

Can we expect more from *Alnus glutinosa* (L.) Gaertn. in a changing climate?

Katharina Tiebel,
Antje Karge

Black alder (*Alnus glutinosa* [L.] Gaertn.) is recognized as a key tree species in moist habitats, riparian ecosystems, and wetland restoration projects. The future success of *A. glutinosa* establishment is believed to be at risk due to the increasing frequency of high-temperature and drought events associated with climate change. However, some studies have indicated that alder may tolerate greater drought stress than previously assumed. In this study, a series of greenhouse experiments was conducted to assess the sensitivity of black alder to drought during seed germination and seedling establishment in its first year. The results showed that alder seeds can withstand unfavourable germination conditions (e.g., radiation, precipitation, heat) for periods exceeding 16 weeks and still germinate successfully thereafter. Consequently, the expected increase in spring and summer droughts due to climate change will not affect the success of alder germination in years with extended periods of precipitation. Additionally, germination success appears unaffected by the absence of cool spring temperatures. Warmer spring temperatures are necessary for germination and the presence of open mineral soil. Covering dry soil with litter and moss proved problematic, and as drought conditions worsen, there are no safe alternatives to exposed mineral soil. Shading was found to significantly enhance germination success. This allows alder to germinate in a changing climate in shaded locations that remain moist for longer. During germination on open soil, alder seeds did not exhibit specific requirements for soil moisture compared to other deciduous pioneer tree species. Furthermore, drought conditions did not significantly affect growth parameters, including shoot and root growth, root collar diameter, and biomass; however, there was a tendency toward reduced shoot length and belowground biomass under drought stress. Importantly, alder seedlings cannot survive dry periods exceeding 3-6 weeks without soil moisture during spring, summer, or autumn, consistent with other pioneer species such as *Betula pendula*, *Salix caprea*, and *Populus tremula*. These findings support the hypothesis that alder trees are more drought-tolerant than previously thought.

Keywords: Black Alder, Drought Stress, Seed, Germination, Seedling, Radiation, Biomass, Riparian Ecosystem

Introduction

Alnus glutinosa (L.) Gaertn., commonly known as black alder, is a typical pioneer tree species that requires light to sunny conditions for establishment. Alder trees exhibit rapid early growth and a short life-span, but suffer from competition by other tree species (Claessens et al. 2010, Houston et al. 2016). Black alder is an important pioneer species in moist habitats and riparian

ecosystems, providing habitat for fauna and flora, enhancing soil nutrient levels via nitrogen fixation, stabilizing the soil to protect against erosion, and filtering pollutants from soil and water (Claessens et al. 2010, Lovely 2019). For alder to exert a positive influence on riverbanks, it is essential that it regenerates and establishes successfully in these areas.

Black alder seeds germinate optimally on

mineral soil with sufficient soil moisture and high sunlight (McVean 1953, 1955, Schalin 1967, Willoughby et al. 2019). Climate change is leading to declines in cool spring temperatures, a general rise in temperatures, an increase in the frequency of high-temperature events, and reduced rainfall during spring and summer, resulting in frequent and prolonged drought periods (IPCC 2021). These changes are also affecting riverbanks and floodplains, causing soil surfaces and upper soil layers to dry out despite the moist environment. This raises the question of how strongly black alder regeneration will be affected by these changing conditions in wetlands.

Certain species necessitate cold temperatures before or during germination, whereas others require warm conditions or a combination of these factors. MacCart-haigh & Spethmann (2000) recommend a cold treatment of alder seeds lasting three to five weeks at temperatures between 0.5 and 1 °C to promote germination. Thus, the

Chair of Silviculture, Institute of Silviculture and Forest Protection, TUD Dresden University of Technology, Piener Str. 8, 01737 Tharandt (Germany)

@ Katharina Tiebel (katharina.tiebel@tu-dresden.de)

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expected decline in cool spring temperatures could negatively affect alder. Alder seeds possess an oily seed coat, a thicker seed testa, and a higher surface-to-volume ratio, which necessitate greater water uptake for swelling and germination, as compared to other pioneer tree species (McVean 1955, Fenner & Thompson 2005, Tiebel et al. 2024). Eschenbach & Kappen (1999) emphasize that alder seeds cannot germinate and establish on dry sites (Lovely 2019). According to Gomes Marques et al. (2022), the future establishment success of *Alnus glutinosa* is likely to be threatened by climate change. The authors highlight potential challenges, particularly concerning the restoration of riverbanks and disturbed wetland sites (Gomes Marques et al. 2022). This raises the question of whether covering or shading the ground could create alternative site conditions that would prolong soil moisture availability, thereby preserving the alder's germination potential. Additionally, it is relevant to consider the duration for which alder seeds can withstand dry conditions and direct sunlight on the soil surface while remaining viable for germination upon re-watering. Further, it is known that seeds stored at room temperature and high humidity, especially when subjected to repeated swelling and drying cycles due to precipitation, tend to lose their germination capacity more rapidly than seeds stored under dry, cold conditions at freezing temperatures, where metabolic activity and reserve consumption are minimized (Schönborn 1964, Schubert 1998).

Zhu et al. (2023) demonstrated that alder trees may tolerate more drought than previously assumed. Nevertheless, most seedlings of pioneer tree species in temperate forests cannot survive dry periods of more than three weeks (Tiebel et al. 2023), though there is still a lack of sufficient studies on this topic. Zhu et al. (2023) wrote: "In the future, more detailed experiments under well-controlled conditions as well as long-term field investigations are recommended to have a deep understanding of

the effects of projected drought and heat events on this tree species".

