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Original Article

More water, less light: how to improve silver fir seeding to convert Norway spruce monocultures into mixed stands in a drier region of Germany

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Abstract

Adaptive forest management gains importance as climate and disturbance regimes continue to change. Norway spruce monocultures are particularly vulnerable to those changes. Thus, there is a strong demand to convert pure spruce stands toward better adapted forest ecosystems. Silver fir has similar wood properties as Norway spruce, but is less vulnerable to droughts. Yet, little is known how to efficiently admix silver fir into Norway spruce monocultures. We analyzed seedling abundance in mature Norway spruce monocultures 1 year after soil scarification and silver fir seeding in a relatively dry region of southern Germany. Our objectives were to study the effect of soil scarification and seeding on regeneration density and to identify drivers of seedling abundance. We collected data on regeneration, forest structure, as well as soil and light conditions at 103 scarified and 25 untreated control plots. We used non-parametric independence tests to compare scarified and untreated plots. Subsequently, we used boosted regression trees to investigate the drivers of seedling abundance. Norway spruce strongly benefited from soil scarification ($P < .001$), with seedling numbers even exceeding those of silver fir. Both species thrived in soils with high plant available water capacity. In contrast, seedling numbers were overall negatively affected by light. Moreover, we found a higher density of silver fir regeneration at greater distance from neighboring trees and in soils devoid of carbonate. Our study indicates that water, not light, is the limiting factor for both Norway spruce and silver fir seedlings in the study region. Seeding silver fir will likely be most effective underneath an intact canopy on deep, fine-textured soils without carbonate, while maximizing the distance to Norway spruce trees. In conclusion, silver fir seeding can be optimized to become an effective adaptive measure to diversify Norway spruce monocultures, and thus to create more resistant and resilient forest ecosystems.

Keywords: adaptive management; forest conversion; Norway spruce; regeneration; soil scarification; silver fir

Introduction

Climate change and intensifying disturbance regimes constitute a great challenge for forest management in Central Europe (Seidl et al. 2016). The adaptation of forests to future environmental conditions is crucial for sustaining the social and economic benefits that forests provide to society (Thom and Seidl 2016, Knoke et al. 2021). As the current distribution of tree species is not adapted to climate change in many forest ecosystems, proactive interventions, such as planting drought-tolerant tree species or provenances, are becoming increasingly important (Mauri et al. 2023, Thom 2023). Tree planting is widely recognized as an important nature-based solution to climate change, as evidenced by initiatives like the EU's Biodiversity Strategy (3 billion trees project). However, the success of planting efforts depends on complex interactions of local climatic, soil, and stand conditions, which are often poorly understood (Park and Talbot 2018). Consequently, there is a need for a more comprehensive knowledge base on the factors determining the successful establishment and survival of seedlings, in order to facilitate efficacious and economical forest adaptation endeavors.

Norway spruce (*Picea abies* [L.]) is the most abundant and commercially important tree species in Central Europe, but, at the same time, highly susceptible to natural disturbances (Stadelmann et al. 2013, Panayotov et al. 2015). Droughts and bark beetle outbreaks have intensified over the past decades (Patacca et al. 2023). In particular, the drought episode from 2018 to 2020 was unprecedented in Central Europe (Büntgen et al. 2021), causing severe growth reductions (Thom et al. 2023) and high mortality of Norway spruce (Obladen et al. 2021). Climate conditions in lowlands of Central Europe are projected to become even less suitable for Norway spruce, while the pressure of disturbances, particularly bark beetles, is expected to increase and thereby cause a shift in species compositions (Temperli et al. 2013). To reduce future disturbance risks, some commercial forest enterprises aim to convert Norway spruce monocultures by admixing other tree species (Löf et al. 2023). Silver fir (*Abies alba* [Mill.]) has been promoted as a promising species to replace Norway spruce, as it has a higher drought tolerance (Vitasse et al. 2019) and similar wood characteristics as Norway spruce (Verkasalo and Leban 2002). Hence, silver fir might become more important for

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the wood-based industry in the future, and buffer some of the economic losses from growth decline and mortality of Norway spruce (Hlásny et al. 2017).

Commonly, silver fir is planted underneath tree canopies, as the species is very shade tolerant and susceptible to late frost (Niinemets and Valladares 2006, Bianchi et al. 2019). However, seeding has gained popularity as an alternative to planting (Baumhauer 2004, Kutscher et al. 2009). Advantages of seeding include, among others, the absence of a planting shock, natural root development, a potentially high regeneration density, and low costs of seeds compared to plants (Huth et al. 2017). Disadvantages of seeding include a high mortality of seeds due to seed predators and pathogens, exposure of seeds to adverse weather conditions (e.g. dry air and consequently dry top soils), and additional efforts for seedbed preparation (Huth et al. 2017). While previous studies have indicated a high potential of silver fir seeding to convert Norway spruce monocultures (e.g. Hamm et al. 2014), the success of silver fir seeding in drier regions of Central Europe remains uncertain. These regions are particularly important for conversions, as this is where Norway spruce is already close to its dry trailing edge. Research is also needed to assess whether Norway spruce is still able to regenerate and persist in these regions or whether a tipping point has been reached after which Norway spruce regeneration fails (Arend et al. 2021). Defining thresholds in seedling requirements for light as well as soil conditions, such as plant available water capacity (i.e. the potential amount of plant available water in the soil), may help forest managers to optimize seeding efforts for the conversion of Norway spruce monocultures to coniferous-rich mixed forests. In addition, further research is required to determine the optimal distance from seeding location to trees as tree roots may either facilitate or compete with regeneration (Karst et al. 2023), and precipitation amounts reaching the ground at given locations vary depending on the distance to tree stems (Jochheim et al. 2022).

