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Provenance Variability and Survival in Black Pine Seedlings: Analysis across two Sowing Years

Herkunftsvariabilität und Überlebensrate bei Schwarzkiefern-Sämlingen – Analyse auf Basis zweier Saatjahrgänge

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Keywords: *Pinus nigra*, intraspecific variation, phenotypic plasticity, forest genetics

Schlüsselbegriffe: *Pinus nigra*, intraspezifische Variation, phänotypische Plastizität, Forstgenetik

Abstract

The European black pine (*Pinus nigra* Arnold) is a widely distributed and ecologically versatile conifer. Its resilience to drought, frost and nutrient-poor soils makes it a promising candidate for climate-adaptive forest management, particularly in Central Europe. This study examines variability in provenance and survival of seedlings from 21 European sources, with a focus on morphological traits, biomass allocation and age-related differences over two cohorts, representing two different sowing years (2008 and 2018). Shoot length, root collar diameter, and above- and below-ground biomass were measured to evaluate intraspecific variation and phenotypic plasticity. Latitude was found to have the strongest influence on biomass allocation, with above-ground biomass increasing and root biomass decreasing towards higher latitudes. Height decreased with elevation, reflecting adaptation to resource-limited high-altitude environments. Comparisons between cohorts revealed stable variability in root traits, but a marked reduction in variability of height from sowing year 2008 to sowing year 2018 seedlings. Field trials also showed that bigger seedlings (sowing year 2018) had a higher survival rate, with root collar diameter emerging as the strongest predictor

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of survival across age classes. By linking trait development across seedling cohorts with provenance-specific differences, this study provides valuable information for evaluating seedling quality and identifying suitable provenances to promote the establishment of resilient *P. nigra* populations in changing environmental conditions.

Zusammenfassung

Die Europäische Schwarzkiefer (*Pinus nigra* Arnold) ist eine weit verbreitete und ökologisch vielseitige Nadelbaumart. Ihre Widerstandsfähigkeit gegenüber Trockenheit, Frost und nährstoffarmen Böden macht sie zu einem vielversprechenden Kandidaten für ein klimaangepasstes Waldmanagement, insbesondere in Mitteleuropa. Diese Studie untersucht die Variabilität der Herkünfte und das Überleben von Sämlingen aus 21 europäischen Populationen, mit besonderem Fokus auf morphologische Merkmale, Biomasseallokation und weitere Unterschiede über zwei Aussaat-Jahrgänge (2008 und 2018). Sprosslänge, Wurzelhalsdurchmesser sowie ober- und unterirdische Biomasse wurden gemessen, um innerartliche Variation und phänotypische Plastizität zu bewerten. Die geografische Breite erwies sich als der stärkste Einflussfaktor auf die Biomasseallokation: Mit zunehmender Breite stieg die oberirdische Biomasse, während die Wurzelbiomasse abnahm. Die Baumhöhe nahm mit der Seehöhe ab, was eine Anpassung an ressourcenbegrenzte Hochgebirgsumgebungen widerspiegelt. Vergleiche zwischen Aussaatjahrgängen zeigten eine stabile Variabilität der Wurzeleigenschaften, jedoch eine deutliche Abnahme der Variabilität in der Höhe von Aussaat-Jahrgang 2008 zu den Sämlingen des Jahrganges 2018, was auf eine Konvergenz im oberirdischen Wachstum hindeutet. Feldversuche zeigten außerdem, dass die kräftigeren Sämlinge des Jahrganges 2018 eine höhere Überlebensrate aufwiesen, wobei sich der Wurzelhalsdurchmesser als stärkster Prädiktor für das Überleben über die Jahrgänge hinweg herausstellte. Durch die Verknüpfung der Merkmalsentwicklung über verschiedene Aussaat-Jahrgänge mit herkunftsspezifischen Unterschieden liefert diese Studie wertvolle Informationen zur Bewertung der Sämlingsqualität und zur Identifizierung geeigneter Herkünfte, um die Etablierung widerstandsfähiger *P.-nigra*-Bestände unter sich verändernden Umweltbedingungen zu fördern.

1 Introduction

The European black pine (*Pinus nigra* Arnold) is a widely distributed and ecologically versatile conifer native to Europe, particularly the Mediterranean basin (*e.g.* Isajev *et a*l. 2004). Renowned for its ability to withstand diverse environmental stresses such as drought, frost, and nutrient-poor soils, this species has proven valuable for afforestation and reforestation efforts, especially in Central Europe, where it successfully establishes on dry and marginal sites (Enescu *et al*. 2016, Vacek *et al*. 2021). Hence, in

the face of accelerating climate change, *P. nigra* has gained renewed interest as a resilient forest tree species that can contribute to climate-adaptive forest management in Central Europe (Vacek *et a*l. 2023).

Tree species differ widely in their ecological requirements, which vary with site and climate and shift across life stages (*e.g.*, Niinemets 2010). Variation within species further modulates population and individual responses along environmental gradients. Accordingly, forest management should account for species-level ecological breadth, population-level variation, and seedling-specific requirements to ensure regeneration and develop resilient stands.

Pinus nigra, exemplifies these complexities. Its natural distribution is broad yet fragmented, spanning from the Iberian Peninsula and southern France through the Balkans and Italy to Anatolia and eastern Austria. This pattern reflects notable ecological plasticity, with occupancy from lowland to montane elevations (250–2200 m a.s.l.), mean annual temperatures of 6–18 °C, and precipitation of 650–2500 mm (Grossoni 2000). The species thrives on calcareous to siliceous substrates and tolerates climatic extremes, including winter temperatures below −20 °C (Bussotti 2002). Such breadth has driven substantial morphological and physiological variation among regional populations (*e.g.*, Röhrig 1966; Ivetic *et a*l. 2021), knowledge of which is essential for management.

This ecological and geographic diversity of the species *P. nigra* resulted in its subdivision into several subspecies, each with distinct phenotypic characteristics (Caudullo *et al*. 2017). *Pinus nigra* ssp. *nigra* (Austrian black pine), grows in the Eastern Alps, the Balkans, and parts of Greece. This subspecies is known for its robust growth and preference for calcareous soils. *P. nigra* ssp. laricio (Corsican or Calabrian black pine) occurs in Corsica, Calabria, and Sicily, characterized by straight stems and dense needle clusters on granitic and volcanic soils. Under humid and semi-arid climates, *P. nigra* ssp. *pallasiana* (Crimean black pine) grows on nutrient-poor soils in regions such as Crimea, Anatolia, and southeastern Europe. In contrast, *P. nigra* ssp. *dalmatica* (Dalmatian black pine) is restricted to the Adriatic coast, where it shows lower growth performance and occupies a narrower ecological niche. Furthermore, the *P. nigra* ssp. *salzmannii* (Pyrenean black pine) occurs in Spain and Southern France, as well as P. nigra ssp. mauretanica (African black pine) growing in Morocco and Algeria (Isajjev *et al*. 2004, for review see Vacek *et al*. 2021).

The current distribution and differentiation of *P. nigra* subspecies are closely linked to postglacial recolonization history (Scotti-Saintagne *et al*. 2019). Although pre-glacial distributions remain uncertain due to sparse pollen records, *P. nigra* likely formed a continuous Mediterranean range during the late Pleistocene that was subsequently fragmented by Miocene–Pleistocene climatic oscillations and geographic isolation (Vernet *et al*. 1983; Scotti-Saintagne *et al*. 2019). Some populations, notably in Corsica and northeastern Sicily, are considered Tertiary relicts that may represent ancestral lineages (Rafii *et al*. 1996).

Genetic studies broadly align with this geographic structuring, recovering western, central, and eastern Mediterranean groups, though boundaries are often diffuse due to postglacial dynamics, human-mediated movements, and afforestation (Afzal-Rafii & Dodd 2007; Bonavita *et al*., 2015; Dias *et al*. 2020; Isajev *et al*. 2003). Across these groups, populations exhibit high within-population diversity and comparatively low among-population differentiation, reflecting ecological plasticity and historical gene flow (Scotti-Saintagne *et al*. 2019).

Given the species' broad ecological amplitude and genetic diversity, it is likely that some provenances harbour traits valuable under changing climatic conditions - potentially found in provenances, which are already growing under drier and warmer conditions compared to populations in Austria. On the other hand, Austria hosts the northernmost natural occurrences of *P. nigra*, with populations concentrated mainly in Lower Austria and fragmented stands in Carinthia. These stands represent refugial remnants from the last Ice Age and potentially date back to the Tertiary period, proposed to survived glaciation in warm microhabitats along the so-called "thermal-line" (*e.g*. Kohlross 2022). According to their most northern distribution, these provenances may also possess traits that are especially useful for Central European forestry (*e.g*. cold hardiness: Röhrig 1966, Kreyling *et al*. 2012).