In this study, we investigated the drought stress sensitivity of *Alnus glutinosa* during seed germination and seedling establishment within the first year under controlled conditions. Four questions guided this research: (i) Could a reduction in cooling periods in winter and spring have negative effects on the germination of alder seeds in a changing climate? (ii) Are there alternative germination sites for alder, such as shady or covered soils, if dry and sunny mineral soils prove to be poor germination sites as a result of climate change? (iii) Can alder seeds withstand dry conditions and direct sunlight on the soil surface and still germinate later? (iv) How long can alder seedlings survive a dry period in spring and summer-autumn?

The findings from these studies are crucial for understanding the drought stress sensitivity of *Alnus glutinosa* and assessing its vulnerability to climate change.

Materials and methods

The study consists of four experiments: (1) germination tests, (2) seedling survival and growth under different site conditions, (3) delayed germination, and (4) seedling survival under drought stress (Fig. 1). Only studies 2 and 3 were linked. All other studies were independent and conducted under different conditions, as shown in Fig. 1 and described below.

The seeds of *Alnus glutinosa* for all four experiments were obtained from the seed kiln of the state forest enterprises of Saxony in Flöhe, Germany. The seeds were collected in 2019 in hilly locations in Saxony, Germany, and exhibited a germination rate of 71% in 2023.

(1) Germination tests

Germination tests were conducted in a climate chamber to determine whether *A. glutinosa* seed germination depends on temperature or light availability. High spring or autumn temperatures and the absence of cold periods can influence the ger-

mination behaviour of tree species (MacCarthaigh & Spethmann 2000). Therefore, germination tests following the ISTA (2012) guidelines were performed in summer and autumn 2023 using Jacobsen seed germination kits with domes. The germination tests included four variants, combining two temperature levels (25 and 5 °C) with two light conditions (16 h light/8 h darkness and 24 h darkness – Fig. 1). Each variant consisted of four replicates (ISTA 2012), corresponding to four seed germination kits per variant. Each germination kit contained 100 alder seeds sown on moist filter paper. The germination kits were placed in a climate chamber, and germination was monitored weekly for 3 weeks. Germination was considered successful when seedlings had developed a root, a shoot, and the first leaves.

(2) Seedling survival and growth under different site conditions

A greenhouse experiment was conducted following the study by Tiebel et al. (2023), to determine whether the seeds of *A. glutinosa* continue to require high radiation, soil moisture, and open soil for successful germination under climate change, or whether the requirements for germination sites will change. We tested three types (variants) of ground cover, three radiation levels, and three soil moisture levels, with two replicates for each of the 27 treatment combinations established in spring 2023 (Fig. 1). It was hypothesized that shaded conditions maintain higher soil moisture; however, it remains unclear whether this is better achieved through ground cover or shading.

For the preparation of treatment variants, 54 pots were filled with a 1:1 substrate mixture of brown podsol soil from the Tharandter Forest, Germany, and the cultivation substrate "Einheitserde" (Typ ED 73) from Meyer shop, Germany. The ground cover variants included: open soil; a 4-5 cm-high layer of spruce litter; and a 3-5 cm-high layer of moss mixture comprising *Pleurozium* sp., *Polytrichum* sp., and *Dicranum* sp., collected from the Tharandter Forest, placed atop the substrate mixture. The shading treatments consisted of 11% and 27% shade, created with shade mats and controlled using the SKP 210 sensor, which measures photosynthetically active radiation (PAR). Due to the inherent reduction in radiation within greenhouses (Seemann 1952, Tiebel et al. 2023), it was not possible to exceed 46% radiation, though alder can tolerate higher radiation levels (Chan et al. 2003). Therefore, the 46% variant was not shaded in the greenhouse and represents the open area radiation variant.

The three soil moisture variants were dry, moist, and wet conditions. The dry variant was maintained above the permanent wilting point at 8-12 vol.%, representing future conditions; the moist variant was at the lower field capacity limit at 15-24 vol.%; and the wet variant was at the upper field ca-

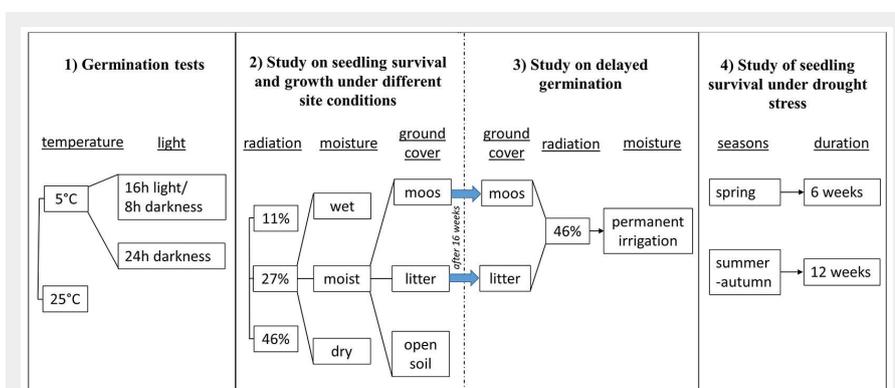


Fig. 1 - Flow chart of the experimental designs for the four experiments: (1) germination tests, (2) seedling survival and growth under different site conditions, (3) delayed germination, and (4) seedling survival under drought stress. The vertical solid lines indicate separate experiments, and a dashed line indicates linked experiments.

capacity limit at 27-35 vol.%, simulating riparian zone conditions.