To address these knowledge gaps, we analyzed seedling abundance in mature Norway spruce monocultures 1 year after soil scarification and silver fir seeding initiated by a private forest company in a relatively dry region in southern Germany. Our objectives were (i) to analyze the effect of soil scarification and seeding on regeneration density as well as (ii) to identify the drivers of seedling abundance. We hypothesized a high abundance of silver fir after seeding, but only few Norway spruce seedlings from natural regeneration due to unfavorable weather conditions in the year 2022 (H1). We expected a threshold after which increasing light availability becomes less favorable for regeneration as solar radiation elevates evapotranspiration (H2). Moreover, we assumed an increasing number of seedlings with distance from trees due to decreased root competition and higher throughfall (H3). Lastly, we hypothesized a positive relationship between available water capacity of soils and seedling abundance (H4).

Materials and methods

Study area

The forest stands of the forestry company “Fürst Wallerstein” are situated in the kolline–sub-montane lowlands of southern Germany (Fig. 1). The topography of the area is homogenous, with elevations ranging from ~500 to 550 m. The climate is sub-oceanic with annual average temperatures of about 10°C and annual precipitation sums of 724 mm (reference period: 1981–2010) (German Weather Service 2023). However, the region has become drier over the past decade and was frequently affected by droughts (Rupp et al. 2021). The geology of the region is shaped by a meteor impact that occurred some 14.5 million years ago. This impact created a bedrock of impactites. The dominant soil types are pseudogleys and brown soils, characterized by high proportions of clay and silt. Carbonate is not widespread in the study region, but can be found as a result of the meteor impact. European beech (*Fagus sylvatica* [L.]) historically dominated the potential natural vegetation in the study region, but as temperatures have increased, the current potential natural vegetation has already shifted toward forest types dominated by oaks (*Quercus* spp.) and European hornbeam (*Carpinus betulus* [L.]) (Fischer et al. 2019). The investigated species, silver fir and Norway spruce, are not naturally abundant in the study area. Norway spruce dominates montane–sub-alpine forests, while silver fir is a common tree species on pseudogleys in montane forests where Norway spruce is less competitive and cannot root deeply into the soils. With the given site conditions of our study area, Norway spruce is already close to the trailing edge of persistence (Honkaniemi et al. 2020), while silver fir is likely able to cope better with drier conditions (Bottero et al. 2021).

Site preparation and silver fir seeding

Silver fir seeding was performed in monocultures that consisted of almost 100% Norway spruce. In addition, very few Scots pine (*Pinus sylvestris* [L.]), European larch (*Larix decidua* [Mill.]), pedunculate oak (*Quercus robur* [L.]), and small-leaved lime (*Tilia cordata* [Mill.]) individuals were found on the studied sites. A contractor utilized a small excavator to scarify the forests’ upper soil layer in order to expose the mineral soil for an improved seed germination (Castro et al. 2002). Scarifications also created basins, concentrating precipitation in the seeded areas, and thus optimizing water availability for germination and growth. In addition, herbaceous plants and grasses were removed to reduce competition. During the seeding period in 2021, the forestry company manually sowed ~12 kg of silver fir seeds per ha (>200 000 seeds). The bulk of the seeds were collected in the company’s own silver fir stands, but ca. 21% of silver fir seeds originate from Romania. Prior to seeding, seeds were harvested and dried until the cones fell apart. Regular turning prevented seeds and cones from molding. Seeding took place in February and March. Weather conditions during spring and summer of 2021 were favorable for germination with high amounts of precipitation (Fig. 2). Yet, the period from September 2021 until data were collected in June 2022 was notably drier and warmer compared to the long-term (1981–2010) average, which potentially led to soil drying and increased seedling mortality.

Data collection

The study area encompassed 11 homogenous stands dominated by even-aged Norway spruce, in which we established a systematic inventory network of 128 plots (Fig. 1). At 103 plots, soils were scarified (Fig. 3), while the remaining 25 plots served as untreated control plots. The location of the first plot was chosen randomly, and all others were based on a 40 × 40 m grid. The 25 control plots were selected using a random number generator. All plot locations were established using a GPS receiver, aiming for close proximity to the designated coordinates. Once the indicated location was reached, a wooden pole was permanently installed at the center of the scarified area. At control plots, the pole was inserted into unscarified soil as close as possible to the corresponding GPS coordinates. The area per plot in which seedlings were recorded was rectangular, measuring 1.5 × 0.4 m (0.6 m^2) (Fig. 3).

