Variation in seed traits, leaf phenology and growth performance among sessile oak provenances from Baden-Württemberg and Alsace

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Abstract

Given the long lifespan of forest trees, their adaptation to climate change may lag behind the pace of global warming. In this context, it is crucial to explore the variation of fitness-related traits. Our study focuses on assessing the adaptive potential of sessile oak (*Quercus petraea*), specifically concerning seed characteristics, as well as leaf phenology and growth performance of seedlings. To investigate this, we conducted a common garden experiment using seeds sampled from 15 relict and four regularly managed sessile oak provenances in Baden-Wuerttemberg, Germany, and Alsace, France. We observed differences in budburst, with the provenances from higher altitude as well as from the Franconian Plateau flushing up to three days later than the provenances from lower altitudes in the other regions. We interpret this phenological behaviour as the result of adaptation to late frosts, which are more common in cold regions. Additionally, we found significant variation in seedling height. These findings highlight adaptive genetic processes in sessile oak populations and underscore the importance of preserving their genetic diversity as a valuable resource for future adaptation to climate change. Such adaptive differentiation should also be considered in seed sourcing. Taking climate change into account, forest reproductive material originating from colder parts of a provenance region should preferably be used locally and ideally enriched with provenances from lower altitude.

Key words: *Quercus petraea*, progeny test, leaf phenology, growth performance, clinal variation, local adaptation

Introduction

As global warming is rapidly progressing, there is an urgent need to establish vital and sustainable forests (Keenan, 2015; Lindner et al., 2010). For this purpose, species with high capability to cope with rapidly changing environmental conditions are needed. Being ecologically diverse and less prone to drought and heat, oaks (genus *Quercus*) are expected to play an important role in increasing the climate-resilience of temperate forests in the Northern Hemisphere, particularly in Europe (Hanewinkel et al., 2013). At the within-species level, it is crucial to explore variation in fitness-related traits in order to identify climate-resilient provenances and use them as seed sources (Aitken & Bemmels, 2016). In Central Europe, sessile oak (*Quercus petraea* (Matt.) Liebl.) is an economically important species and displays a wide ecological amplitude (Aas, 2008). Therefore, adaptation studies on sessile oak within this area have a particular practical significance as they can be used as an important basis to inform seed sourcing policies in the face of climate change.

Tree phenology plays a crucial role in forest tree adaptation to local climatic conditions (Schüler et al., 2012). Consequently, clinal and ecotypic variation of phenological traits can be observed in several forest tree species due to their adaptation to diverse environmental conditions. This is assumed to be caused by natural selection locally favoring phenotypes with increased fitness, as well as their underlying genotypes. Common garden experiments have been widely used to investigate such genetically fixed variation of fitness-related traits in forest trees (Ducousso et al., 1996; Kuser & Ching, 1980; Vitasse et al., 2009).

The onset of the growing season is determined by budburst. During this period, trees are particularly vulnerable to adverse climate conditions such as cold, heat, or drought. For

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frost-sensitive deciduous trees, late frost events during budburst can be detrimental to their subsequent growth (Dittmar et al., 2006; Ningre & Colin, 2007). If freshly formed leaves are destroyed by frost, the tree must utilize its energy reserves to produce new leaves, resulting in a competitive disadvantage in terms of growth. However, if the tree delays budburst for too long, the growing season is shortened, also leading to a competitive disadvantage.

Compared to budburst in spring, autumn leaf senescence has received relatively little attention (Gallinat et al., 2015), although a recent common garden experiment highlighted its significance in the context of global warming (e.g. Torres-Ruiz et al., 2019). While early senescence provides an immediate advantage of resource preservation and stress mitigation, it also limits the tree's ability to utilize sunlight for optimal energy production and its growth potential in late summer. Conversely, the benefits of prolonged photosynthesis and competitive advantage offered by late leaf senescence are counterbalanced by the heightened risk of disease, resource depletion, and vulnerability to cold damage (Hagen-Thorn et al., 2006; Keskitalo et al., 2005). This highlights the critical role of timing for the growing season as one of the most important adaptation-related characteristics.