Identifying site-adapted, high-performing provenances is central to sustainable forestry and climate-resilient afforestation. Provenance trials provide essential insights into physiological ranges and intraspecific trait variation (Kleinschmidt 1974, Morgenstern 1996). Although provenance tests for *Pinus nigra* date back to the 1960s and 70s in Europe and the USA (Wheeler *et al*. 1976, Klumpp 2021), comprehensive trials across its full range - especially in Central Europe - remain scarce, particularly for seedling-stage morphological traits (Hinckley *et al*. 2011). Seedlings, the foundation of future forest stands, are particularly vulnerable to biotic and abiotic stress due to exposure to dynamic ground-level microclimates with pronounced diurnal fluctuations in temperature, humidity, and radiation (Johnson *et al*. 2011). Hence, this study evaluates early-stage seedling traits, their interannual variability, and first-year survival under field conditions to link phenotypic variation with provenance origin. Specifically, we aimed to

(a) characterize growth traits and variation among provenances within and among four subspecies,
(b) assess provenance-level variability between two nursery cohorts (2010 and 2019),
(c) determine the influence of environmental conditions at seed origin on seedling morphological traits, and
(d) test correlations between seedling traits and first-year survival under field conditions.

2 Material and Methods

2.1 Plant material and site conditions

Within this study we analysed seedling growth performance of *Pinus nigra* provenances, associated with the international *P. nigra* provenance test series initiated by the Bavarian State Institute for Forest Genetics (AWG) in 2010, when several provenance trials were established together with project partners from Germany and Austria (Huber 2011). Seeds from 49 provenances were collected by the Bavarian State Institute of Forest Genetics during 2007 and 2008, and BOKU contributed with seed samples from Austria and Türkiye. Besides the main international test series from 2010, a second field experiment was established for Austria in Wiener-Neustadt in autumn 2019.

The seeds for the Austrian experiments were obtained from the Bavarian State Institute AWG and stored at the forest research facility "Knödelhütte" of BOKU University (Vienna, Austria) in a regular freezer at –19 °C in sealed plastic bags. In total 26 different *P. nigra* provenances are represented in our study (Tab. 1 and Fig. 1). All analysed seedlings were sown and raised at the nursery of forest research facility "Knödelhütte". Alltogether, two cohorts of two year aged seedlings ("A", "B") were harvested in 2010 and 2019, respectively (see also Tab. 2).

The nursery of forest research facility "Knödelhütte" is located at the western border of the Austrian forest eco zone 8.1 "Pannonian Lowland and Hills" at 290 m a.s.l. (Fig. 1, Tab. 1). Seed beds and nursery beds are managed in traditional way, where the clayic soil is steadily improved with organic fertilizer and sand admixture.

After seedling production, two field trials were established: Site "A" was established with provenances from cohort "A", which was sown in 2008, and site "B" was established with provenances from cohort "B" sown in 2018 (Tab. 02). Both experiment sites were located in Lower Austria (Site A: Hernstein, Site B: Wiener Neustadt) including provenances of the four different subspecies: *Pinus nigra* subsp. *nigra*, subsp. *laricio*, subsp. *pallasiana*, and subsp. *dalmatica*. A geographic overview of all provenances analysed is provided in Fig. 1 and Table 1, where details of the Austrian test sites are given as well.

For experiment "A": seeds were drill sown in July 2008 (Tab. 2), using 3g/m of seeds per provenance with three replications. Altogether, seeds from 21 provenances were sown, and seedlings were raised in seedbeds for two growing seasons (2008 and 2009). After lifting the planting stock in April 2010, seedlings were sorted into three height classes (small, medium, tall) by visual assessment and then labeled and packed in bundles with equal representation of each class. Afterwards seedlings were sealed in and stored at +4 OC in a cooling chamber. Finally, 20 provenances were harvested in nursery, as one provenance failed for germination (see also Jansen 2011).

Another provenance had only few surviving seedlings from seedbed and was excluded from analysis, so that 19 provenances were available for experiment "A" of this study (Tab. 1).

The field experiment "A" was established in the pine forests of Hernstein / Lower Austria (Fig. 1, Tab. 1) at an elevation of 640 m a.s.l., using a small clear cut, surrounded by mixed pine stands. The site is found in the Austrian forest eco zone "5.1. Eastern Edge of the Lower Austrian Alps" at the lower foothills of the Alps in close vicinity to eco zone 8.1. The brown soil developed from tertiary gravel and provided low to medium water capacity, depending on the sand content. We used a randomized complete block design with three blocks. Each experimental plot comprised 6 rows × 7 seedlings planted at 2×1 m spacing (2 m between rows, 1 m within rows). Provenances were randomized within each block.

For experiment "B": seeds were drill sown in May 2018 (Tab. 2), following the same protocol as for experiment "A". Seedlings were raised also for two seasons (2018, 2019). Planting stock was lifted in October 2019 and sorted, packed and stored as described for experiment A. From experiment B 22 provenances were used for laboratory analysis, of which 16 provenances were from seed lots identical with experiment "A" (Tab. 1).

Field experiment "B" was established in pine forests named "Grosser Föhrenwald" owned by the municipality of Wiener Neustadt / Lower Austria (Fig. 1, Tab. 1) at an elevation of 330 m a.s.l.. The site is situated in the southwestern corner of Austrian forest eco zone 8.1 "Pannonian Lowland and Hills". Brown soil developing from tertiary gravel with low to medium water capacity is dominating the landscape. The experimental design was the same as in experiment A. It is important to note, that all three Austrian experiment locations are located at the western border of the Austrian forest eco zone 8.1 "Pannonian Lowland and Hills": nursery and field experiment "B" (Wiener Neustadt) are inside eco Zone 8.1. Both field experiments (A, B) are located in the immediate vicinity, even though field experiment "A" is in forest eco zone 5.1. (Fig. 1). A closer look to weather conditions during the two different experiments reveals similarities between local weather at the nursery site during the periods 2008-2009 and 2018-2019 with the trend of decreasing precipitation and increasing maximum temperatures (Tab. 2) resulting from climate change effects. Moreover, site "A" clearly shows lower average temperature of the year in comparison to nursery site, but comparable temperature extremes (Tab. 2). Site "B", located in the south-western plain of the Viennese Basin, shows higher average temperature and low level of yearly precipitation in comparison to the other sites (Tab. 2).

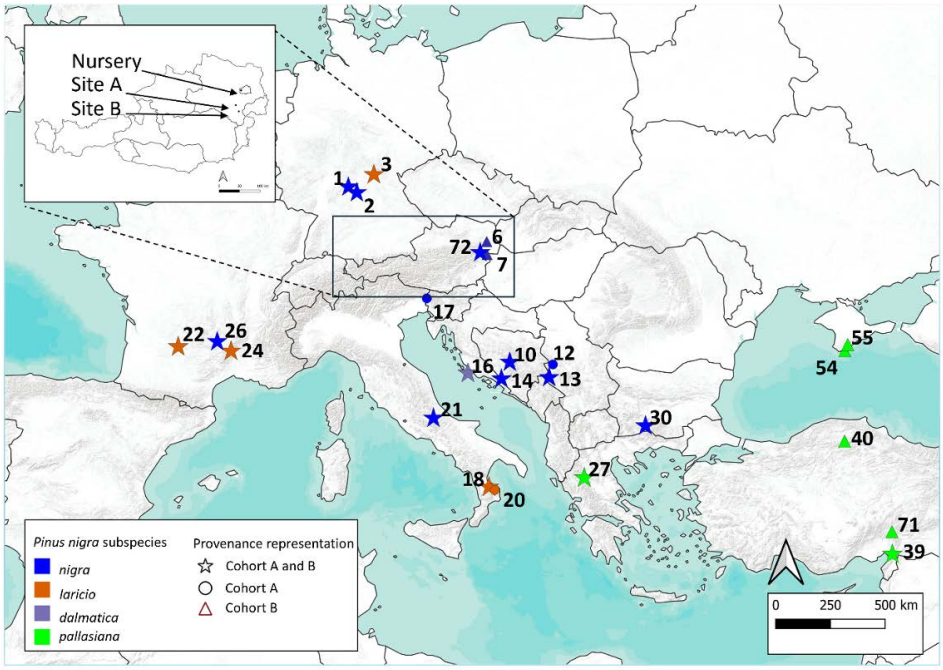

Figure 1: Overview about the study populations and locations of the nursery and field trials (site A and B) in Austria (top left). Colour of symbols represents the subspecies of Pinus nigra. Provenances illustrated by a star are represented in both cohorts and site A and B, dots represent provenance exclusively in cohort and site A, rectangle represents provenances in cohort and site B.

Abbildung 1: Überblick über die Herkunftsgebiete der Studienpopulationen sowie die Standorte der Aufzucht- und Freilandversuche (Standort A und B) in Österreich (oben links). Die Farbe der Symbole gibt die Unterart von Pinus nigra an. Mit einem Stern gekennzeichnete Herkünfte sind in beiden Kohorten sowie an den Standorten A und B vertreten. Punkte kennzeichnen Herkünfte, die ausschließlich in der Kohorte und am Standort A vertreten sind; Rechtecke stehen für Herkünfte in der Kohorte und am Standort B.

Table 1: Overview about studied populations with ID in the study, original name, country of origin, representation in seedling cohorts, subspecies (Subsp.), geographic position in decimal degrees (Longitude, Latitude) and its original ID from the international P. nigra provenance trial series (Original ID Bavaria).

Tabelle 1: Übersicht der untersuchten Populationen mit Studien-ID, Originalbezeichnung, Herkunftsland, Repräsentation in den Sämlingskohorten (Cohort), Unterart (Subsp.), geographischer Lage in Dezimalgrad (Länge, Breite) sowie der Original-ID aus der internationalen P. nigra Herkunftsversuchsserie (Original-ID Bayern).