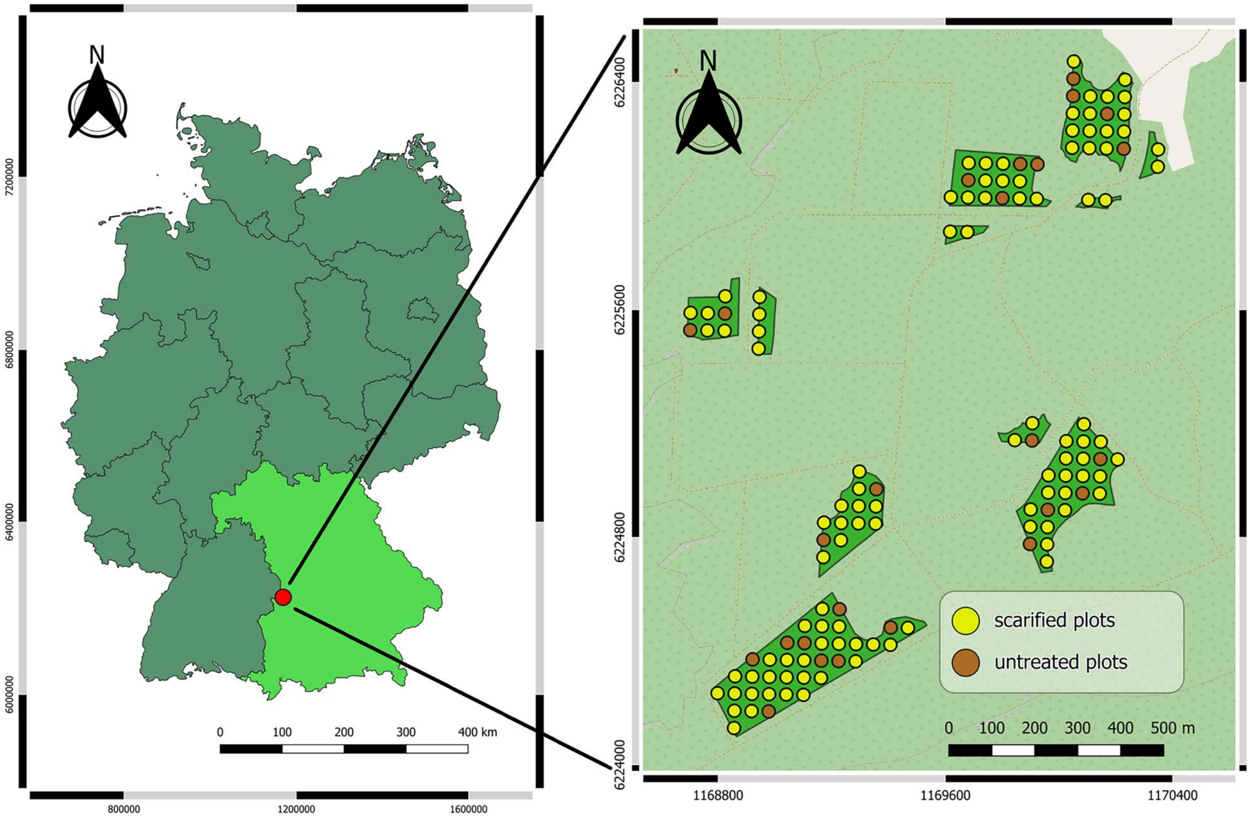

Figure 1. Location of the study area and inventory design. Coordinate reference system: EPSG:3857-WGS 84.

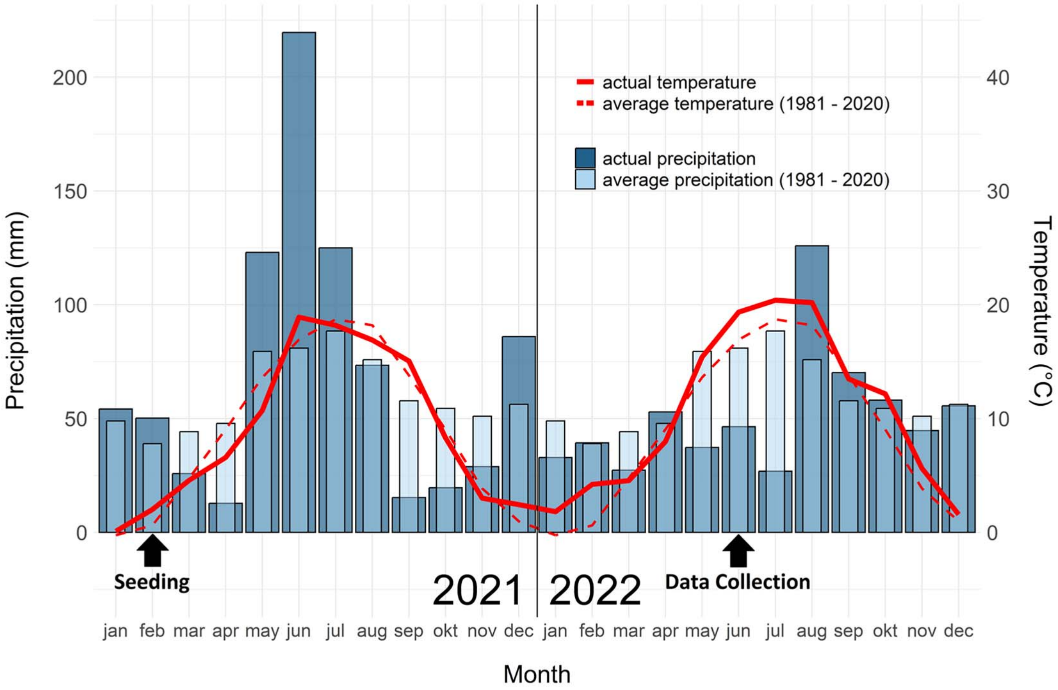

Figure 2. Weather conditions of the studied landscape during 2021 and 2022.