Especially in temperate regions, where the length of the growing season is strongly dependent on temperature, the effects of climate warming are considered particularly significant for plant phenology (Vitasse et al., 2009). Under climate change, increasing heat and drought periods pose severe challenges for forests in northern and temperate latitudes, necessitating silvicultural adjustments. A way to mitigate the effects of climate change is the use of reproductive material originating from forests where current climatic conditions are similar to those predicted at the plantation site in the future (assisted migration). This may include material transfer within the natural range of a given species (assisted gene flow) or just beyond its poleward or uppermost (in terms of altitude) distribution limit into areas predicted to be suitable for the species in the future (assisted range expansion) (Stanturf et al., 2024).

During the last three decades, the average (pedunculate and sessile) oak proportion in German forests has steadily risen, from 9.6 % in 2002 (Jablonski, 2014) to 10.4 % in 2012 and 11.5 % in 2022 (National Forest Inventory of Germany available at https://bwi.info). The genus *Quercus* is likely to play an even larger role in the future (Hanewinkel et al., 2013). Oaks continue to have significant economic importance as a potential high-value timber source (Aas, 2008). They are also ecologically significant as key carriers of biodiversity (e.g., Bußler, 2014). Particularly sessile oak is considered well-equipped for climate change due to its ecological adaptability and thus received particular attention in forest genetic research (Ducousso et al., 1996, Sáenz-Romero et al., 2017, Le Provost et al., 2023). To identify appropriate seed sources for harvesting and establish climate-resilient forests with this species, it is essential to understand the patterns of local adaptation and characterize the adaptive potential of oak populations.

In this context, Central European sessile oaks growing on relict, mainly dry sites with a long habitat continuity have been in the focus of recent investigations (Neophytou et al., 2024). Given the relict character of these forests, natural selection might have acted over many generations on the oaks growing there. Thus, such stands are ideal to study fitness-related traits (Neophytou et al., 2020). To evaluate these populations as potential seed stocks, here we examine provenance-specific variation in seed traits, leaf phenology and growth performance in a common garden experiment.

In our study, we focused on 19 provenances of sessile oak in Southern Germany and Alsace, several of which are considered drought-adapted (Neophytou et al., 2024). We worked under the assumption that genetically fixed, biparentally inherited phenological differences are already expressed in the first life years and are affecting the juvenile growth of the seedlings (Schwinning et al., 2022). Additionally, we investigated the effect of seed mass on seedling growth presuming that it reflects maternal effects (González-Rodrígues et al., 2011). Maternal effects refer to the influence of the mother tree on the phenotype and fitness of the offspring that is not transmitted via nuclear maternal alleles into the next generation. They include i) effects due to the maternal inheritance of plastid DNA (e.g. chloroplasts and mitochondria for angiosperms), ii) the effect of the endosperm, which is dominated by maternal nuclear DNA and iii) seed coat which consists of maternal tissue, as well as iv) maternal provisioning with nutrient resources, hormones, proteins and transcripts. These effects are under the influence of both the genotype and the environment experienced by the maternal tree (Donohue 2009, Ramírez-Valiente et al. 2009). Maternal effects are particularly strong in the juvenile phase and decrease with increasing age of the progenies (Roach & Wulff, 1987; Van Dooren et al., 2016; Vivas et al., 2020). Seed mass is both under strong influence of the maternal genotype and environment and has a significant effect on seedling growth (Ramírez-Valiente et al. 2009, González-Rodríguez et al., 2011). Thus, we interpret an association between seed weight and juvenile growth as a maternal effect.

