremula* and *Salix caprea* are not able to form a soil seed bank or a seedling bank (Thompson et al. 1997; Tiebel et al. 2018; Tiebel 2020). Dry periods of several weeks (IPCC 2021) before and after germination (Tiebel et al. 2023) will significantly limit the natural regeneration success of all tree species under climate change.

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Author contribution KT created the study concept. All authors contributed to the study design. The investigation, data collection, and literature search were performed by all authors. The data analysis, preparation of figures, and the initial draft of the manuscript were undertaken by KT. All authors commented on previous versions of the manuscript and read and approved the final manuscript. KT was responsible for data curation, project administration, and funding acquisition.

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Data availability The datasets generated and analyzed during this study are available from the corresponding author upon reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors have no competing interests to declare that are relevant to the content of this article.

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