ID	Name	Country	Cohort	Subsp.	Longitude	Latitude	Original ID Bavaria
1	Zellingen	DE	A/B	*nigra*	9.72	49.88	Skie 01
2	Leinach	DE	A/B	*nigra*	9.92	49.78	Skie 02
3	Oberwohlsbach	DE	A/B	*laricio*	10.97	50.27	Skie 03
6	Wiener Neusatdt	AT	B	*nigra*	16.18	47.86	Skie 06
7	Dreistetten	AT	A/B	*nigra*	16.18	47.76	Skie 07
10	Bugojno	BA	A/B	*nigra*	17.63	44.02	Skie 10
12	Kremanske	RS	A	*nigra*	19.59	43.83	Skie 12
13	Prijepolje	RS	A/B	*nigra*	19.56	43.48	Skie 13
14	Imotski	HR	A/B	*nigra*	17.22	43.43	Skie 14
16	Brac	HR	A/B	*dalmatica*	15.58	43.63	Skie 16
17	Triestino	IT	A	*nigra*	13.41	46.23	Skie 17
18	Sila Cosenza	IT	A/B	*laricio*	16.61	39.45	Skie 18
20	Sila Fosiata	IT	A	*laricio*	16.74	39.42	Skie 20
21	Viletta Barrea	IT	A/B	*nigra*	13.89	42.01	Skie 21
22	Sologne	FR	A/B	*laricio*	1.38	44.56	Skie 22
24	Ponteils Bresis	FR	A/B	*laricio*	3.97	44.41	Skie 24
26	Lanujols	FR	A/B	*nigra*	3.57	44.50	Skie 26
27	Milia Metsova	GR	A/B	*pallasiana*	21.28	39.80	Skie 30
30	Zadapni Rhodopi	BG	A/B	*nigra*	24.28	41.73	Skie 30
39	Camurlu	TR	A/B	*pallasiana*	36.38	36.86	Skie 39
40	Karadere	TR	B	*pallasiana*	34.04	41.17	Skie 40
54	Alupka	UA	B	*pallasiana*	34.05	44.43	Skie 54
55	Gursuf	UA	B	*pallasiana*	34.19	44.53	Skie 55
71	Akifiye	TR	B	*pallasiana*	36.36	37.74	Skie 35
72	Wiener	AT	B	*nigra*	16.13	47.90	Skie 06_2
Nursery	Vienna	AT	A/B	na	16.24	48.22	na
Site A	Hernstein	AT	A	na	16.07	47.90	na
Site B	Wiener-Neustadt	AT	B	na	16.16	47.76	na

Table 2: Overview of temperature and precipitation for the time of sowing and raising the seedlings as well at the field experiments. Climate data presented for the nursery, cohort A and cohort B (Geosphere Austria 2025).

Tabelle 2: Übersicht über Temperatur- und Niederschlagsverhältnisse während der Aussaat und Aufzucht der Sämlinge sowie an den Standorten der Freilandversuche. Klimadaten sind für die Baumschule, Kohorte A und Kohorte B dargestellt (Geosphere Austria 2025).

Cohort	Site	Activity	Time	Local weather (month)		Local weather (year)				
				T average [oC]	precip. [mm]	T average [°C]	Tmax (abs.) [oC]	Tmin (abs.) [oC]	precip. [mm]	precip. Max [mm]
A	Nursery	sowing	10.07.2008	20.7	115					
	Nursery	raising	2008			11.5	32.3	-12	1056	85
	Nursery	raising	2009			10.9	33.1	-18.4	826	52
A	A (Hernstein)	outplanting	10.05.2010	13.8	176					
	A (Hernstein)	observation	2010			9	34	-20.1	853	55
B	Nursery	sowing	18.07.2018	21.3	85					
	Nursery	raising	2018			11.4	35.4	-17.4	791	56
	Nursery	raising	2019			11.3	37.6	-10.9	725	34
B	B (Wiener Neustadt)	outplanting	October 2019	11.5	24					
	B (Wiener Neustadt)	observation	2019			12.7	35.9	-11.3	563	44
	B (Wiener Neustadt)	observation	2020			12.2	35.1	-9	639	38

2.2 Assessment of Seedling Quality

The successful establishment of a forest trial site depends not only on the genetic adaptiveness of the planting material but also on its overall quality. Morphological traits are particularly valuable, as they provide early indications of a seedling's developmental potential. In the present study, we selected dry weight, shoot length, root length, and root collar diameter as metric traits for data collection. Given the extensive literature on this subject, reference is made here to key scientific works (Olberg 1933; Schmidt-Vogt 1961; Aksoy 1965; Duryea *et al*. 1984).

2.3 Data collection

Plants were removed from cold storage immediately before measurement; only the number that could be measured promptly was taken out, and samples were kept in slightly moistened cloth to prevent desiccation.

In total, we analysed 1,142 seedlings representing 25 provenances. In cohort A, 661 seedlings were measured, with an average of 35 seedlings per provenance (ranging from a minimum of 19 seedlings in provenance 17 to a maximum of 50). In cohort B, 481 seedlings were assessed, with an average of 22 seedlings per provenance, ranging from 13 seedlings in provenance 55 to 50 in the largest group (Table S6). Across both cohorts, 16 provenances overlapped, representing all four subspecies (see Fig. 1).

The following morphological traits were assessed:

- Dry Weight: Seedlings were oven-dried at 112 °C for 24 h in a circulating-air oven until constant weight was reached. Shoot and root dry weights were determined separately.

- Shoot Length: Total seedling height was measured from the root collar to the apical bud, providing a direct indicator of aboveground growth and overall vigor.

- Root Length: The length of the longest root was measured from the root collar downwards.

- Root Collar Diameter (RCD): RCD was measured at the root collar using a caliper (precision 1 mm).

- Root-to-Shoot Ratio (R/S ratio): Based on root dry weight relative to total dry weight, the R/S ratio was calculated to quantify biomass allocation. A balanced partitioning of biomass between root and shoot is considered indicative of efficient resource use and high-quality planting stock (Olberg 1933, Aksoy 1965, Duryea *et al*. 1984).

- Height-Diameter Ratio (HD): HD was calculated as quotient of shoot length and RCD.

Together, these metrics provided a comprehensive evaluation of seedling growth, biomass allocation, and plant quality. All length measurements were made with a folding ruler (precision 1 mm). RCD was determined with a caliper (precision 1 mm), and fresh and dry weights were measured with a digital scale (precision 0.01 g).

To evaluate the success of provenances and seedlings at trial sites, survival was evaluated for each site after the first year of experiment including the first winter and the first summer, respectively. Mortality of cohort A was analysed by measuring the total number of 2229 plants of experiment "A" (Hernstein), whilst cohort "B" was assessed by measuring a subsample of 50 % (=1580 plants) of all plants at "Wiener Neustadt" site (experiment "B").

2.4 Statistical Analysis

To address the study objectives, subsets of the original dataset were compiled and analyzed according to each research question. Provenance variability and differences between cohorts were assessed using overlapping provenances across sites, while correlations with environmental variables and survival were evaluated separately for cohorts A and B. All analyses were conducted in R (v. 4.5.1). Growth metrics were first summarized

by provenance and cohort as mean values to provide an overview of trait distributions. Group means and their precision are reported as mean standard error (SE).

Differences among groups were assessed at three hierarchical levels: among subspecies, among provenances within subspecies, and overall among provenances. Assumptions of normality and homogeneity of variances were evaluated using the Shapiro-Wilk test (Royston, 1982; stats package) and Levene's test (car package), respectively. Metrics violating these assumptions were log-transformed and reassessed. Analyses were conducted on transformed data if assumptions were sufficiently improved; otherwise, non-parametric methods were applied. Depending on data distribution, one-way ANOVA (equal variances), Welch's ANOVA (unequal variances; Welch 1951), or Kruskal-Wallis tests were used. Significant results were followed by pairwise comparisons using Tukey's HSD, Games-Howell, or Dunn's tests with Bonferroni correction.

Correlations between growth metrics, survival, and environmental variables were calculated using Pearson or Spearman methods, depending on assumptions described above. Environmental predictors included geographic coordinates, elevation (from Copernicus DEM, 30 m resolution; Guth *et al*. 2021), and distance from the nursery to provenance origin. Bioclimatic variables were extracted from CHELSA 2.1 to calculate climate similarity indices between provenances and both nursery and experimental sites (Karger *et al*. 2017). Dissimilarity was calculated as the difference between provenance and site values, divided by the site value. For experimental sites, dissimilarity was calculated using site A for cohort A and site B for cohort B, while nursery dissimilarities were assessed across both years.

Trait variability across cohorts was quantified at the subspecies and provenance levels. Within-group variability was calculated separately for cohort A and B and compared between years using Levene's test, providing insight into the consistency of trait expression across generations.

The influence of geographic variables on seedling traits was assessed using linear models. Response variables included height, RCD, shoot dry weight, and root dry weight. Traits were tested for skewness; positively skewed traits with only positive values were log-transformed. Each trait (raw or transformed) was regressed against four predictors: latitude, longitude, elevation, and distance from the nursery (Dist_Nurs). Linear models were fitted using ordinary least squares (OLS), and diagnostics included variance inflation factors (VIF) to assess multicollinearity, Shapiro-Wilk tests for residual normality, Breusch-Pagan tests for heteroscedasticity, and residual skewness calculations.