In particular, we aim to address the following hypotheses: (i) The timing of phenological transitions of sessile oak populations in Baden-Württemberg and Alsace is under selection pressure, resulting in patterns of local adaptation. Therefore, we anticipate that the progenies of colder provenances will show a pattern of delayed budburst in spring and early leaf senescence in autumn. (ii) Provenances from warmer sites are adapted to a longer vegetation period resulting in a better growth performance if growth is not hindered by frosts. Thus, progenies with early budburst and/or late senescence are expected to have a higher growth performance under common garden conditions in the lack of late frost in spring and / or early frost in autumn. Given that our field trial site displays a warm climate compared to almost all tested provenances, we assume that progenies with early budburst and/or late senescence do not face a disadvantage due to frost susceptibility and can profit from a longer growth period. (iii) Seed weight has a positive impact on germination rate and growth performance, since a higher seed weight results in a lower risk of seed desiccation and a better nutrient supply of the seedlings. Thus, we expect that higher seed weight is positively correlated with

germination rate and juvenile growth indicating a maternal effect.

Materials and Methods

Seed sources and study site

Our study area includes Baden-Württemberg in southwestern Germany and Alsace in eastern France. In this area, we harvested seeds from 19 sessile oak stands, hereinafter named provenances, during autumn 2020 (Figure 1). The stands were situated across varying elevations ranging from 224 to 783 m (Table 1). To set up a common garden experiment, we used seeds from five open-pollinated mother trees per provenance. In the case of inadequate fructification, we bulked seeds from five mother trees of a given provenance. For establishing open-pollinated families, seeds were acquired either from the forest floor (ground harvest) or directly from the tree crown (tree harvest). Afterwards, thousand seed weight (TSW) was documented for each seed lot by counting, weighing the number of acorns (usually 100) and extrapolating the weight for 1000 acorns. TSW is a standard measure used to describe seed mass in plant species, and here serves as an important variable for testing some of our hypotheses. Within 3-4 weeks after the harvest, seeds underwent a thermotherapy at 41°C for two hours in a water bath and then were stored at -3°C until spring 2021.

A common garden experiment was subsequently established in the nursery of the Forest Research Institute (FVA) of Baden-Württemberg in Freiburg in spring 2021, including 64 seed lots (single-tree or bulked, Table 1) from the 19 provenances. To account for ecoregional differences, we subdivided the provenances into five groups: Southern Upper Rhine Lowlands (Southern URL), Northern Upper Rhine Lowlands (Northern URL), Franconian Plateau, Black Forest, and Vosges Mountains (Table 1). The common garden comprised around 20,000 seedlings. Among them, about 2,200 individuals were systematically selected and labeled for intensive monitoring, amounting to a minimum of 25 saplings per seed lot (either single-tree or bulked seed lot). Throughout the data collection period, the total number of recorded plants varied from 2,041 to 2,228 seedlings due to various factors, such as mortality or label loss due to rain and/or wind. The common garden was exposed to local climatic conditions and was regularly watered.