Each of the 54 pots was sown with 100 untreated *A. glutinosa* seeds. All pots were randomly arranged within the greenhouse, weighed three times weekly, and irrigated as needed to compensate for weight loss and maintain the designated moisture levels (Tiebel et al. 2023). The greenhouse conditions ranged from an average daily minimum temperature of 5 °C to a maximum of 36 °C, with relative humidity between 31% and 86%. The seedlings were counted weekly for 16 weeks. At the end of the experiment in August 2023, all seedlings were harvested, thereby destroying the substrate structure within each pot. Measurements of shoot and root lengths were taken using a folding ruler; root collar diameter was measured with a calliper. Seedlings were then oven-dried for 2 days at 105 °C, and their above- and below-ground biomass were determined using a precision scale.

(3) Delayed germination

Following the completion of the previous study (2) on seedling survival and growth under different site conditions, all pots in which no germination had occurred after 16 weeks and the substrate remained intact were subjected to 46% radiation in the cold greenhouse with an automatic irrigation system (Fig. 1). This marked the start of the third experiment. The aim was to determine whether alder seeds could withstand repeated cycles of swelling and desiccation and still germinate successfully weeks later. The study included 36 pots with moss and litter cover. The open soil pots were excluded, as germination was observed in every open soil pot. Only undisturbed pots containing 100 seeds each were included in this delayed-germination assessment. Germination was recorded once a week for the first three weeks. After four weeks, no new germinations were observed. During this period, the average daily minimum and maximum temperatures ranged from 6 to 21°C, with relative humidity between 63% and 85%.

(4) Seedling survival under drought stress

Two drought stress experiments were conducted on April 24, 2023 (spring) and July 31, 2023 (summer-autumn) to investigate the duration of survival of *A. glutinosa* seedlings under drought conditions when the topsoil dries out. The methodology followed the procedures outlined by Tiebel et al. (2023). For the spring experiment, four pots (each serving as a replicate) were filled with the described 1:1 substrate mixture of brown podzol soil and “Einheitserde”, and watered to 30-35 vol.%. Similarly, eight pots (eight replicates) were used for the summer-autumn experiment. Each pot was sown with 100 *A. glutinosa* seeds. Seed germination and seedling development were allowed to proceed for six

weeks before watering was discontinued to induce drought stress (Fig. 1).

Temperature and humidity data were the same of the experiment (2) on survival and growth of seedlings under different site conditions. We counted the living seedlings and measured the soil moisture every week. The spring drought stress experiment was concluded once all seedlings had died. The summer-autumn experiment was terminated after 12 weeks of observation in December 2023, as no further seedling mortality occurred and the vegetation period had ended.

Statistical analyses

The Kruskal-Wallis H test was used to analyse the germination test results, as the data were not normally distributed (Zar 2010).

The structure of the experiment (2) on seedling survival and growth under different site conditions corresponded to a full factorial design, with the response variables “surviving seedlings” and “delayed germination” being binomially distributed. Each surviving seedling and germinated seed was considered as a replicate in the analyses (Castro et al. 2005, Tiebel et al. 2021), since seedling survival and seed germination were binary events (absence = 0, presence = 1). Generalized linear mixed models (GLMM) were used to assess the influence of the fixed effects – soil cover (categorical variable), soil moisture (categorical variable), and radiation (continuous variable) – on the response variables (Zuur et al. 2009). Pots were included as a random effect, as each of the 100 seeds sown per pot was treated as one observation in the dataset. No overdispersion was observed in the models, as the data consisted of independent binary observations, with the only parameter also determining the variance. The analyses of growth parameters (response variable) – shoot length, root length, root collar diameter, and biomass – in experiment 2 were conducted using linear mixed-effects models (LMMs), with soil moisture and ground cover as categorical variables, radiation as a continuous variable, and pot number as a random effect. The growth data were log-transformed to meet assumptions of normality and homogeneity of variance prior to analysis.

The data on seedling survival under drought stress (4), which were also binomially distributed, were analysed using GLMMs. In this study, soil moisture was treated as a continuous variable, while season was modelled as a categorical fixed effect. The pot number was included as a random effect.

The effects of fixed factors were evaluated using backward selection based on Akaike Information Criterion (AIC) values to identify the optimal model fit (Tiebel et al. 2023). All modeling was performed using the “lme4” package (version 1.1-35.1) and the “glmmTMB” package (version

1.1.8) in R Studio v. 2022.12.0 (Bates et al. 2015, Brooks et al. 2017, R Core Team 2022).