Relationships between survival and seedling traits were assessed via pairwise correlations between survival rates and trait means for each provenance and year. Traits with high skewness (skewness > 1) were analyzed using Spearman's rank correlation; otherwise, Pearson's correlation was applied.

3 Results

3.1 Metric traits of *Pinus nigra* seedlings

Laboratory analysis of metric traits showed that 2-year-old seedlings in cohort A, raised between 2008 and 2009, are smaller than in cohort B, raised during the years 2018 and 2019 (Tab. 3). Shoot length of cohort B shows a total average of 12.57 cm, whilst cohort A exhibit 10.02 cm. A similar trend can be found in shoot dry-weight, where the average value of the seedlings of experiment B reaches 147% (1.29 g) versus the seedlings of experiment A (0.88 g). At the other hand, there are only slight differences in root parameters, where RCD values of cohort B seedlings increases 15% in comparison of experiment "A" and the root dry weight increases only by 4.6%.

A closer look to the average values for each of the subspecies groups reveals the fact, that there is no clear tendency between the subspecies. Height increases clearly from experiment "A " to experiment "B" in *P. nigra* subsp. *nigra* as well as in *P. nigra* subsp. *pallasiana*, but not in *P. nigra* subsp. *laricio*, where even the RCD average values are the same for both experiments (Tab. 3).

Statistical analyses first focused on differences between subspecies and among provenances within the two seedling generations (cohort A and cohort B). Overall, differentiation was high, as indicated by the frequent significance of variance analyses (see also Fig.2 and Table S1). We observed differences among subspecies for multiple traits in both years. For height, significant contrasts were detected in cohort A between *laricio-dalmatica*, *nigra-laricio*, and *pallasiana-laricio* ($p = 0.0004$). In cohort B, fewer differences remained, with only *nigra-dalmatica* and *nigra-laricio* showing significant separation ($p = 4.12 \times 10^{-6}$). HD displayed strong differentiation in cohort A, but these contrasts were less pronounced in cohort B. In contrast, traits such as RCD and R/S ratio exhibited consistent differences across both years; for example, *nigra-laricio* and *pallasiana-laricio* differed significantly in RCD in both cohort A ($p = 1.83 \times 10^{-5}$) and cohort B ($p = 3.72 \times 10^{-6}$). In general, *pallasiana* shows the highest biomass allocation in root development. Especially, in cohort A root biomass allocation (R/S ratio), was increased and showed higher variation between subspecies (Table 3a).

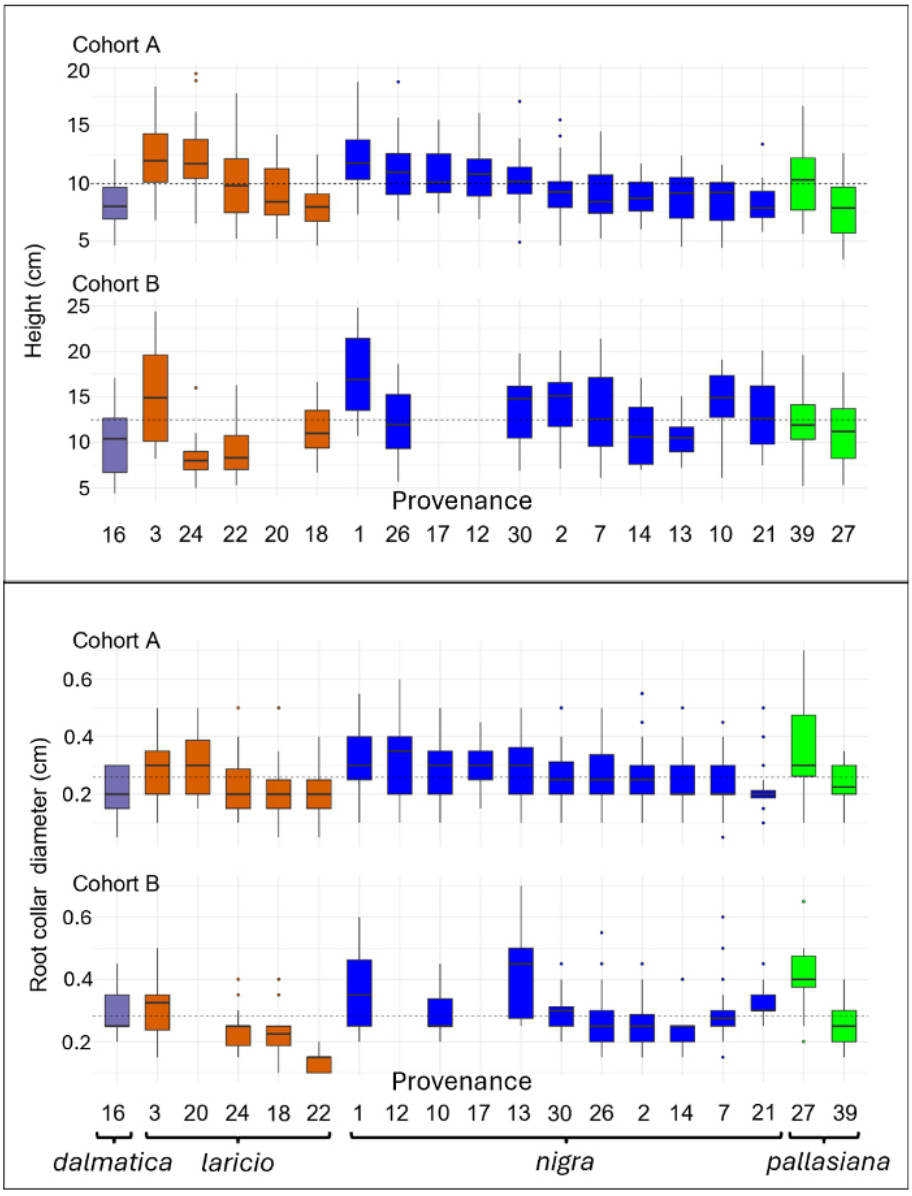

Figure 2: Overview of provenances for height (top) and root collar diameter (bottom) in cm across both cohorts. Colours indicate the subspecies, and the black dotted line represents the cohort average.

Abbildung 2: Übersicht der Herkünfte hinsichtlich Höhe (oben) und Wurzelhalsdurchmesser (unten) in cm in beiden Kohorten. Farben kennzeichnen die Unterarten, die schwarze gestrichelte Linie zeigt den Durchschnitt der Kohorte.

Table 3: Seedling characteristics presented as average values and standard error for each cohort (A, B) and each group of P. nigra provenances (subspecies: subsp.): Height (cm), Root collar diameter (RCD; cm), Height diameter ratio (HD), Shoot weight dry (g), root weight dry (g), Root shoot ratio (RSR), and length of the longest root (cm).

Tabelle 3: Merkmale der Sämlinge, dargestellt als Mittelwert und Standardfehler für jede Kohorte (A, B) und jede Gruppe von P. nigra-Herkünften (Unterarten: subsp.): Höhe (cm), Wurzelhalsdurchmesser (cm), HD (Höhen-Durchmesser-Verhältnis), Spross Trockenmasse (g), Wurzel Trockenmasse (g), Wurzel-Spross-Verhältnis (%), und Länge der längsten Wurzel (cm).

Subsp.	Cohort	Height	RCD	HD	Shoot weight dry	Root weight dry	RSR	Root length
nigra	A	9.87 ± 0.13	0.27 ± 0.01	0.39 ± 0.01	0.98 ± 0.04	0.74 ± 0.03	0.43 ± 0.00	22.49 ± 0.31
	B	13.26 ± 0.25	0.30 ± 0.01	0.47 ± 0.01	1.24 ± 0.05	0.65 ± 0.03	0.34 ± 0.02	25.36 ± 0.29
laricio	A	10.41 ± 0.21	0.24 ± 0.01	0.50 ± 0.01	0.75 ± 0.04	0.50 ± 0.03	0.40 ± 0.01	20.64 ± 0.32
	B	11.03 ± 0.51	0.23 ± 0.01	0.53 ± 0.03	0.91 ± 0.07	0.46 ± 0.04	0.32 ± 0.01	27.61 ± 0.64
pallasiana	A	9.05 ± 0.48	0.29 ± 0.02	0.35 ± 0.02	0.94 ± 0.12	0.84 ± 0.10	0.48 ± 0.01	22.49 ± 0.86
	B	12.56 ± 0.34	0.33 ± 0.01	0.42 ± 0.01	1.38 ± 0.10	0.74 ± 0.05	0.37 ± 0.01	26.96 ± 0.59
dalmatica	A	8.30 ± 0.44	0.21 ± 0.02	0.47 ± 0.04	0.54 ± 0.08	0.44 ± 0.06	0.45 ± 0.01	23.50 ± 1.02
	B	10.07 ± 1.02	0.29 ± 0.02	0.35 ± 0.03	1.14 ± 0.19	0.74 ± 0.06	0.42 ± 0.02	28.61 ± 1.19
experiment total	**A**	**9.96 ± 0.11**	**0.26 ± 0,004**	**0.43 ± 0.01**	**0.88 ± 0.03**	**0.65 ± 0.02**	**0.43 ± 0.00**	**21.88 ± 0.22**
	B	**12.62 ± 0.19**	**0.30 ± 0.005**	**0.47 ± 0.008**	**1.22 ± 0.04**	**0.65 ± 0.02**	**0.35 ± 0.00**	**26.23 ± 0.25**

Table 3a: Summary about measured traits for each subspecies (Subsp.), provenance (ID), Cohort, Height (cm), Root collar diameter (RCD, cm), Height diameter ration (HD), shoot weight dry (g), root weight dry (g), root shoot ration, and length of the longest root (cm). Data are presented as arithmetic mean and standard error.