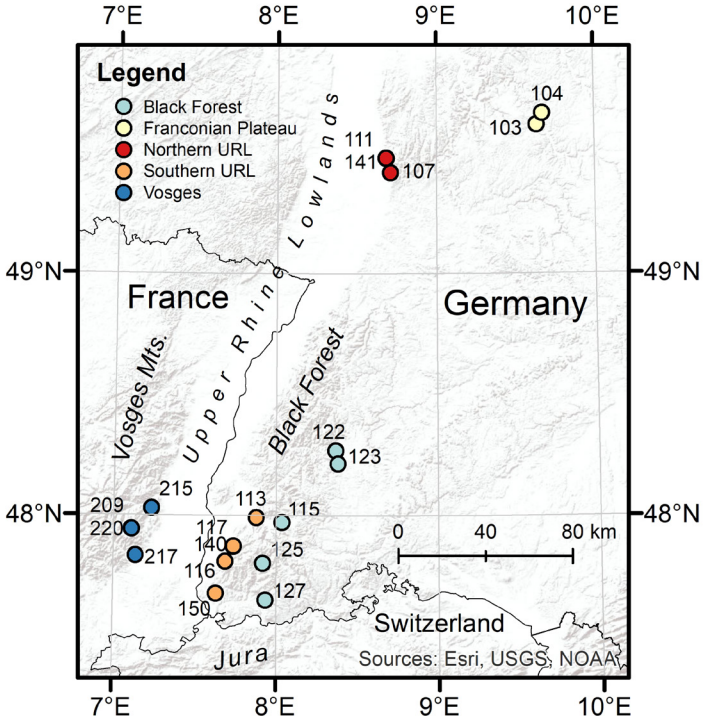

Figure 1
Geographic distribution of the 19 provenances across Baden-Württemberg and Alsace. Different colors represent provenance groups, with shading indicating relative temperature differences, ranging from cold (dark blue) to warm (red). The names of the provenances can be found in Table 1.

Table 1
Number of mother trees, altitude, annual mean temperature (Fick & Hijmans, 2017), and geographic location of the provenances included in this study. Under "Number of sampled mother trees", we denote as "bulked" those provenances for which seed of the harvested mother trees was mixed before sowing. Geographic and climatic data are also provided for the site of the common garden. All provenances underlie dry soil conditions, except for those explicitly labeled as moist.

Region	Provenance			Altitude a.s.l. (m)	Annual mean temperature (°C)	Geographic location	
	Name	Provenance ID	No. of sampled mother trees			Latitude	Longitude
Southern Upper Rhine Land	Freiburg	113	5	340	9.72	47.992	7.878
	Kandern	150	5	345	9.79	47.679	7.631
	Staufen	117	bulked	383	9.94	47.874	7.738
	Staufen moist	140	bulked	420	9.91	47.875	7.738
	Badenweiler	116	bulked	443	9.10	47.811	7.688
Northern Upper Rhine Land URL	Heidelberg	107	5	244	9.65	49.418	8.708
	Schriesheim	111	5	224	9.80	49.477	8.682
	Schriesheim moist	141	5	256	9.80	49.479	8.681
Franconian Plat.	Tauberbischofsheim	103	5	244	8.92	49.662	9.670
	Impfingen	104	3	303	8.77	49.615	9.635
Black Forest	Welschdorf	122	4	485	8.53	48.269	8.366
	Buchenbach	115	5	524	8.25	47.973	8.036
	Wehratal	127	5	557	7.51	47.651	7.935
	Falkenstein-Schramberg	123	5	588	8.00	48.215	8.381
	Schönau-Utzenfluh	125	5	661	7.64	47.804	7.918
Vosges	Linthal	209	bulked	603	7.60	47.944	7.109
	Linthal moist	220	bulked	552	7.61	47.942	7.112
	Uffholtz	217	bulked	731	7.96	47.834	7.136
	Le Stauffen	215	bulked	783	7.95	48.030	7.233
Site of the common garden							
Nursery of FVA-BW, Freiburg				297	10.18	47.975	7.844

Phenological observations and tree height measurements

We recorded the phenology of budburst and senescence for the labeled seedlings over several weeks in spring and autumn 2022. Budburst of the one-year-old seedlings was evaluated every two to three days between April 12th and 28th, 2022 on seven days in total. The phases of budburst of the labeled seedlings were classified according to Table 2.

Table 2
Description of the phases for budburst and leaf senescence

Phase	Budburst	Leaf senescence
0	The bud is at rest.	-
1	The bud is slightly elongated at its distal end. Embryonic, small, yellow to green leaves can be differentiated in the second half of the bud, but these leaves still closely adhere along the axis of the bud at their ends. The overall shape of the bud is still present.	Leaves are fully green.
2	One or two green leaves detach from the bud axis at their ends. In some cases, the buds bend. The lower brown scales are still present and adhere to the base of the bud.	Leaves have begun to transition to red color but very few are fully red/orange. About 20% of the leaves are red/orange.
3	All leaves "open up like a flower" and begin to separate from the bud.	Most leaves are now orange. Less than 40% of the leaves remain green.
4	At least one leaf is completely separated from the bud and stands vertically to the axis of the bud.	Leaves are now dark red/orange. Less than 10% of the leaves remain green.
5	The main stem elongates, and internodes become visible. Several leaves are now standing upright to the stem axis and are almost fully unfolded.	Leaves are completely dark red. There are no green leaves remaining. Leaves are either falling or easy to remove.