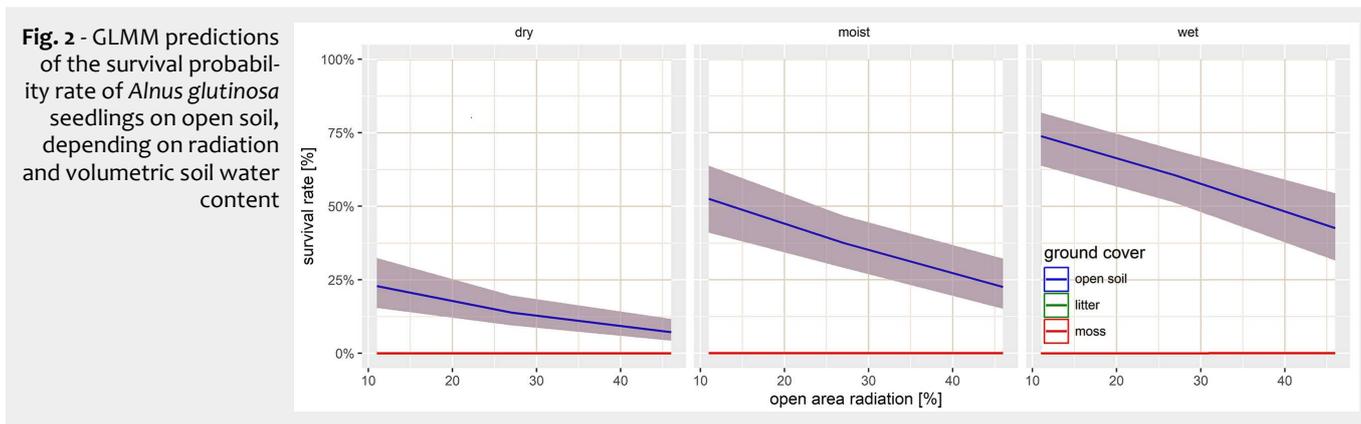
Results and discussion

Germination tests

The germination of *Alnus glutinosa* seeds is closely linked to warm and light conditions. The highest average germination percentage (75%) was observed when the seeds were exposed to 25 °C with a 16-hour light cycle (Fig. S1 in Supplementary Material). These conditions promote good germination success, as supported by previous studies (McVean 1953, 1955, Schalin 1967, De Atrip et al. 2007). When seeds were kept at 25 °C in darkness, the average germination percentage dropped to about 12%, suggesting that light is an important factor for germination. McVean (1953), Schalin (1967), Gosling et al. (2009), and Houston et al. (2016) also came to this conclusion. However, in our experiment, light had no significant effect on germination (Kruskal test, p-value = 0.369). McVean (1955) showed that seeds of *Alnus glutinosa* germinate in the dark. Depending on the seed batch, germination rates in the dark ranged from 25 to 62% (McVean 1955). This indicates that the germination rate of alder seeds may be lower in the dark. Temperature, on the other hand, has proven to be important for germination (Kruskal test, p-value < 0.001). Temperatures of 5 °C did not activate the germination process despite the presence of light. McVean (1953), Gosling et al. (2009), and Aniszewska et al. (2019) showed that germination of black alder seeds typically begins with rising temperatures in late February or early March, around 10-15 °C or 20 °C. Therefore, it can be hypothesized that the expected decrease in cool spring temperatures due to climate change is unlikely to negatively affect the success of Black alder germination.

Seedling survival and growth under different site conditions

During the entire study period, no *Alnus glutinosa* seeds germinated on moss and litter cover. The results revealed that black alder seeds require exposure to mineral soil to germinate (McVean 1953, 1955, Schalin 1967). This finding was somewhat unexpected, as other species for which litter and moss are not considered safe sites under climate change scenarios, such as *Salix caprea* and *Populus tremula*, demonstrated limited germination on these substrates (Tiebel et al. 2023). A possible explanation is the presence of an oily seed coat in *A. glutinosa*, which may hinder seed swelling and germination (McVean 1953, 1955). On moss and litter, there is no direct contact between seeds and soil (Oleskog & Sahlén 2000, Rautio et al. 2023), and the organic layer has a high water-absorbing capacity (Schalin 1967, Oleskog & Sahlén 2000). Also, alder seeds and seedlings require approximately one month of high soil moisture and humidity for successful establish-



ment; main humidity levels above 50% are crucial during the first month of germination (McVean 1953, 1955, Schalin 1967, Claessens et al. 2010, Houston et al. 2016).

On open soil, the highest germination rate was observed after four to five weeks, ranging from 12% (23 seeds) to 72% (143 seeds), depending on soil moisture and radiation levels. The oily testa may have contributed to the prolonged germination period, as also reported by previous research

(Schalin 1967, Kaliniewicz et al. 2018). Gomes Marques et al. (2022) emphasize that climate change, characterized by increasing temperatures and drought, could lead to extended germination and establishment periods in black alder, a trend consistent with our findings.

By the end of the study, survival rates ranged from nine to 136 seedlings (Fig. 2). Statistical analysis revealed a significant negative effect of increasing radiation and

decreasing soil moisture on seedling survival (Tab. 1). No significant interactions between these parameters were detected. The seedling survival of black alder was significantly constrained on dry, open soil, corroborating the findings of Eschenbach & Kappen (1999), who reported that alder seeds are unable to germinate and establish in dry sites. The challenges posed by drought and the associated stress responses in seedlings are exacerbated by higher levels of radiation. Our results demonstrated significantly lower survival rates with increasing radiation. This vulnerability to drought stress suggests that successful seedling establishment of *Alnus glutinosa* may become more difficult under climate change scenarios involving fluctuating water levels, altered watercourses, and reduced precipitation (Gosling et al. 2009, Lovely 2019, Gomes Marques et al. 2022). It is therefore highly beneficial that alder seedlings can establish in shaded conditions, where moisture retention is often longer. However, it should be noted that this does not imply that the seedlings and mature trees can persist or grow permanently in shaded environments (see experiment 2 – McVean 1953, Schalin 1967). Black alder is a shade-intolerant tree throughout its entire life span and, like other pioneer tree species, requires light to sunny sites with ± 20% of open area radiation for estab-

Tab. 1 - Results of the survival rate model (GLMM, left) and delayed germination model (GLMM, right) as a function of radiation, volumetric soil water content, and ground cover. The parameter estimation for the final models with the lowest AIC value are shown. The intercept represents shady, wet moss or shady, wet open soil. (SE): standard error; (SD): standard deviation.