Tabelle 3a: Zusammenfassung der gemessenen Merkmale für jede Unterart (Subsp.), Herkunft (ID), Kohorte, Höhe (cm), Wurzelhalsdurchmesser (cm), Höhen-Durchmesser-Verhältnis (HD), Spross Trockenmasse (g), Wurzel Trockenmasse (g), Wurzel-Spross-Verhältnis (RSR) und Länge der längsten Wurzel (cm). Die Daten werden als Arithmetisches Mittel und Standardfehler dargestellt.

Subsp.	ID	Cohort	Height	RCD	HD	Shoot weight dry	Root weight dry	RSR	Root length
nigra	1	A	11.99 ± 0.43	0.33 ± 0.02	0.38 ± 0.02	1.55 ± 0.15	1.04 ± 0.08	0.41 ± 0.01	27.69 ± 0.53
	2	A	9.32 ± 0.38	0.25 ± 0.02	0.39 ± 0.02	0.85 ± 0.10	0.70 ± 0.09	0.45 ± 0.01	20.99 ± 0.73
	7	A	8.90 ± 0.30	0.24 ± 0.01	0.42 ± 0.03	0.73 ± 0.07	0.56 ± 0.05	0.43 ± 0.01	18.08 ± 0.69
	10	A	8.45 ± 0.48	0.31 ± 0.03	0.29 ± 0.02	1.00 ± 0.14	0.95 ± 0.14	0.49 ± 0.02	23.06 ± 0.91
	12	A	10.80 ± 0.39	0.32 ± 0.02	0.39 ± 0.03	1.19 ± 0.13	0.85 ± 0.08	0.42 ± 0.01	26.42 ± 0.92
	13	A	8.68 ± 0.48	0.30 ± 0.02	0.33 ± 0.03	1.02 ± 0.22	0.85 ± 0.14	0.47 ± 0.02	23.41 ± 1.69
	14	A	8.75 ± 0.36	0.24 ± 0.02	0.40 ± 0.03	0.64 ± 0.10	0.51 ± 0.10	0.44 ± 0.01	20.59 ± 0.69
	17	A	10.88 ± 0.54	0.30 ± 0.02	0.38 ± 0.02	1.19 ± 0.13	0.88 ± 0.09	0.43 ± 0.01	25.12 ± 1.10
	21	A	8.19 ± 0.28	0.22 ± 0.01	0.41 ± 0.02	0.56 ± 0.07	0.46 ± 0.07	0.44 ± 0.01	17.06 ± 0.53
	26	A	11.05 ± 0.35	0.27 ± 0.01	0.45 ± 0.02	1.09 ± 0.10	0.73 ± 0.08	0.39 ± 0.01	21.64 ± 0.70
	30	A	10.24 ± 0.38	0.28 ± 0.02	0.39 ± 0.01	0.96 ± 0.11	0.84 ± 0.09	0.46 ± 0.02	26.47 ± 0.83
	Total	**A**	**9.87 ± 0.13**	**0.27 ± 0.01**	**0.39 ± 0.01**	**0.98 ± 0.04**	**0.74 ± 0.03**	**0.43 ± 0.00**	**22.49 ± 0.31**
	1	B	17.22 ± 1.00	0.37 ± 0.03	0.51 ± 0.04	2.03 ± 0.31	0.88 ± 0.11	0.32 ± 0.01	27.58 ± 1.11
	2	B	14.26 ± 0.58	0.26 ± 0.01	0.58 ± 0.03	1.10 ± 0.10	0.53 ± 0.05	0.32 ± 0.01	21.96 ± 0.77
	6	B	10.23 ± 0.55	0.37 ± 0.03	0.30 ± 0.03	1.95 ± 0.27	1.15 ± 0.14	0.38 ± 0.01	28.22 ± 1.11
	7	B	13.04 ± 0.60	0.28 ± 0.01	0.49 ± 0.03	1.06 ± 0.09	0.53 ± 0.04	0.33 ± 0.01	23.82 ± 0.39
	10	B	14.31 ± 1.02	0.28 ± 0.02	0.52 ± 0.04	1.11 ± 0.15	0.65 ± 0.07	0.38 ± 0.01	28.01 ± 0.86
	13	B	10.60 ± 0.58	0.41 ± 0.04	0.27 ± 0.02	1.90 ± 0.43	1.35 ± 0.24	0.42 ± 0.02	30.14 ± 1.68
	14	B	10.97 ± 0.93	0.25 ± 0.02	0.47 ± 0.05	0.81 ± 0.12	0.43 ± 0.08	0.34 ± 0.02	20.73 ± 1.03
	21	B	13.02 ± 0.95	0.32 ± 0.02	0.41 ± 0.03	1.51 ± 0.13	0.76 ± 0.06	0.34 ± 0.02	28.62 ± 1.32
	26	B	12.50 ± 0.51	0.28 ± 0.01	0.48 ± 0.02	0.97 ± 0.08	0.53 ± 0.05	0.35 ± 0.01	25.62 ± 0.53
	30	B	13.87 ± 0.82	0.29 ± 0.02	0.50 ± 0.04	1.07 ± 0.14	0.49 ± 0.08	0.30 ± 0.02	26.36 ± 0.95
	72	B	14.94 ± 1.25	0.32 ± 0.02	0.47 ± 0.03	1.11 ± 0.14	0.54 ± 0.08	0.32 ± 0.02	23.82 ± 0.92
	Total	**B**	**13.26 ± 0.25**	**0.30 ± 0.01**	**0.47 ± 0.01**	**1.24 ± 0.05**	**0.65 ± 0.03**	**0.34 ± 0.02**	**25.36 ± 0.29**
laricio	3	A	12.19 ± 0.42	0.29 ± 0.01	0.44 ± 0.02	1.13 ± 0.09	0.72 ± 0.06	0.39 ± 0.01	23.57 ± 0.56
	18	A	7.99 ± 0.26	0.20 ± 0.01	0.45 ± 0.03	0.47 ± 0.05	0.42 ± 0.05	0.46 ± 0.01	16.90 ± 0.66
	20	A	9.17 ± 0.44	0.29 ± 0.02	0.33 ± 0.01	0.77 ± 0.09	0.74 ± 0.10	0.48 ± 0.01	20.13 ± 0.79
	22	A	10.27 ± 0.49	0.20 ± 0.01	0.56 ± 0.03	0.62 ± 0.07	0.33 ± 0.03	0.37 ± 0.01	20.83 ± 0.59
	24	A	11.93 ± 0.38	0.21 ± 0.01	0.64 ± 0.03	0.78 ± 0.07	0.39 ± 0.04	0.34 ± 0.01	21.53 ± 0.63
	Total	**A**	**10.41 ± 0.21**	**0.24 ± 0.01**	**0.50 ± 0.01**	**0.75 ± 0.04**	**0.50 ± 0.03**	**0.40 ± 0.01**	**20.64 ± 0.32**
	3	B	15.16 ± 1.15	0.31 ± 0.02	0.56 ± 0.07	1.39 ± 0.16	0.76 ± 0.10	0.35 ± 0.02	28.51 ± 1.17
	18	B	11.36 ± 0.68	0.23 ± 0.02	0.53 ± 0.04	0.81 ± 0.09	0.43 ± 0.05	0.35 ± 0.01	26.71 ± 0.85
	22	B	9.01 ± 0.73	0.14 ± 0.01	0.66 ± 0.05	0.33 ± 0.03	0.10 ± 0.01	0.22 ± 0.03	23.08 ± 1.06
	24	B	8.18 ± 0.54	0.24 ± 0.02	0.39 ± 0.05	0.97 ± 0.10	0.49 ± 0.06	0.33 ± 0.01	31.24 ± 1.27
	Total	**B**	**11.03 ± 0.51**	**0.23 ± 0.01**	**0.53 ± 0.03**	**0.91 ± 0.07**	**0.46 ± 0.04**	**0.32 ± 0.01**	**27.61 ± 0.64**
pallasiana	27	A	7.86 ± 0.60	0.33 ± 0.04	0.27 ± 0.02	1.16 ± 0.20	1.05 ± 0.16	0.50 ± 0.01	23.48 ± 1.29
	39	A	10.36 ± 0.66	0.24 ± 0.01	0.44 ± 0.02	0.70 ± 0.10	0.60 ± 0.07	0.47 ± 0.01	21.41 ± 1.11
	Total	**A**	**9.05 ± 0.48**	**0.29 ± 0.02**	**0.35 ± 0.02**	**0.94 ± 0.12**	**0.84 ± 0.10**	**0.48 ± 0.01**	**22.49 ± 0.86**
	27	B	11.07 ± 0.94	0.42 ± 0.03	0.28 ± 0.03	1.90 ± 0.25	1.16 ± 0.14	0.38 ± 0.01	32.06 ± 2.36
	39	B	12.18 ± 0.44	0.25 ± 0.01	0.49 ± 0.02	0.69 ± 0.07	0.42 ± 0.03	0.40 ± 0.01	22.72 ± 0.59
	40	B	10.37 ± 0.86	0.26 ± 0.02	0.43 ± 0.05	0.78 ± 0.15	0.49 ± 0.06	0.42 ± 0.02	26.39 ± 0.62
	54	B	12.61 ± 0.49	0.35 ± 0.03	0.41 ± 0.03	1.84 ± 0.33	0.80 ± 0.15	0.31 ± 0.02	29.49 ± 1.65
	55	B	15.51 ± 1.03	0.38 ± 0.03	0.43 ± 0.04	1.90 ± 0.27	0.96 ± 0.14	0.33 ± 0.02	29.32 ± 1.21
	71	B	15.04 ± 1.56	0.47 ± 0.02	0.32 ± 0.03	2.83 ± 0.33	1.40 ± 0.10	0.35 ± 0.02	31.81 ± 1.43
	Total	**B**	**12.56 ± 0.34**	**0.33 ± 0.01**	**0.42 ± 0.01**	**1.38 ± 0.10**	**0.74 ± 0.05**	**0.37 ± 0.01**	**26.96 ± 0.59**
dalmatica	16	A	8.30 ± 0.44	0.21 ± 0.02	0.47 ± 0.04	0.54 ± 0.08	0.44 ± 0.06	0.45 ± 0.01	23.50 ± 1.02
	Total	**A**	**8.30 ± 0.44**	**0.21 ± 0.02**	**0.47 ± 0.04**	**0.54 ± 0.08**	**0.44 ± 0.06**	**0.45 ± 0.01**	**23.50 ± 1.02**
	16	B	10.07 ± 1.02	0.29 ± 0.02	0.35 ± 0.03	1.14 ± 0.19	0.74 ± 0.06	0.42 ± 0.02	28.61 ± 1.19
	Total	**B**	**10.07 ± 1.02**	**0.29 ± 0.02**	**0.35 ± 0.03**	**1.14 ± 0.19**	**0.74 ± 0.06**	**0.42 ± 0.02**	**28.61 ± 1.19**