To record seedlings, a 10 × 10 cm grid was implemented within a wooden frame used for standardized measurements. Seedlings were typically between 5 and 10 cm in height and not affected by ungulate browsing (see also Borkowski et al. 2017). To measure light conditions at a standardized height of 1.5 m, a Solariscope 300 was positioned on the frame in the plot center after counting of seedlings. The Solariscope takes hemispherical photographs and differentiates between vegetation and sky in the images. We took one photo and applied seven different models to enhance the contrast between gaps and canopy cover per plot and selected the visually best fit. Based on these images and variation in the trajectories of the sun during the year, the Solariscope quantifies

Figure 3. Tree regeneration in a scarified plot.

different indicators for solar radiation. These include the indirect site factor (ISF) as measure of indirect (diffuse) light, the direct site factor (DSF) expressing direct light, and a combination of both, which is indicated by the total site factor (TSF). Moreover, the Solariscope estimates the gap fraction and the leaf area index. Basal area and stand density were determined using angle count sampling. Moreover, the diameter at breast height (dbh) of trees inside the angle count sampling were measured. Next, we extracted a soil probe of the plot. In particular, a soil sample was taken from a depth of 0.8 to 1 m, located 1.2 m north of the plot center to avoid damage to the seedlings. The sample was used to derive the soil's plant available water capacity, maximum rooting depth, and the presence of carbonate. The distance to the nearest tree was measured from the plot center to the closest stem. Plant available water capacity and potential rooting depth were estimated by separating the soil sample into different sections and determine the soil type (i.e. silt, sand, clay) and the depth and compaction of each section (Arbeitsgemeinschaft Forsteinrichtung Arbeitskreis für Standortskartierung 2016).

Analysis

To investigate the effect of soil scarification on Norway spruce seedling abundance, we first conducted a preliminary test to verify that stand and site conditions were similar between scarified and untreated control plots. In particular, we compared indirect site factor, basal area, and plant available water capacity using an independence test. Independence tests are non-parametric significance tests based on permutations. Thus, they do not rely on specific data distribution assumptions and can be applied to an unbalanced number of observations. As we did not find any significant differences between stand and site conditions ($P > .05$), we conducted an independence test for differences in seedling abundance between scarified and control plots. All subsequent analyses focused on the scarified plots only.

Addressing our first hypothesis, we used an independence test to compare regeneration density between silver fir and Norway spruce. All other hypotheses were addressed by an analysis of regeneration drivers using Boosted Regression Tree (BRT) models with a Poisson distribution. First, we conducted a variable selection procedure to reduce the number of candidate variables explaining seedling abundance. As all variables indicating light conditions (ISF, DSF, TSF) were highly correlated ($r > 0.8$), we only maintained ISF that had the highest unimodal correlation coefficient ($r = -0.13$) with total seedling abundance. Moreover, photosynthesis of trees is often even more strongly influenced by diffuse than direct light (Mercado et al. 2009). In total, we analyzed the effects of six covariates (i.e. plant available water capacity, indirect site factor, tree distance, basal area, potential rooting depth, and carbonate depth) on two response variables (i.e. silver fir and Norway spruce seedling numbers). We used the condition number to analyze the multicollinearity among explanatory variables. The condition number is a common metric to quantify multicollinearity in statistical models and has been recommended to not exceed a value of 2.2 (log-scale) (Dormann et al. 2013). The log-scaled conditional number among explanatory variables was 1.02, indicating only little remaining multicollinearity of our BRT models.

BRT models are ensemble models composed of decision trees (Elith et al. 2008). The covariates were sequentially added to the decision trees (100 trees per run), with the aim of explaining the remaining error from previously added covariates. BRT models are well suited for capturing non-linear effects and interactions, exhibiting high predictive accuracy even in the presence of high collinearity among covariates (Dormann et al. 2013). Moreover, BRT models provide a direct measure of variable importance by considering the frequency of a variable being selected for tree splits, weighted by the squared improvement in the model resulting from those splits (Elith et al. 2008). Throughout multiple model iterations, slight variations in outcomes were observed, owing to the utilization of different subsets of the original dataset during each model training cycle. Consequently, we fitted 100 BRT models for which we derived average effect sizes and uncertainties across models. We evaluated the goodness-of-fit of all models based on their variance explained (R^2). All covariates were z-transformed prior to model fitting. As the effect directions of covariates are challenging to estimate in BRTs and might slightly vary across models, we used all models to conduct a sensitivity analysis. That is, we decreased and increased each covariate by 1 SD, while retaining values of all other explanatory variables, and calculated the difference in predicted values.

All analyses were performed in R. For dataset management, we used the packages "readxl" (Wickham et al. 2023) and "tidyverse" (Wickham 2019a). For the independence test and variance inflation, we used the "coin" (Hothorn et al. 2008), "psych" (Revelle 2023), and the "car" (Fox et al. 2019) packages. For BRT models, we used the packages "gbm" (Greenwell et al. 2022) and "dismo" (Hijmans et al. 2017). The figures were made with the packages "ggplot2" (Wickham 2019b) and "MetBrewer" (Mills 2022).

Results

Tree regeneration after soil scarification

Silver fir seedlings were only present in the scarified plots, where seeding took place. For Norway spruce, we found a highly significant ($P < .001$) difference in the abundance of seedlings between

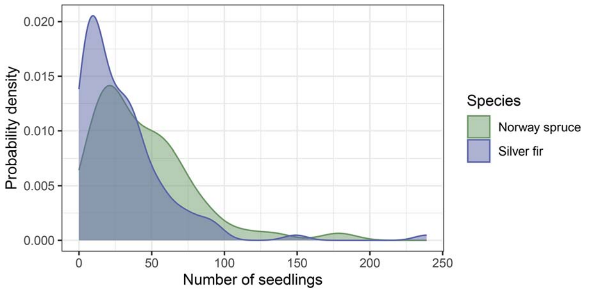

Figure 4. Distribution of Norway spruce and silver fir seedling abundance across scarified plots.