Leaf senescence was monitored 15 times, once a week from September 7th to December 14th, 2022. In the case of heavy rain, data were recorded one day earlier or later, resulting in an interval of six to eight days difference between the data collection time points. Each week, selected seedlings from each progeny were assigned to one of the five leaf senescence phases (Table 2). The process of leaf senescence ended due to frost on December 14th, 2022, at which point all seedlings were classified into the fifth phase due to the loss of leaf functionality from the cold.

For height growth, measurements were taken in July and December 2022. For these measurements, we used the individuals labeled for phenological observations. Using a ruler, we measured the height of the first node (its vertical distance from the ground) in July 2022 and defined that as the height growth in year 2021. In December 2022, after the end of the vegetation period of the second year's growth, we measured the height of each sapling (i.e., the vertical distance of the shoot tip from the ground).

Statistical analysis

To calculate the germination rate, we first estimated the number of sown seeds by dividing their weight by TSW of the respective provenance and then multiplying the result by 1000. Afterwards, we determined the germination rate by dividing the number of seedlings that had germinated in 2021 by the calculated number of sown seeds.

For each progeny and each day of data collection, the arithmetic means of budburst $(\overline{P_{bb}})$ and senescence phase $(\overline{P_{sen}})$ were calculated using the formula (1). The number of individuals present in a phase (N_{P_k}) was multiplied by the number of the corresponding phase.
(for $\overline{P_{bb}}$: P_k ranging from 0-5; for $\overline{P_{sen}}$: P_k ranging from 1-5, see Table 2)
We calculated the sum of the products of the five phases and divided it by the total number of individuals considered.

$$\overline{P_{bb}}, \overline{P_{sen}} = \frac{\sum_{k=1}^{5} N_{P_k} P_k}{\sum_{k=1}^{5} N_{P_k}} \quad (1)$$

Budburst onset was defined as the Julian day when Phase 1 was reached specifically when a given progeny had a $\overline{P_{bb}}$ of 1. To calculate the budburst onset day (JD_{bb}), we used the formula (2) to interpolate between the Julian day of scoring before reaching Phase 1 (JD_{x+1}) and the Julian day of scoring after reaching Phase 1 (JD_{x+1}). $\bar{P}_{x+1}$ describes the exact average phenological score when a phenological score of > 1 was recorded for the first time (called here as the date of scoring x + 1). $\bar{P}_x$ is the previous $\bar{P}$-value recorded in the field right before a phenological score of > 1 was recorded (called here as the date of scoring x). The difference between JD_{x+1} and JD_x was multiplied by the fraction derived from the difference between 1 (denoting the phenological score of exactly 1) and $\bar{P}_x$ divided by the difference between $\bar{P}_{x+1}$ and $\bar{P}_x$. The result was added to the Julian day of scoring before reaching Phase 1 (JD_x).

$$JD_{bb} = JD_x + (JD_{x+1} - JD_x)\frac{1 - \bar{P}_x}{\bar{P}_{x+1} - \bar{P}_x} \quad (2)$$

Senescence onset was defined as the Julian day when Phase 2 was reached, specifically when a given progeny had a $\overline{P_{sen}}$ of 2 (Table 2). Hence, senescence onset day JD_{sen} was calculated similarly, with interpolation between the Julian days of scoring before and after reaching Phase 2 (formula 3).

$$JD_{sen} = JD_x + (JD_{x+1} - JD_x)\frac{2 - \bar{P}_x}{\bar{P}_{x+1} - \bar{P}_x} \quad (3)$$