Fixed Effects	Survival rate			Fixed Effects	Delayed germination		
	Estimate	SE	p-value		Estimate	SE	p-value
(Intercept)	1.456	0.302	<0.001	(Intercept)	0.597	0.205	0.004
moss	-0.274	0.000	0.999	litter	0.447	0.147	0.002
litter	-0.274	0.000	0.999	moist	-0.004	0.180	0.979
moist	-0.935	0.275	0.001	dry	-0.219	0.179	0.222
dry	-2.249	0.289	<0.001	radiation	-0.030	0.005	0.000
radiation	-0.038	0.008	<0.001	-	-	-	-
Random Effects	Name	Variance	SD	Random Effects	Name	Variance	SD
pot number	Intercept	0.179	0.423	pot number	Intercept	0.150	0.387

Tab. 2 - LME results for the logarithm-transformed dependent variables shoot length, root length, and root collar diameter of *Alnus glutinosa* seedlings growing on open soil. The parameter estimates for the final model with the lowest AIC are shown. The intercept represents shady, wet soil. (SE): standard error; (SD): standard deviation.

Fixed Effects	Shoot length (cm)			Root length (cm)			Root collar diameter (mm)		
	Estimate	SE	p-value	Estimate	SE	p-value	Estimate	SE	p-value
(Intercept)	1.535	0.106	<0.001	1.599	0.112	<0.001	-1.204	0.101	<0.001
moist	0.004	0.159	0.979	-0.162	0.172	0.368	-0.134	0.154	0.409
dry	0.000	0.194	0.999	-0.056	0.222	0.804	0.289	0.199	0.160
radiation	0.026	0.003	0.002	0.023	0.003	<0.001	0.034	0.003	<0.001
radiation:moist	-0.001	0.006	0.808	0.011	0.006	0.105	0.008	0.006	0.169
radiation:dry	-0.019	0.007	0.022	-0.009	0.008	0.307	-0.012	0.008	0.123
Random Effects	Name	Variance	SD	Name	Variance	SD	Name	Variance	SD
pot number	Intercept	0.008	0.089	Intercept	0.006	0.079	Intercept	0.005	0.072
residual	-	0.351	0.592	-	0.563	0.750	-	0.447	0.669

lishment (McVean 1953, Götz 2003, Claessens et al. 2010, Houston et al. 2016).

The effect of drought stress, in combination with other environmental conditions such as dryness, shading, and soil cover, can be inferred not only through germination success but also from growth parameters, including shoot and root length, root collar diameter, and biomass. The analysis of these growth parameters and their differences provides insights into how trees allocate their growth energy and enables evaluation of environmental factors that affect juvenile growth rates.

When the black alder seedlings were established on open soil, a significant, positive effect of radiation on shoot growth, root growth, root collar diameter, and biomass was found (Tab. 2, Tab. 3). The mean shoot length and root length of the germinated seedlings on open soil varied from 4.8 to 17.8 cm and 5.7 to 19.6 cm, respectively. The seedlings exhibited an average root collar diameter of 0.5-2.3 mm. The average above-ground biomass ranged from 22 to 548 mg, while the average below-ground biomass varied between 4 and 152 mg. In the first few years, shoots can grow up to approximately 1.5 m per year (Claessens et al. 2010). In the present study, an average shoot length of 17.8 cm was achieved after 16 weeks of growth under sufficient moisture and light, which is consistent with the growth rates reported by Lovely (2019). Radiation levels of 20% lead to stagnating growth rates (Claessens et al. 2010), which explains the significantly reduced shoot lengths of 7.1 cm observed in our study at 11% radiation, despite adequate moisture (Lovely 2019). The reduced shoot length confirms that alder, as a pioneer tree species, requires sufficient light for optimal growth (McVean 1953, Götz 2003, Claessens et al. 2010, Houston et al. 2016). Furthermore, the seedlings showed the lowest biomass yields on dry open soil with 11% radiation, while the highest biomass was recorded on moist, open soil with 46% radiation.

Surprisingly, drought did not significantly impact any growth parameters; however, a clear trend of reduced shoot growth, root growth, root collar diameter, and biomass under drought conditions was observed (Fig. 3). The seedlings of *Alnus glutinosa* showed significantly higher below-ground biomass in moist soil conditions (Tab. 3), while shoot growth was reduced in dry, open soil conditions as radiation increased (Tab. 2). The higher below-ground biomass indicates that more fine roots were formed with increasing moisture, as root lengths and root collar diameters did not differ significantly. The reduction in shoot growth during drought and under high-light conditions occurs even though the above-ground biomass remains relatively unchanged. This can be explained by noting that black alder does not adapt well to shade, as it does not develop shade leaves (Eschenbach & Kappen 1999, Claessens et