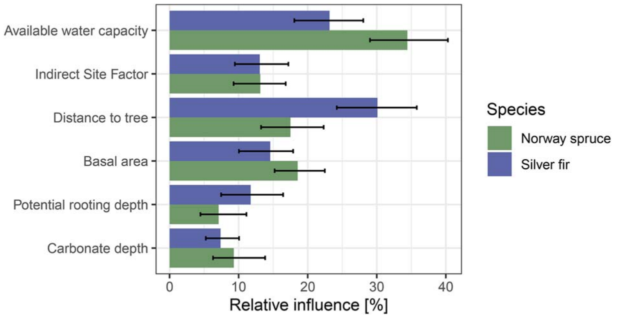

Figure 5. Relative influence of covariates on seedling numbers based on Boosted Regression Tree models. Bars show the average relative influence and error bars indicate the 95% confidence interval of the relative influence values across 100 models.

unscarified and scarified plots. Specifically, the median abundance of Norway spruce seedlings on untreated plots was 86% lower compared to scarified soil. This major contrast highlights the positive impact of scarification on the regeneration of Norway spruce.

The number of Norway spruce recruits from natural regeneration was significantly higher ($P = .013$) than the number of silver fir recruits following seeding in scarified plots (Fig. 4). Silver fir abundance varied from 0 to 239 individuals with a median number of 22, while Norway spruce exhibited a slightly lower variation, ranging from 0 to 183 individuals, with a median value of 36.

Drivers of silver fir seedling abundance

Our BRT models were able to explain, on average, 34.3% of the variance in silver fir seedling abundance. Among all covariates, distance to the nearest tree had the highest relative influence (on average, 30.0%) (Fig. 5). Plant available water capacity was the second most important variable in the model (22.8%), followed by basal area (14.9%), indirect site factor (13.3%), potential rooting depth (11.9%), and carbonate depth (7.2%).

Covariates exhibited non-linear relationships and threshold behaviors with silver fir seedling abundance (Fig. 6). Partial effect plots indicate the greatest number of silver fir seedlings at a distance to the nearest tree above 2.5 m. Moreover, we identified a decrease in seedling numbers at plant available water capacities below 110 mm/dm^2. Seedling abundance increased when the basal area of Norway spruce was below 38 m^2. Seedling numbers decreased with higher amounts of diffuse light and remained low after the indirect site factor reached 0.1. The absence of carbonate in upper soil layers was generally beneficial for silver fir seedlings, especially within the first 60 cm of soils. Seedling numbers decreased with potential rooting depth beyond 30 cm.

Standardized effect sizes expressed as an increase of each covariate by 1 SD revealed three variables with an overall positive and three variables with an overall negative impact on silver fir seedling abundance (Fig. 7). Of those, indirect site factor had the greatest impact on seedlings. That is, an increase in indirect site factor from −1 to +1 standard deviation (Table 1) reduced seedling numbers, on average, by eight. Potential rooting depth and basal area also showed negative effects, but to a lower extent (on average, −4 and −2 individuals, respectively). Distance to the nearest tree had the greatest positive impact on silver fir seedling abundance among all covariates (on average, +6 individuals). Also, carbonate depth and plant available water capacity increased silver fir seedlings (on average, +4 and +3 individuals, respectively). The sensitivity analysis was only significant ($P < .05$) for three of the six covariates, including indirect site factor, distance to the next tree, and carbonate depth. In effect, the interpretation of non-significant standardized effect sizes depends on the conditions for comparisons and their directionality cannot be generalized.

Drivers of Norway spruce seedling abundance

Boosted Regression Tree models could explain, on average, 33.8% of the variance in Norway spruce seedling abundance. In contrast to silver fir, plant available water capacity was, by far, the most important variable explaining Norway spruce seedling abundance with an average relative influence of 34.4% (Fig. 5). The second and third most important variables explaining the number of Norway spruce seedlings were basal area (18.2%) and distance to the nearest tree (17.6%). Similar to silver fir, the indirect site factor had a relative influence of 13.7%. Carbonate depth and potential rooting depth had the lowest relative influence on the model (9.1% and 7.1%, respectively).

We found a steep increase in the number of Norway spruce seedlings beyond an available water capacity of ~130 mm/dm^2 (Fig. 6). Similar to silver fir, seedling abundance of Norway spruce was particularly low with diffuse light levels above 10%. However, in contrast to silver fir, we identified an optimum with seedling numbers peaking at an indirect site factor of 0.06 (i.e. 6% diffuse light). Seedling numbers were lowest at a basal area of ~36 m^2. Contrary to the findings for silver fir, the response curves of Norway spruce seedlings to tree distance and carbonate depth were almost flat. Seedling numbers decreased if the potential rooting depth was greater than ca. 35 cm.

Only one covariate in the sensitivity analysis was clearly positively associated with Norway spruce seedling abundance, whereas two covariates showed almost no effect and three covariates had a negative relationship with seedling numbers (Fig. 7). Plant available water capacity had, by far, the strongest effect. That is, an increase of the variable from −1 to +1 SD (Table 1) resulted in an increase of 28 Norway spruce seedlings. Potential rooting depth had the second strongest impact, decreasing seedling numbers by 12. Similarly, an increase in diffuse light caused a reduction of 9 individuals. Marginal changes in seedling numbers were found for increasing basal area (−3) and carbonate (−1), while distance to the nearest tree showed a neutral relationship with Norway spruce seedlings (±0). The effects of three covariates on seedling numbers were statistically significant ($P < .05$), including available water capacity, potential rooting depth, and indirect site factor. The interpretation of standardized effects of other covariates remains highly uncertain.