The significance of differences among provenances in budburst onset, seed weight (TSW), as well as height growth among progenies in 2021 and 2022 and sapling height in December 2022 were evaluated applying a one-way analysis of variance (ANOVA) in R (R Core Team, 2022). To test for pairwise differences between provenances, we performed a post-hoc analysis using the Tukey Honest Significant Difference method with the function TukeyHSD() in R. To verify that the assumptions of ANOVA were met, we i) tested for normality of the residuals with a Shapiro-Wilk Test using the function shapiro.test() in R and ii) performed a Levene Test for homogeneity of variances using the leveneTest() function in the R package car (Fox et al., 2012). In this part of the analysis, we included only the 12 provenances with open pollinated families raised separately and excluded the remaining seven established with bulked seed lots (Table 1).

To test for correlation between seed weight and juvenile growth and to address adaptation of phenological traits along altitudinal or latitudinal gradients, we applied correlation tests based on Kendall's Tau correlation coefficient. We opted for the Kendall's Tau as a non-parametric correlation coefficient because in all cases mentioned below we had two non-normally distributed ordinal or metric variables. In particular, we tested i) whether progeny seed weight correlates with seedling height at the end of year 2021 and 2022, respectively, ii) whether the Julian day of budburst or senescence correlate with the altitude and the latitude of origin, respectively. Finally, we defined the duration of vegetation period as the period spanning from the onset of budburst to the onset of leaf senescence. We then tested whether the length of the vegetation period correlates with growth performance (height growth in 2021 and 2022).

Results

Phenological observations

Budburst onset occurred, on average, around Julian day 104 (April 14th) (mean across provenances = 103.85 ± 0.18). Significant differences were observed among the provenances (ANOVA, p = 0.002, Table 3, Figure 2). The provenance 107 – Heidelberg (Northern URL) had a significantly earlier budburst than some provenances from the Black Forest region (123 – Falkenstein-Schramberg, and 127 – Wehratal), as well as from the Franconian Plateau (103 – Tauberbischofsheim, 104 – Impfingen) (Table 3, Figure 2). The largest difference of 3.1 days was between provenances 107 – Heidelberg (early flushing) and 104 – Impfingen (late flushing).

Table 3
Mean ± standard error for thousand seed weight (TSW), height growth in 2021 and 2022, total height in 2022, and the onset of budburst and leaf senescence for the 19 sessile oak provenances. The onset of budburst and leaf senescence (in Julian Days) were defined using the formula (2). Significant differences among the provenances consisting of open-pollinated families (in white) are based on ANOVA and are highlighted in bold font. (a) and (b) indicate the groups of provenances that differed significantly from each other for a certain trait based on post-hoc tests for pairwise differences. For provenances established with bulked seeds (in grey), neither standard errors could be calculated, nor a test could be carried out.