Within subspecies, *nigra* showed the greatest provenance-level variability across traits. For height, significant differences were found especially for provenance "1" (Zellingen, DE) and "26" (Lanujols, FR) towards the remaining provenances in cohort A, while beside provenance "1" and "13" (Prijepolje, RS) in cohort B. By contrast, *laricio* and *pallasiana* displayed fewer significant within-subspecies differences, indicating greater uniformity.

The variability analysis between both cohorts revealed clear differences in how subspecies responded to nursery conditions (Table S2). *Laricio* and *nigra* exhibited the most pronounced shifts across traits, whereas *dalmatica* and *pallasiana* were comparatively stable. In subsp. *laricio*, significant differences between cohorts were detected for height ($F = 5.26$, $p = 0.0226$), HD ($F = 4.32$, $p = 0.0387$), and R/S ratio ($F = 4.21$, $p = 0.0410$), while traits such as shoot dry weight and root length remained unchanged ($p > 0.05$). This suggests moderate variability, with certain traits more sensitive to nursery effects. *Nigra* displayed substantial variability, with strong year-to-year differences across multiple traits including height ($F = 84.79$, $p = 7.26 \times 10^{-19}$), HD ($F = 53.61$, $p = 8.92 \times 10^{-13}$), root dry weight ($F = 12.22$, $p = 0.0005$), R/S ratio ($F = 17.54$, $p = 3.29 \times 10^{-5}$), and root length ($F = 10.97$, $p = 0.00099$). These results indicate that nigra is particularly sensitive to nursery conditions, with multiple traits showing strong variability across the two cohorts. By contrast, *pallasiana* showed little variability, with most traits stable between years ($p > 0.05$). Only root dry weight approached significance ($F = 3.91$, $p = 0.0507$), suggesting limited sensitivity. Subspecies *dalmatica* also exhibited low variability, with significant year-to-year differences observed only for height ($F = 9.07$, $p = 0.0049$), although interpretation is constrained by its limited representation in the dataset.

At the provenance level, variability between cohort A and cohort B was not uniform, even within the same subspecies. Significant year-to-year differences were detected for traits such as height, HD, root dry weight, and R/S ratio, while other traits remained stable (Table S2).

Within *nigra*, several provenances showed marked variability across multiple traits, consistent with the high variability observed at the subspecies level. For example, provenance "7" differed significantly in height ($F = 28.44$) and HD ($F = 8.61$), as well as in R/S ratio ($F = 4.86$) and root length ($F = 17.96$), indicating sensitivity in both above- and below-ground traits. Provenance "26" similarly displayed significant differences in root dry weight ($F = 6.31$, $p = 0.0136$) and R/S ratio ($F = 4.89$, $p = 0.0293$). For *laricio*, provenances "3," "18," and "22" exhibited moderate variability, with significant shifts in height (e.g., provenance "3": $F = 13.95$, $p = 0.0004$) and R/S ratio (e.g., provenance "18": $F = 6.51$, $p = 0.0129$). Provenance "22" was particularly dynamic, showing significant differences in RCD ($F = 14.13$, $p = 0.0004$), shoot dry weight ($F = 7.22$, $p = 0.0092$), and root dry weight ($F = 13.20$, $p = 0.0006$). In contrast, *pallasiana* provenances displayed low variability, with only isolated traits differing between years. For example, provenance "39" differed significantly in HD ($F = 4.09$, $p = 0.0471$) and root dry weight ($F =$

4.82, p = 0.0316), while most other traits remained stable. Similarly, *dalmatica* provenances exhibited minimal year-to-year variability, with height being the only trait showing significant differentiation (F = 9.07, p = 0.0049).

The following correlation analysis demonstrated that geographic and environmental factors - including latitude, longitude, and elevation- significantly influenced seedling traits, with some relationships persisting across years and others shifting between cohorts (Tab. 4). Latitude was strongly associated with above-ground traits. Height was positively correlated with latitude in both cohort A (r = 0.28) and cohort B (r = 0.18), indicating that provenances from higher latitudes tended to grow taller. Similarly, shoot dry weight showed a positive correlation in cohort A (r = 0.22), though this relationship weakened in cohort B (r = 0.14). In contrast, R/S ratio was negatively correlated with latitude (r = –0.34 in cohort A; r = –0.25 in cohort B), suggesting greater shoot allocation at higher latitudes. Longitude primarily influenced below-ground allocation. R/S ratio was positively correlated with longitude in both years (r = 0.46 in cohort A; r = 0.25 in cohort B), while HD showed a consistent negative correlation (r = –0.34 in cohort A; r = –0.13 in cohort B), reflecting a more balanced HD in eastern provenances. RCD was also positively associated with longitude, though effects were weaker (r ≈ 0.13–0.15). Elevation effects were consistent across years. R/S ratio increased with elevation (r = 0.33 in cohort A; r = 0.29 in cohort B), while HD decreased (r = –0.25 in cohort A; r = –0.15 in cohort B), indicating that seedlings from higher elevations developed more balanced above- and below-ground proportions. RCD also showed weak but positive associations with elevation

Additionally, linear regression models provided a quantitative assessment of environmental influences on seedling traits. Latitude consistently emerged as the strongest predictors across multiple traits, while longitude exerted weaker but notable effects (Table S3). Above-ground traits, such as height and shoot dry weight, were positively associated with latitude in both years. Height, for example, increased with latitude (cohort A: estimate = 0.235, p < 0.001; cohort B: estimate = 0.497, p < 0.001). Longitude became a significant positive predictor of height in cohort B (estimate = 0.101, p < 0.001. Below-ground traits were following the same directions as above ground traits. highlighting the dominant role of latitudinal gradients in shaping growth and allocation patterns across provenances. Detailed regression estimates for all traits are provided in Table S4.

Table 4: Overview about morphological traits (Root shoot ratio (RSR), Height, Root weight dry, Shoot weight dry, Root collar diameter (RCD), height-diameter ratio (HD), Root length) and Spearman correlations with latitude, longitude, elevation, and the distance of a provenance origin to nursery (Dist_to_Nursery).

Tabelle 4: Übersicht der morphologischen Merkmale (Spross Wurzel Verhältnis (RSR), Höhe, Wurzel Trockenmasse, Spross Trockenmasse, Wurzelhals Durchmesser (RCD), Höhe-Durchmesser Verhältnis (HD), Längste Wurzel) und Spearman-Korrelationen mit Breite, Länge, Höhe und der Entfernung des Herkunftsortes zur Baumschule (Dist_to_Nursery).

	Latitude		Longitude		Elevation		Dist_to_Nursery	
Metric/ variable	**Cohort A**	**Cohort B**	**Cohort A**	**Cohort B**	**Cohort A**	**Cohort B**	**Cohort A**	**Cohort B**
RSR	-0.34	-0.25	0.46	0.25	0.33	0.29	-0.11	-0.1
Height	0.28	0.18	-0.25	n.s.	-0.11	n.s.	n.s.	-0.13
Root weight dry	0.09	n.s.	0.16	0.11	0.14	0.11	-0.2	-0.12
Shoot weight dry	0.22	0.14	n.s.	n.s.	n.s.	n.s.	-0.14	-0.17
Total Weight Dry	0.17	0.11	n.s.	n.s.	0.08	n.s.	-0.17	-0.16
RCD	0.09	n.s.	0.13	0.15	0.1	0.13	-0.16	n.s.
HD	0.14	0.12	-0.34	-0.13	-0.25	-0.15	0.21	n.s.
Root length	0.17	n.s.	n.s.	n.s.	n.s.	0.14	-0.1	n.s.