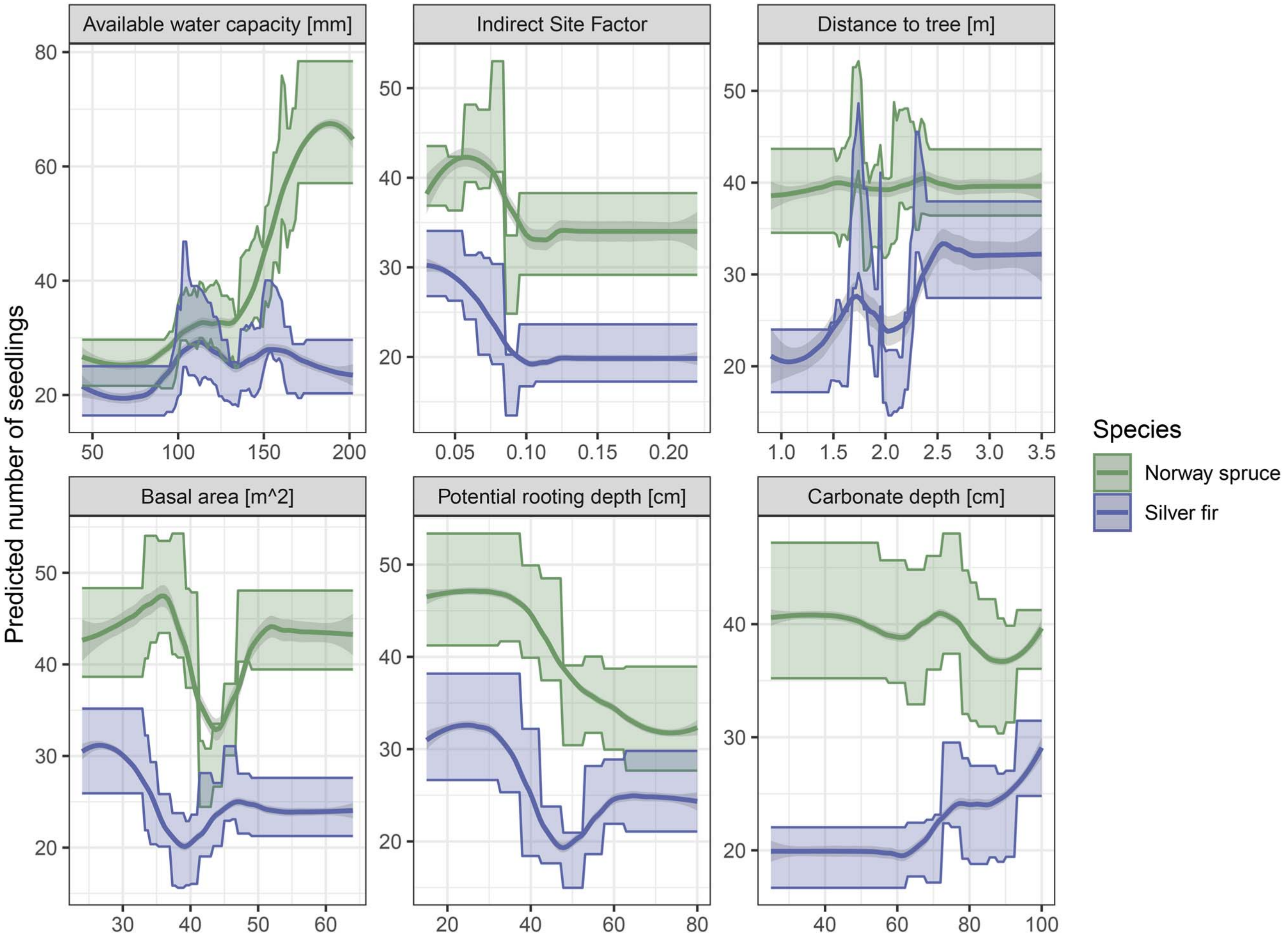

Figure 6. Partial dependence plots of the relationship between covariates and seedling numbers. Smoothed lines present averages and the interval highlights the range of predicted values based on 100 Boosted Regression Tree models.

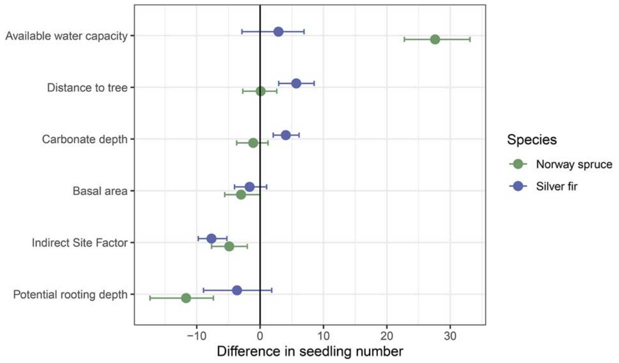

Figure 7. Sensitivity of seedling numbers on standardized covariates. Effects were derived by predicting seedling numbers when modifying each covariate individually by −1 to +1 SD and calculating the difference in predicted values. Dots indicate average values and bars show the 95% confidence interval across outputs from 100 models.