Region	Provenance name and ID	TSW (g)	Height 2021 (cm)	Height 2022 (cm)	Onset of budburst (JDbb)	Onset of senescence (JDsen)
Southern Upper Rhine	Freiburg 113	**1730 ±261 (b)**	10.5 ± 1.3	26.2 ± 2.8	102.9 ± 0.4	307.2 ± 8.6
	Kandern 150	4080 ± 386 (a)	**14.9 ± 1.5 (a)**	38.4 ± 1.5	103.6 ± 0.6	306.6 ± 8.0
	Staufen 117	1320	9.5	25.3	103.0	310.5
	Staufen moist 140	2500	13.1	33.2	103.6	306.6
	Badenweiler 116	1620	9.7	26.8	103.5	312.7
Northern Upper Rhine	Heidelberg 107	3278 ± 347	**15.0 ± 1.0 (a)**	36.5 ± 4.0	**102.3 ± 0.3 (a)**	295.7 ± 4.2
	Schriesheim 111	2644 ± 528	11.3 ± 0.4	28.3 ± 2.1	103.2 ± 0.4	310.9 ± 2.5
	Schriesheim moist 141	2450 ± 329	12.2 ± 1.3	37.6 ± 4.6	103.3 ± 0.6	311 ± 3.6
Franconian Plateau	Tauberbischofsheim 103	2746 ± 486	12.4 ± 1.0	37.7 ± 6.1	**104.9 ± 0.6 (b)**	312.4 ± 1.3
	Impfingen 104	2257 ± 202	11.2 ± 2.1	26.3 ± 4.4	**105.4 ± 1.1 (b)**	309.2 ± 4.2
Black Forest	Welschdorf 122	3350 ± 425	11.1 ± 0.3	36.5 ± 3.9	104.6 ± 0.8	317.6 ± 3.8
	Buchenbach 115	3275 ± 519	**8.9 ± 0.6 (b)**	31.5 ± 3.7	103.7 ± 0.3	305.0 ± 5.0
	Wehratal 127	3580 ± 351	12.0 ± 0.5	26.4 ± 1.9	**105.1 ± 0.6 (b)**	298.6 ± 7.6
	Falkenstein-Schramberg 123	3150 ± 288	10.8 ± 0.3	35.0 ± 2.4	**104.8 ± 0.4 (b)**	309.7 ± 2.4
	Schönau-Utzenfluh 125	3160 ± 404	**15.5 ± 1.6 (a)**	40.4 ± 4.8	103.8 ± 0.3	311.9 ± 2.4
Vosges	Linthal 209	3500	10.6	24.4	103.6	317.0
	Linthal moist 220	3090	12.8	29.2	103.9	306.0
	Uffholtz 217	3470	13.4	29.6	103.6	311.2
	Le Stauffen 215	1320	10.3	24.0	103.8	316.2
	p-value	ANOVA	ANOVA	ANOVA	ANOVA	ANOVA
		0.012*	<0.001***	0.053	0.002**	0.228

We also observed differences in the variance of budburst onset among progenies within a provenance (Table S1). Thus, progenies of the mother trees from 122 – Welschdorf exhibited a maximum pairwise difference of 3.8 days in reaching Phase 1, whereas budburst dates among progenies from 125 – Schönau-Utzenfluh differed at maximum by 1.6 days. However, we could not test the significance of these differences as we could only calculate average values within a progeny.