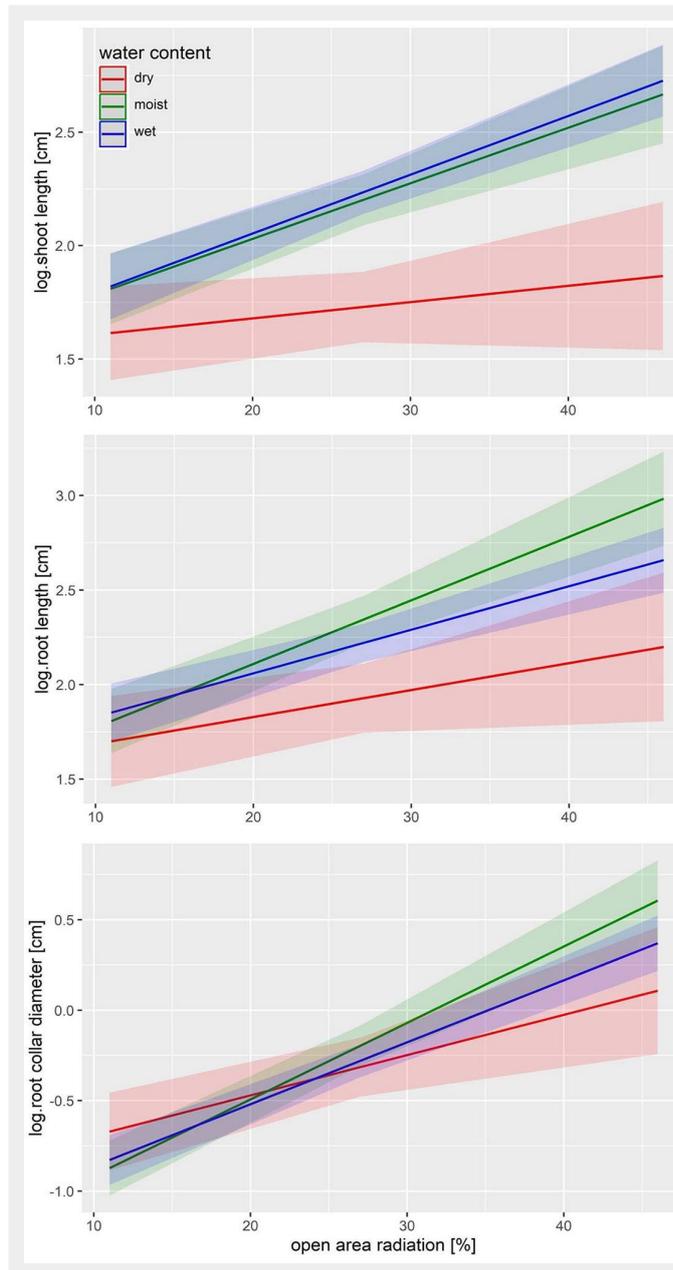


Fig. 3 - LME predictions of the shoot length (cm), root length (cm), and root collar diameter (mm) of *Alnus glutinosa* seedlings growing on open soil, depending on radiation and volumetric soil water content.

al. 2010). As a result, leaf biomass remained stable, and the shoot length was reduced under drought stress, with no significant effect on overall above-ground biomass.

Lovely (2019) demonstrated that drought can influence sprout growth and root length but does not significantly affect root collar diameter or above- and below-

Tab. 3 - LME results for the logarithm-transformed dependent variables above-ground biomass and below-ground biomass of *Alnus glutinosa* seedlings growing on open soil. The parameter estimates for the final model with the lowest AIC are shown. The intercept represents shady, wet soil. (SE): standard error; (SD): standard deviation.

Fixed Effects	Above-ground biomass (g)			Below-ground biomass (g)		
	Estimate	SE	p-value	Estimate	SE	p-value
(Intercept)	-4.754	0.149	<0.001	-7.801	0.387	<0.001
moist	0.093	0.132	0.497	0.881	0.345	0.027
dry	-0.183	0.167	0.289	0.354	0.399	0.387
radiation	0.067	0.005	<0.001	0.100	0.011	<0.001
Random Effects	Name	Variance	SD	Name	Variance	SD
pot number	Intercept	0.014	0.118	Intercept	0.224	0.473
residual	-	1.627	1.276	-	5.298	2.302