Discussion

Performance, limiting factors, and drivers of tree regeneration

Our study indicates that water, not light, is the limiting factor for both Norway spruce and silver fir seedlings in a drier region of Germany. Contrary to our initial hypothesis (H1), we found that Norway spruce seedlings were highly abundant on scarified plots. This suggests that environmental conditions have not yet reached a tipping point at which initial Norway spruce regeneration would fail. Our statistical models identified a threshold (H2) for the impact of light on Norway spruce regeneration. Initially, the number of seedlings increased with greater light availability until diffuse light levels reached ~6% (ISF = 0.06). Beyond this point, the abundance of seedlings decreased. In contrast, we observed no threshold for silver fir, indicating a consistently negative effect of light on silver fir seedlings. The distance to the nearest Norway spruce tree played a significant role for silver fir regeneration (H3), possibly due to root competition and limited precipitation amounts reaching the ground at close proximity to trees. Interestingly, the abundance of Norway spruce seedlings did not vary with tree distance, which may be attributed to intraspecific facilitation of regeneration through a common mycorrhizal network (but see Karst et al. 2023). Instead, the most influential factor explaining the abundance of Norway spruce seedlings was the soil's plant available water capacity (H4). For silver fir, this variable also exerted a positive effect on the abundance of seedlings, but it was less important than for Norway spruce, potentially suggesting a lower sensitivity of fir seedlings to drought.

Our findings show that soil scarification has a notable impact on the regeneration of Norway spruce, which is partially corroborated by other research. According to Fløistad et al. (2018), both the germination rate and height growth of seedlings experience significant enhancements through soil scarification. Their investigation reveals a decreasing trend in germination rate and seedling

Table 1. Summary of regeneration densities, as well as stand and site conditions of scarified plots ($n = 103$).

Category	Attribute	Unit	Description	Mean (SD)
Regeneration	Silver fir seedlings	n	Abundance of fir seedlings	30.05 (33.16)
	Norway spruce seedlings	n	Abundance of spruce seedlings	43.66 (34.59)
Forest structure	Basal area	$m^2\ ha^{-1}$	The cross-sectional area of all stems within an angle count sample	41.96 (7.8)
	Distance to nearest tree	m	Distance from the plot center to the nearest stem of a living tree	1967 (0.49)
Light conditions	Indirect site factor	Ratio	Indicator for diffuse light, measured in the plot center at 1.5 m height	0.073 (0.03)
Soil conditions	Plant available water capacity	$mm\ dm^{-1}$	The ability of soils to physically hold plant available water against the force of gravity	132.4 (36.18)
	Potential rooting depth	cm	The potential depth a tree can grow limited by soil compaction and bedrock	49.51 (14.71)
	Carbonate depth	cm	The depth where carbonate was found (a max. depth of 100 was assumed, if not present)	83.2 (22.3)

Presented are means and standard deviations (SD, in parentheses)

growth over time following soil scarification, underscoring the importance of promptly seeding after the scarification process to optimize seeding outcomes.

Although leaf photosynthesis increases with diffuse photosynthetically active radiation (Mercado et al. 2009), our study indicated a negative relationship between light levels and seedling numbers (Fig. 5). While, in particular, silver fir seedlings were sensitive to an increase in light levels, our findings also reflect the high shade tolerance of silver fir which enables it to outperform other species like Norway spruce under a rather dense canopy. Light availability is widely recognized as a crucial factor influencing both the density and growth of regeneration (Bednář et al. 2022). Yet, light availability is of greater importance for taller tree recruits compared to smaller ones (Dyderski et al. 2018) and may thus become a stronger indicator for regeneration success during future stand development. In addition, light increases evapotranspiration, causing soils and plants to dry out during prolonged warm and dry weather periods (Oren and Pataki 2001). Given that our study region is close to the drier trailing edge of the investigated species, light may not be a limiting factor for regeneration, as worsening drought conditions may be more important (see also Simon et al. 2019).

Basal area correlates with light conditions (Korhonen et al. 2007), but is also an indicator for seed availability (Halpern and Antos 2021). We used a statistical approach that is well able to deal with high correlations between explanatory variables (Dormann et al. 2013), and thus to disentangle the individual effects of light and basal area on seedling density. Although light levels decrease with basal area, suggesting a positive relationship with seedling density, we found that Norway spruce basal area had mainly negative effects on regeneration of both species. This result is not surprising for silver fir as a higher competition with Norway spruce can be expected. For instance, also Axer et al. (2023) observed a lower number of European beech seedlings as Norway spruce basal area increases. However, we anticipated a positive response from Norway spruce regeneration, given that basal area is correlated with the quantity of seeds released onto the ground (Paluch 2011).

In contrast to light and stocking density, plant available water capacity was positively associated with seedling abundance. In particular, our study revealed a very strong response of Norway spruce to an increase in plant available water capacity as the species is less drought tolerant than silver fir (Niinemets and Valladares 2006). Top soils may dry out quickly under prolonged warm temperatures and a lack of precipitation. A high plant available water capacity may partially offset dry weather conditions (Thom et al. 2023) and thus ensures an adequate water supply for seedlings. For silver fir, the distance to the nearest tree was even more important than the soil's available water capacity. As Norway spruce was not influenced by tree distance, it remains unclear whether higher precipitation amounts between trees might have supported silver fir seedlings. Instead, a closer proximity of silver fir seedlings to Norway spruce trees might have resulted in higher interspecific root competition (Schmid 2002). Potential rooting depth exerted a significant negative effect on Norway spruce seedlings and a moderately adverse effect on silver fir seedlings. Shallow soils might warm quicker after winter, supporting germination. Yet, this might only improve initial regeneration density. Moreover, mature tree roots might prefer deeper soils to improve geochemical cycling (Pierret et al. 2016), thereby intensifying root competition in areas with higher potential rooting depth. However, it is also conceivable that tree roots become more densely concentrated in shallow soils when they are unable to penetrate deeper soil layers (Pierret et al. 2016), which should have resulted in a higher abundance of seedlings in plots with greater potential soil depth. Further research is therefore needed to elucidate the mechanisms underlying the influence of potential rooting depth on regeneration success. Moreover, we observed a greater abundance of silver fir seedlings at plots where upper soil layers were lacking carbonate, whereas Norway spruce seedlings were almost indifferent about carbonate soil depth. Previous studies found a preference of both silver fir and Norway spruce for acidic soils over those containing carbonate (Boncina et al. 2002, Dobrowolska et al. 2017). However, our study solely focused on identifying the presence of carbonate and did not measure its quantity or other indicators of soil acidity, such as pH. Thus, our study provides only limited information about the effect of soil chemistry on silver fir and Norway spruce regeneration.