3.2 Survival versus metric traits

Survival was measured after the first year of the experiment (Table 5). Overall, experiment A exhibited lower survival than experiment B, with total averages of 78.16% and 90.5%, respectively. The largest group, subspecies *nigra*, performed slightly above the overall experiment averages. All provenances in this group showed higher survival in experiment B, except for provenance 14 (Imotski, Croatia), which remained stable at approximately 86% (Table 5). The subspecies *pallasiana* exhibited survival rates close to the experiment averages. While only one provenance was included in experiment A (Nr. 39, B. Camurlu), the six provenances in experiment B showed a survival rate of ~90 %. The single provenance of subspecies *dalmatica* performed near the average in experiment A, but slightly below the total average in experiment B. Low survival were observed in subspecies *laricio*, which consistently performed below the experiment averages (Table 5, Fig. 3).

Table 5: Total survival of provenances at experiment site A (Hernstein) and B (Wiener Neustadt), values given as average percentage over all experiment cells per provenance and experiment.

Tabelle 5: Gesamtes Überleben der Herkünfte an den Versuchsstationen A (Hernstein) und B (Wiener Neustadt). Die Werte sind als durchschnittlicher Prozentsatz über alle Versuchsflächen pro Herkunft und Versuch angegeben.

Subsp.	ID	Cohort A	Cohort B
nigra	1	76.00	100.00
	2	85.00	96.66
	6	n.a.	87.50
	7	79.00	96.25
	10	76.00	88.33
	12	80.00	n.a.
	13	89.00	100.00
	14	86.00	86.66
	16	78.00	87.50
	17	94.00	n.a.
	21	85.00	93.10
	26	62	68.30
	30	70.00	98.33
	72	n.a.	91.00
	average	**80.00**	**91.1**
laricio	3	89.00	94.87
	18	68.00	87.50
	20	88.00	n.a.
	22	62.00	68.30
	24	52.00	85
	average	**71.80**	**83.9**
pallasiana	27	n.a.	85.00
	39	77.00	91.25
	40	n.a.	95.00
	54	n.a.	90.00
	55	n.a.	93.30
	71	n.a.	90.00
	average	**77.00**	**90.80**
dalmatica	**16**	**78.00**	**87.50**
	Total average	**78.16**	**90.50**

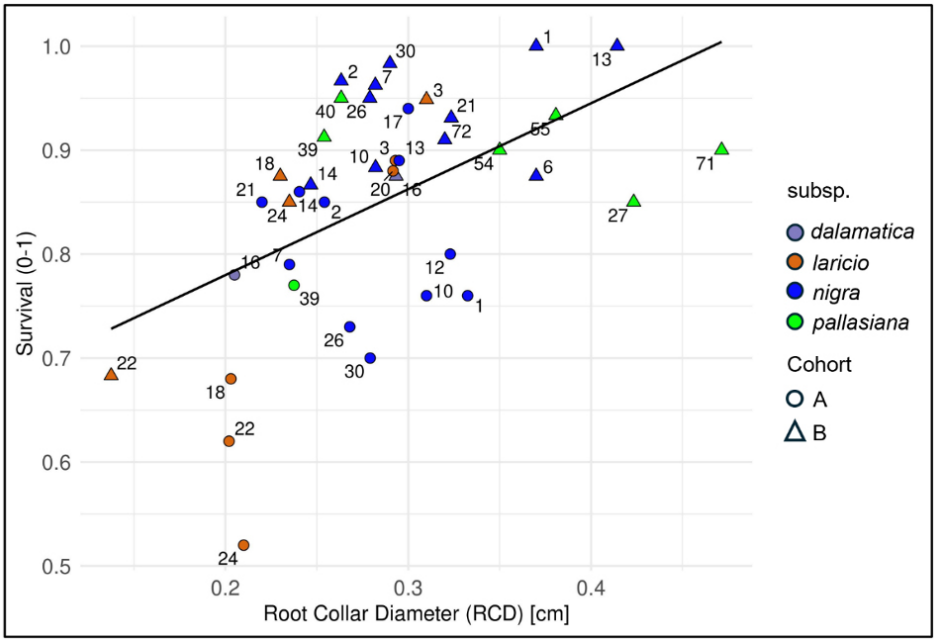

Figure 3: Survival by provenance and site as a function of root collar diameter (RCD). Colors denote subspecies (subsp.); circles indicate Site A and triangles indicate Site B. The black line shows the linear regression (line of best fit).

Abbildung 3: Überleben nach Herkunft und Standort in Abhängigkeit vom Wurzelhalsdurchmesser (RCD). Die Farben codieren die Unterart (subsp.), Kreise markieren Standort A und Dreiecke Standort B. Die schwarze Linie ist die Ausgleichs-/Regressionsgerade.

3.3 Survival, morphological traits and environmental variables

Finally, we investigated the relationship between seedling morphological traits, provenance origin distances, and plant survival at the two experimental sites. Correlation analyses revealed significant associations between survival, seedling traits, and geographic and climatic variables (Table S5).

In cohort A, RCD showed a positive correlation with survival ($r = 0.474$, $p = 0.047$), while HD was strongly negatively correlated ($r = -0.732$, $p < 0.001$). Among climatic variables, temperature seasonality (bio4) was positively associated with survival ($r = 0.509$, $p = 0.031$). Geographic distance to the planting site was only significant for site A negatively correlated with survival (Site A: $r = -0.518$, $p = 0.028$).

In cohort B, height ($r = 0.568$, $p = 0.006$) and RCD ($r = 0.436$, $p = 0.042$) remained significant positive predictors of survival, while HD was no longer significant. Several cli-

matic variables were negatively correlated with survival, including mean annual temperature (bio1; r = –0.446, p = 0.037), maximum temperature of the warmest month (bio5; r = –0.571, p = 0.006), minimum temperature of the coldest month (bio6; r = –0.502, p = 0.017), mean temperature of the driest quarter (bio9; r = –0.444, p = 0.038), mean temperature of the warmest quarter (bio10; r = –0.522, p = 0.013), and mean temperature of the coldest quarter (bio11; r = –0.545, p = 0.009).

Figure 3 illustrates survival and RCD across subspecies and provenances. The low performance of subspecies *laricio* is evident in both experiments, except for provenance No. 3 (Oberwohlsbach, Bavaria), which ranked among the top-performing provenances in both cohorts. Additionally, the positive correlation between higher RCD values and better survival is clearly demonstrated and statistically significant in both experiments, as described above.

4 Discussion

4.1 Experimental design

Whilst the main timber species of Europe, Norway spruce and Scots pine, are well analysed by several provenance trials and world-wide test series (Giertych & Oleksyn 1992, Morgenstern 1996, Erikson & Ekberg 2001), field tests in European black pine are rarely to be found (Seho *et al*. 2010). The *Pinus nigra* seed collection, which was carried out by the Bavarian State Institute of Forest Genetics between 2007 and 2008 (Huber 2011) provides a valuable tool, not only for the international *Pinus nigra* provenance test series implemented in autumn 2009 and spring 2010, but also for different research in black pine (*e.g.* Thiel *et al*. 2012, Scotti-Saintagne *et al*. 2019). Within this framework 23 provenances were tested in Austria, and seedling development were analysed for 16 provenances in open seed beds for two sowing years (Table 2). Early nursery-stage tests are valuable because seedling establishment is a critical and failure-prone phase of reforestation (*e.g.* Grossnickle & MacDonald, 2018). They provide rapid, low-cost feedback on provenance performance under standardized conditions, allowing managers to identify weak or promising sources before committing to large, slow, and costly field trials. This is particularly important given that high-quality seed is expensive and not always readily available. Early traits (*e.g.*, RCD, RSR, or plant height) can help to predicted survival, reduce risk and guide smarter seed purchases, prioritizing provenances for broader deployment or further testing.

4.2 Impact of local weather conditions

Because the seeds were sown in open seed beds without environmental control, weather conditions during the experiments may have affected seedling development. Average weather conditions in July 2008 and July 2018 (Table 2) showed comparably higher precipitation in 2008 (115 mm vs. 84 mm) and slightly lower mean temperature (20.7 °C vs. 21.4 °C). More critical for seedling production, however, were the conditions during 2018 and 2019, which were characterized by prolonged heat waves and drought periods. As shown in Table 2, maximum temperatures were considerably higher in 2018–2019 than in 2008–2009, while annual precipitation was lower. As a result, seedlings harvested in October 2019 (cohort "B") exhibited longer shoots and greater dry weight than seedlings from cohort "A," harvested in April 2010 (Table 3). This suggests that absolute maximum temperatures below 38 °C and average maximum temperatures of 28.3–29.2 °C during June–August 2019 were favorable for the growth of the analysed provenances compared to the 2009 conditions (Table 2). By contrast, two-year-old *Pinus nigra* seedlings exposed to temperatures above 40 °C, as observed in the Mediterranean region during the summer of 2025, suffered severe foliar damage regardless of provenance (Ivetić *et al.* 2021). Similarly, Mataruga *et al*. (2012) tested one-year-old seedlings under drought stress in open "stressbeds," which resulted in remarkably low height increment compared to ordinary nursery management due to reduced soil moisture. However, average monthly temperatures in their study ranged from 27 °C to 33.5 °C during June–August (Mataruga *et al*. 2012), which were considerably higher than those recorded in our Austrian experiments.