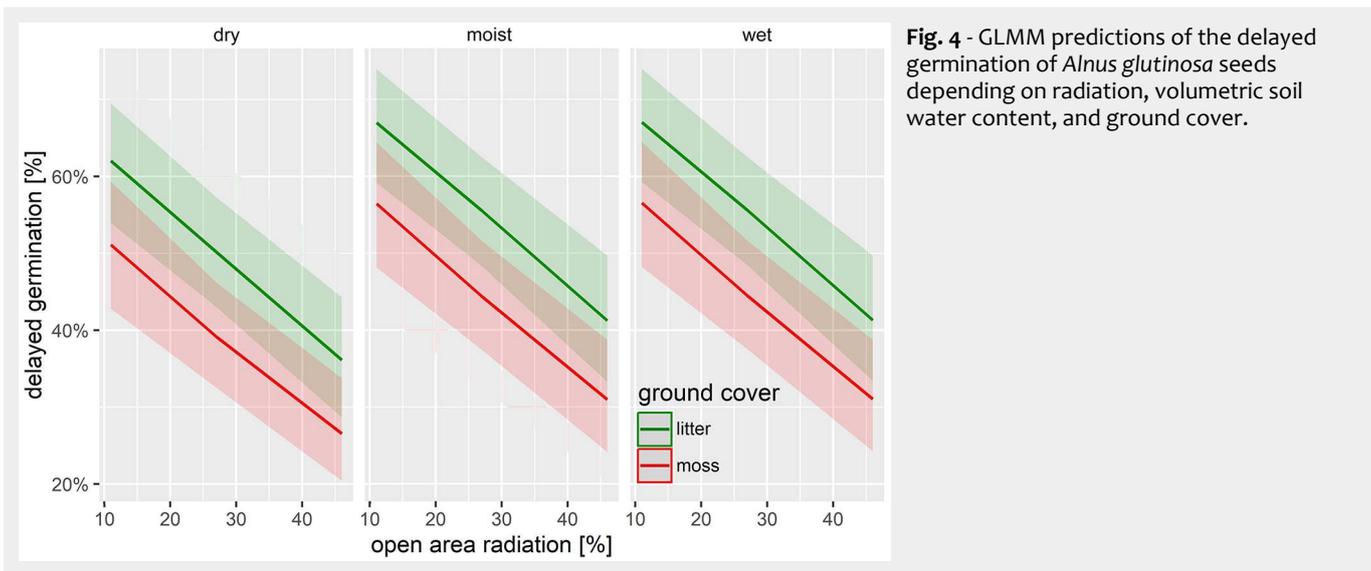


Fig. 4 - GLMM predictions of the delayed germination of *Alnus glutinosa* seeds depending on radiation, volumetric soil water content, and ground cover.

Tab. 4 - Results of the seedling survival (GLMM) during drought periods in spring and summer-autumn for *Alnus glutinosa* as a function of soil water content and period. The parameter estimates for the final model with the lowest AIC are shown. The Intercept represents the drought period in the summer-autumn. (SE): standard error; (SD): standard deviation.

Fixed Effects	Estimate	SE	p-value
(Intercept)	-1.834	0.147	<0.001
soil moisture	0.077	0.003	<0.001
spring	-1.216	0.270	<0.001
soil moisture:spring	0.058	0.007	<0.001
Random Effects	Name	Variance	SD
pot number	Intercept	0.094	0.307

dicating that *Alnus glutinosa* is less sensitive to drought stress than expected for a riparian tree species. Nonetheless, slow growth caused by limited light or drought can prolong the juvenile phase, thereby increasing the risk of pathogen infection, herbivory, and browsing, as well as mortality from permanent flooding or further drought stress (Lovely 2019, Gomes Marques et al. 2022, Miettinen et al. 2024).

Delayed germination

After 16 weeks without germination in moss and litter pots (experiment 2), germination began just a week after automatic, continuous watering started and was complete in most pots within three weeks (experiment 3). Maintaining consistent moisture levels facilitated the successful germination of alder seeds on moss and litter, aligning with the results of Claessens et al. (2010). Germination rates ranged from 19 to 64% on moss and from 18 to 78% on litter. In general, the germination percentage of *Alnus glutinosa* can vary widely, typically between 15 and 80% (Schalin 1967, Hall & Nyong'o 1973, De Atrip et al. 2007, Gosling et al. 2009, Kaliniewicz et al. 2018, Gomes Marques et al. 2022).

The statistical analysis revealed that the variations in soil moisture conditions (from wet to dry) over the 16 weeks prior to germination, did not significantly influence the success of delayed germination (Tab. 1, Fig. 4). This could be due to the accelerated desiccation of seeds on moss and litter substrates, which determines the lack of contact with soil (Oleskog & Sahlén 2000, Rautio et al. 2023), reducing the water absorption by the organic layer (Schalin 1967, Oleskog & Sahlén 2000) and ultimately hampering the germination process on these substrates. The previously applied varying radiation levels negatively affected seed germination capacity after the storage period. Only 18-52% of seeds from the 46% radiation variant germinated after 16 weeks. Seeds exposed to continuous shading were protected from damaging UV ra-

ground biomass. According to Seiler & Johnson (1984), Eschenbach & Kappen (1999), Copolovici et al. (2014), and Lovely (2019), prolonged drought stress reduces transpiration, photosynthetic, and growth rates in black alder seedlings. In our experiment, the increased radiation appears to largely mitigate the effects of drought, in-

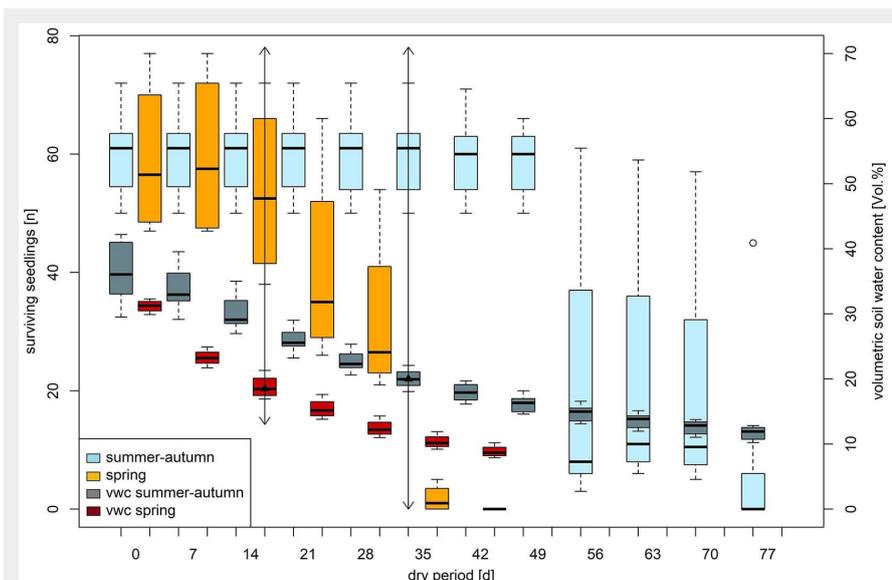


Fig. 5 - Effect of decreasing cumulated volumetric soil water content (vwc) on the seedling survival (n) of *Alnus glutinosa* over time (dry period) in spring and summer-autumn. The arrow indicates the moment when the measured soil moisture has fallen below the permanent wilting point.

diation, whereas seeds exposed to full sunlight experienced persistent UV exposure (Harrington 1972, Dadlani et al. 2023). It appears unlikely that the reduction in germination capacity was due to excessive seed desiccation caused by radiation, as low seed moisture content is generally associated with improved storability (Schönborn 1964, Aniszewska et al. 2019, Tiebel et al. 2024). Therefore, we conclude that alder seeds can survive extended periods without germinating, even when subjected to repeated cycles of watering, swelling, drying, and irradiation.