Conversion of Norway spruce monocultures via silver fir seeding

A number of management implications can be drawn from our results to effectively convert Norway spruce monocultures to coniferous mixed forest in drier regions of Central Europe by means of silver fir seeding. First, light conditions should be optimized to improve seeding success. Our findings reveal that forest canopies play a crucial role in protecting the seedlings of both silver fir and Norway spruce. The abundance of silver fir seedlings increased with shade, suggesting low seedling mortality (see also Reventlow et al. 2023), while the greatest number of Norway spruce seedlings were found in diffuse light conditions of ~6%. This suggests that small canopy openings are beneficial for Norway spruce regeneration. Yet, there was little difference in seedling abundance of both species beyond diffuse light levels of 10%. Therefore, we recommend avoiding preparation cuts before seeding and instead suggest conducting silver fir seeding underneath an intact canopy in regions where water availability is a limiting factor for regeneration. Instead, silver fir seedlings should be allowed to grow slowly under closed canopies until they have developed a deeper root system, to prevent them from dehydration (see also Dobrowolska et al. 2017). The same holds true for Norway spruce, but careful interventions could be necessary earlier, as the species is less shade tolerant than silver fir (Niinemets and Valladares 2006). As we investigated plants 1 year after soil scarification and seeding, the importance of light for regenerating silver fir successfully needs to be determined in following years in order to provide more robust recommendations.

Second, the horizontal stand structure should be considered to reduce competition with trees. While Norway spruce seedlings were indifferent to the distance from trees, we found a positive relationship between silver fir seedlings and distance from trees. As a result, it is advisable to concentrate silver fir seeding in the center between Norway spruce trees to maximize seedling abundance. However, it is important to note that our study focused only on early seeding success. As the seedlings get older, their requirements and competition might change. In the longer term, facilitating silver fir regeneration might require the removal of trees to provide the regeneration with more resources. Finding the right balance between ideal shading conditions and reduced competition can be challenging and will require further research in order to determine ideal thinning intensities over the curse of regeneration development.

Third, soil conditions should be considered to concentrate seeding efforts on suitable locations. We have shown that soil scarification is not only essential to establish silver fir via seeding, but also strongly benefits Norway spruce, so that the current species composition of the regeneration allows a conversion to mixed silver fir–Norway spruce forests. Moreover, simple soil analyses can help identify suitable locations to further improve regeneration success. Our results reveal a positive but weak association between plant available water capacity and silver fir seedling abundance. In contrast, plant available water capacity was the most important variable to foster Norway spruce seedlings. Thus, Norway spruce could potentially outcompete silver fir at sites with high plant available water capacity. Future studies should investigate competition between these two species during stand development. If Norway spruce has a competitive advantage, regulation of Norway spruce may be necessary at sites with high plant available water capacity to promote a higher proportion of silver fir, whereas silver fir is more likely to be successful at drier sites without further interventions. Our results also indicate that the upper soil layers should not contain carbonate to maximize the number of silver fir seedlings, while carbonate did not have a notable effect on Norway spruce seedlings. Therefore, a higher proportion of Norway spruce at the expense of silver fir can be expected if soil scarification is done at sites with carbonate. Lastly, we detected a negative correlation between potential rooting depth and seedling abundance for both species. While seedling numbers might increase on shallower soils, it is important to note that tree growth and survival will likely be greater on deeper soils. Silver fir is more capable to deal with soil compaction zones than Norway spruce, making it a better species choice under such conditions. Therefore, we conclude that silver fir seeding is a useful approach regardless of potential rooting depth, as long as a minimum is met to support future tree growth.

Although our study provides some relevant results for silvicultural recommendations, we acknowledge that our study area reflects specific site conditions. Hence, our recommendations should be considered carefully when applying them to a different region. In addition, we recognize the constraints of our study due to a limited sample size. Consequently, our recommendations contain some degree of uncertainty.

Conclusions

In drier regions of Central Europe, admixing Norway spruce monocultures with silver fir by seeding might be a viable option to create coniferous-rich mixed forests. Soil scarification was not only important to establish silver fir, but also greatly increased the number of Norway spruce seedlings, indicating that Norway spruce is still well able to regenerate in drier lowland regions of Germany. Yet, for both species, water availability is key for successful regeneration. It is crucial to identify the right balance between ideal shading conditions and reduced competition with overstory trees to provide a suitable microclimate, and preventing high losses of water through evapotranspiration during hot and dry periods in order to optimize conditions for silver fir regeneration. With proceeding stand development, the regulation of Norway spruce might become necessary to obtain high proportions of silver fir. In conclusion, silver fir seeding might be a useful adaptive measure of economic forest enterprises to diversify Norway spruce plantations, and thus to create more resistant and resilient forest ecosystems, but further research covering a range of different site conditions and regeneration development stages is needed to generalize these results.

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Conflict of interest

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Data availability

The data underlying this article are available in Zenodo, at https://doi.org/10.5281/zenodo.8164627.

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