In general, the seedling size of our experiment appears small compared to other studies. The shoot length of the two-year-old cohort "A" averaged 10 cm, while that of cohort "B" reached 12.57 cm. In contrast, Gülcü and Üçler (2008) reported shoot lengths of 33.8 cm for one-year-old seedlings in a study conducted near Isparta, Türkiye. Similarly, raising *Pinus nigra* seedlings in open seed beds at 850 m a.s.l., under average yearly temperatures of 6.5 °C and annual precipitation of 1009 mm, resulted in shoot lengths of 6 cm after one year and 10 cm after two growing seasons (Ivetić & Škorić 2013). These comparisons raise an important question: to what extent does temperature during plant production influence seedling growth?

Our study highlights distinct growth and resource allocation patterns among the four subspecies, reflecting inherent differences and potential adaptations to their respective environments. *Laricio* and *nigra* were the tallest subspecies, suggesting a prioritization of aboveground growth, potentially to maximize light capture in more competitive environments. Lower temperatures may reduce photosynthetic activity, which could make investment in aboveground biomass an advantageous strategy to capture limited light (Johnson *et al*. 2011). In contrast, *pallasiana* and *dalmatica* exhibited the highest R/S ratios, indicating a greater allocation of biomass to roots. This result aligns with Padilla *et al*. (2007), who reported elongated root development in Mediterranean shrub seedlings from drier sites compared to seedlings from more

mesic conditions. Such a strategy may enhance water and nutrient uptake under resource-limited environments.

4.3 Variability among subspecies

The degree of variability in traits differed markedly among subspecies, with *nigra* exhibiting the highest variability and *pallasiana* the lowest. The pronounced variability in *nigra* across traits such as height, root dry weight, and R/S ratio suggests that this subspecies is highly responsive to environmental conditions. This variability may reflect greater genetic diversity or environmental heterogeneity within its provenances. In contrast, *pallasiana* exhibited minimal variability across traits, both within and between age cohorts, indicating a more uniform growth strategy. However, since Gülcü and Üçler (2005) reported substantial growth differences among 21 *pallasiana* populations, our interpretation should be made cautiously given the limited representation in our dataset. *Laricio* showed moderate variability, with some traits (*e.g.*, height) being sensitive to nursery-related changes, while others (*e.g.*, shoot dry weight) remained stable. The limited representation of *dalmatica* in the dataset restricts broader conclusions.

4.4 Cohort related changes in traits

Although previous studies have not found provenance-specific responses to extreme weather conditions such as frost, heat or drought (Thiel *et al.* 2012, Mataruga *et al.* 2012, Ivetić *et al*. 2021), we observed clear shifts in growth traits when comparing seedling cohorts A and B, which were raised under different weather conditions in open seed beds. Comparing the two cohorts revealed marked changes in growth and resource allocation as the plants matured. Height increased significantly from cohort A to cohort B across all subspecies, reflecting the expected progression of aboveground growth under the moderately higher temperatures of 2018–2019. In contrast, the R/S ratio decreased consistently, indicating a developmental shift in biomass allocation towards shoots. This trend was most pronounced in *nigra*, which exhibited the largest reduction in R/S ratio, suggesting a stronger developmental emphasis on shoot growth. By contrast, *pallasiana* maintained a relatively high R/S ratio, highlighting its continued investment in root biomass. These results suggest that, while some traits, such as height, are strongly influenced by moderately higher summer temperatures, others, such as RCD, remain relatively stable and are likely to be governed more by genetic factors. The observed decline in the R/S ratio under the slightly warmer conditions of cohort B may reflect a shift in the allocation of resources: seedlings in cohort A invested heavily in their root systems to establish themselves, whereas seedlings in cohort B prioritized shoot growth to compete for light. Similar trends have been reported in other conifer species (Liu *et al.* 2024, 2025).

4.5 Subspecies responses to weather conditions

For *laricio*, significant differences in height, HD, and RSR between cohort A and cohort B suggest moderate variability, with some traits being sensitive to developmental changes while others remain stable. This variability may reflect broader genetic diversity or environmental adaptability, given its representation across multiple provenances. In *nigra*, the pronounced variability across traits such as height, HD, root weight dry, and root length reinforces its characterization as the least uniform subspecies. The high variability in both above-ground and below-ground traits suggests that *nigra* is particularly responsive to environmental conditions or developmental processes, making it less predictable in terms of growth and resource allocation. In contrast, *pallasiana* showed minimal variability across traits, with no significant differences between cohorts for most traits. This stability aligns with its uniform growth strategy and suggests that it is less influenced by weather-related changes compared to *laricio* and *nigra*.

4.6 Trait correlations

The results reveal a complex interplay between environmental factors and seedling traits, with latitude, longitude, and elevation shaping growth and biomass allocation. Among these factors, latitude emerged as a particularly strong driver. Provenances from higher latitudes tended to grow taller, as shown by the positive correlation with height. Similar observations are reported from experiments with *Fraxinus americana* in Wisconsin (see review by Eriksson & Ekberg 2001). This pattern likely reflects adaptations to shorter growing seasons or cooler climates, where rapid vertical growth enhances light capture. At the same time, the negative correlation between latitude and R/S ratio indicates that northern provenances allocate proportionally more resources to shoots than to roots, a strategy that likely maximizes photosynthetic capacity in environments with restricted growing seasons.

Longitude primarily influenced below-ground traits. Eastern provenances exhibited higher R/S ratios and larger RCD, indicating adaptations to drier or less fertile soils, where greater R/S investment enhances water and nutrient uptake. The negative correlation between longitude and HD suggests that eastern provenances develop a more balanced HD, potentially improving stability and resource allocation efficiency. These results highlight the role of longitude in shaping below-ground growth strategies, particularly in response to soil and water availability. Elevation consistently influenced multiple traits, particularly root allocation. Higher-elevation provenances showed increased R/S ratios, larger root collars, and more balanced HD, supporting the idea that these provenances invest more in below-ground structures to enhance water and nutrient uptake in resource-limited or harsh environments. These effects were observed across both cohorts, emphasizing the role of elevation as a driver of

seedling performance. Elevation of provenances shows a slightly negative correlation for height (significant for cohort A), but positive association with below biomass, which may be linked to the hypotheses that resources to roots on infertile sites to optimize nutrient uptake (Cairns *et al*. 1997). Overall, linear models and correlation analyses consistently highlight latitude as the strongest determinants of seedling growth and biomass allocation.

4.7 Survival vs Traits and climatic mismatch

Our results highlight the importance of both morphological traits and climatic factors in determining seedling survival, with some differences between cohorts A and B. In cohort A, survival was strongly influenced by RCD and HD, suggesting that seedlings with larger root collars and more balanced HD were better able to establish. This is in line with several other studies, recognizing root biomass is as a key predictor for post-planting survival rates (Olberg 1933, Schmidt-Vogt 1961, Aksoy 1965, Duryea & Landis 1984). The significant positive correlation with temperature seasonality (bio4) indicates that provenances originating from regions with higher seasonal temperature variation were better adapted to the planting sites. Negative correlations with geographic distance measures suggest that local provenances, originating closer to the planting sites, experienced higher survival rates, likely due to reduced environmental mismatches.

In cohort B, height and RCD remained important predictors of survival, reflecting the continued importance of seedling morphology. However, climatic variables played a more prominent role, with several temperature-related indices (bio1, bio5, bio6, bio9, bio10, bio11) showing significant negative correlations with survival. These results suggest that provenances from warmer climates may have been less suited to the planting sites, particularly as seedlings grew larger with lower R/S ratios and experienced environmental stressors. In contrast, provenance 39 (subsp. *pallasiana*) exhibited above-average growth performance and good survival rates in Austria. Overall, the observed survival rates are consistent with previous studies. In Turkish experiments, survival ranged from 69.3% to 98.7% after the first year (Oner *et al*. 2015). In southern German provenance trials of the international *Pinus nigra* test series (2009/2010), average survival after ten years was 60% for subspecies pallasiana and 70% for *nigra* and *laricio* (Schirmer *et al*. 2023). Moreover, six Turkish provenance trials established in 1984 reported total average survival rates between 34% and 79% after 25 years (Gökdemir *et al*. 2011).

5 Conclusion

This study demonstrates that early-stage seedling traits, their variability across years, and survival are shaped by both provenance origin and environmental conditions. Subspecies differ in growth strategy and responsiveness, with *nigra* and *laricio* being more sensitive to nursery conditions and environmental variability, while *pallasiana* and *dalmatica* are more stable. Latitude is the most influential environmental factors, whereas longitude and elevation have secondary effects. These findings provide actionable guidance for provenance selection and forest management under changing climatic conditions. German provenances (IDs 1–3; two subsp. *nigra* and one subsp. *laricio*) generally exhibited strong growth, balanced above- and belowground biomass allocation, and high survival on Austrian sites. Likewise, the consistently good performance and survival of the most south-eastern provenance, 39 (subsp. *pallasiana*; TR), highlight its broad adaptive potential and identify it as a promising candidate for future use under climate change.

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Supplementary Material

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