Seedling survival under drought stress

Following a three-week period of drought stress in spring and summer-autumn, during which soil moisture levels fell below the permanent wilting point, a decline in seedlings was observed (Fig. 5). A prolonged drought lasting four to six weeks led to the death of nearly all seedlings. More frequent and severe droughts are expected as a consequence of climate change, and this can often dry out the topsoil in typically moist areas like riverbanks, thus hampering the establishment of black alder seedlings. In contrast, mature trees of *A. glutinosa* with extensive and deep root systems can generally tolerate drought periods of four to six weeks without significant adverse effects. Old trees are primarily affected when deeper soil layers desiccate, typically after droughts lasting 2-3 months, accompanied by a decline in the groundwater table (Eschenbach & Kappen 1999, Roloff 2021, Zhu et al. 2023). Although *Alnus glutinosa* can close its stomata during drought conditions (Copolovici et al. 2014), its stomatal regulation is less efficient compared to species like *Fagus sylvatica* (Herbst et al. 1999, Zhu et al. 2023). Water consumption remains largely unchanged during drought periods (Eschenbach & Kappen 1999, Claessens et al. 2010), making black alder seedlings sensitive to drought stress (McVean 1953, 1955, Copolovici et al. 2014, Aniszewska et al. 2019). However, alder seedlings are no more susceptible to drought than seedlings of other deciduous pioneer tree species like *Betula pendula*, *Populus tremula*, and *Salix caprea*, which also hardly survive drought periods longer than three weeks (Tiebel et al. 2023).

The comparison of the impacts of drought stress across seasons revealed that spring drought had a significantly greater effect on seedling mortality than summer-autumn drought. At the onset of the drought stress experiments in both seasons, there were approximately 60 seedlings. The analysis revealed a significantly lower survival rate over time during the spring study. After stopping the irrigation in spring, the soil moisture reached the permanent wilting point after two weeks, and four weeks later, all *Alnus glutinosa* seedlings had died (Fig. 5). In contrast, during the summer-autumn study, the permanent wilting point was reached

after five weeks without irrigation, with the first seedlings dying after an additional three weeks. After six weeks of severe drought, an average of only 7% of the seedlings remained alive in December 2023. For both drought stress studies, a positive influence of soil moisture on the survival rate could be proven (Tab. 4). This positive effect was even more pronounced in the spring study (Tab. 4). In addition, the seedlings were also exposed to intense radiation and high temperatures, which further increased environmental stress on the plants (Copolovici et al. 2014, Roloff 2021). In autumn, these factors are significantly less intense and do not contribute additional stress to the seedlings. We hypothesize that the observed seedling mortality from autumn until December was primarily due to the continued photosynthetic activity of the alder leaves.

Conclusion

Black alder (*Alnus glutinosa*) is an important tree species in riparian ecosystems, which are affected by heat waves and drought periods driven by climate change. In view of climate change, the most significant challenge for the species is the drying of the topsoil, which negatively affects the germination and establishment of alder trees. Nevertheless, this study also identified strengths of alder that give hope in the context of climate change.

The germination success of *Alnus glutinosa* does not appear to be hindered by the absence of cool spring temperatures. However, the more frequent and intense spring and summer droughts is not expected to limit successful germination to years with prolonged periods of rainfall. It has been demonstrated that alder seeds can survive unfavourable germination conditions for over 16 weeks and still germinate successfully afterward. Alder is typically regarded as a species characteristic of riparian ecosystems (Zhu et al. 2023). Nonetheless, it has moisture requirements during germination similar to those of other pioneer tree species such as *Betula pendula*, *Salix caprea*, and *Populus tremula*, which colonise disturbed areas and are generally considered more drought-tolerant than alder (Tiebel et al. 2023). In dry locations near the permanent wilting point, alder seedlings can successfully establish and grow in open soil. Shading can significantly enhance germination success on dry soils. If *Alnus glutinosa* could reduce its water consumption under drought stress, a potential for reforestation of disturbed terrestrial forest areas would be possible (Zhu et al. 2023). However, covering the soil with litter and moss presents challenges. Alder requires mineral soil for successful germination. Seeds can only germinate on litter and moss when sufficient moisture is persistently available, which is unlikely in riparian ecosystems due to climate change. Droughts hamper the germination and development of *Alnus glutinosa* seedlings by

delaying and prolonging these processes. However, drought does not entirely prevent germination and the establishment of alder seedlings in dry locations.

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KT conceived the study, conducted the greenhouse measurements, performed the statistical analyses, and wrote the manuscript; AK conducted the greenhouse measurements and helped draft the manuscript.

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Supplementary Material

Fig. S1 - Results of seed germination under different conditions.

Link: Tiebel_4842@suppl001.pdf