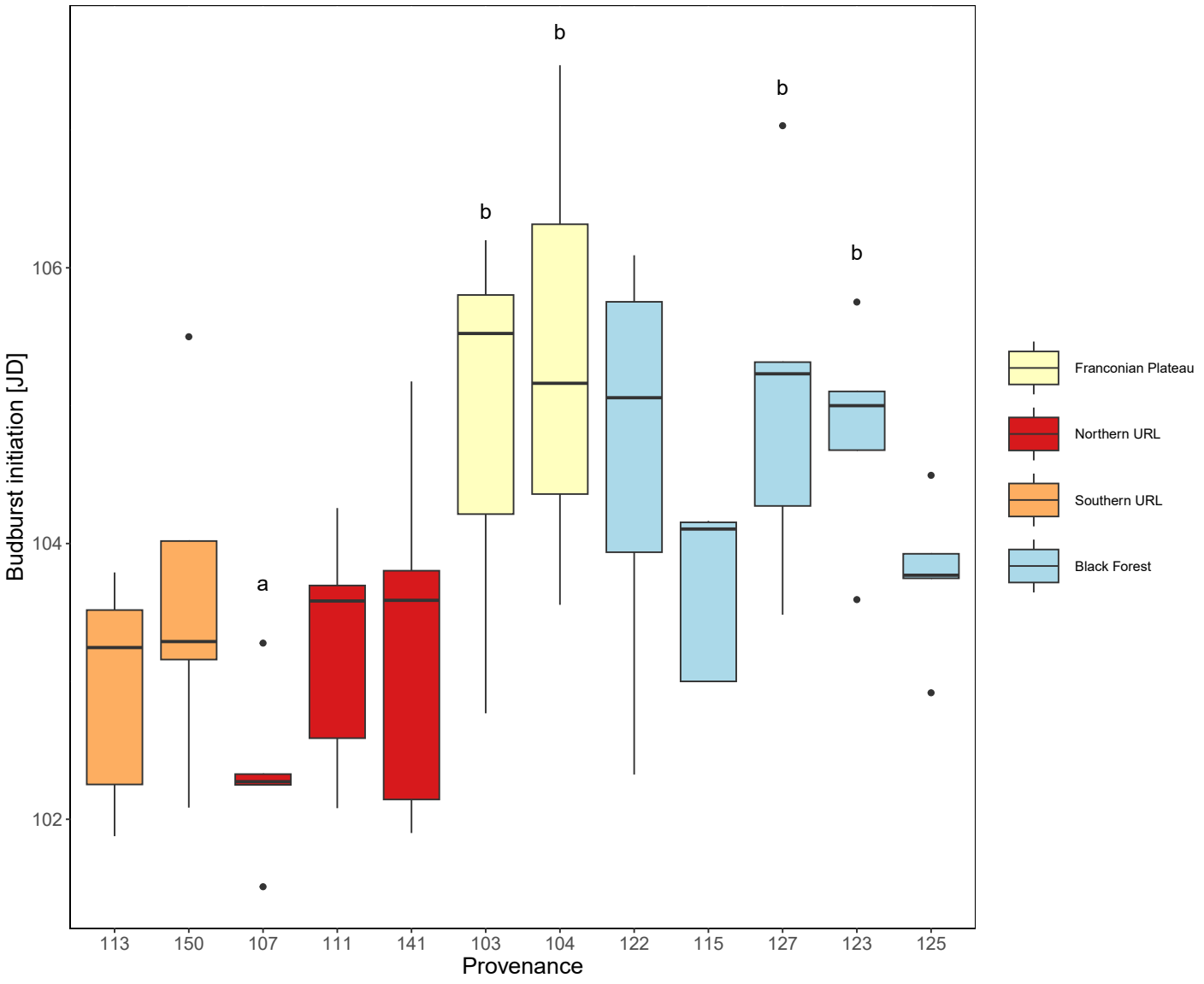

Figure 2
Onset of budburst (in Julian days; JD) of provenances consisting of open-pollinated progenies (ANOVA $p < 0.001$). Different letters above boxes indicate significant differences. Different colors represent provenance groups, with shading indicating relative temperature differences, ranging from cold (blue) to warm (red). The names of the provenances can be found in Table 1.

In our experiment, the mean onset of leaf senescence across provenances was Julian day 309 (November 4th; mean across provenances = 309.27 ± 1.28). On average, 127 – Wehratal was the earliest provenance where senescence began on day 299 (October 26th), whereas 122 – Welschdorf was the latest provenance where the average onset of leaf senescence occurred on day 318 (November 14th). Due to an intense frost event, leaf senescence monitoring of all seed lots ended on day 348 (December 14th). The differences in the onset of senescence among provenances were not significant (Table 3).

Correlation of seed weight with germination rate and growth performance

Progeny seed weight differed strongly among provenances. The highest value of TSW, 4080 g, was observed for provenance 150 – Kandern and the lowest, 1730 g, for 113 – Freiburg. This pairwise difference was significant, as indicated by the post-hoc test (Table 3).

For assessing growth performance we assessed thee height at the end of the vegetation periods of the years 2021 (Figure 2) and 2022 (Figure 3). The mean height in 2021 across all provenances (also those without separately kept progenies) was 11.85 ± 0.44 cm while in 2022 it was 31.24 ± 1.25 cm. Height at the end of 2021 differed significantly among provenances (Table 3, Figure 3), but this was not the case for 2022 (Table 3, Figure 4). In 2021, the provenance 115 – Buchenbach had a significantly lower height growth compared to the provenances 107 – Heidelberg, 125 – Schönau-Utzenfluh and 150 – Kandern.

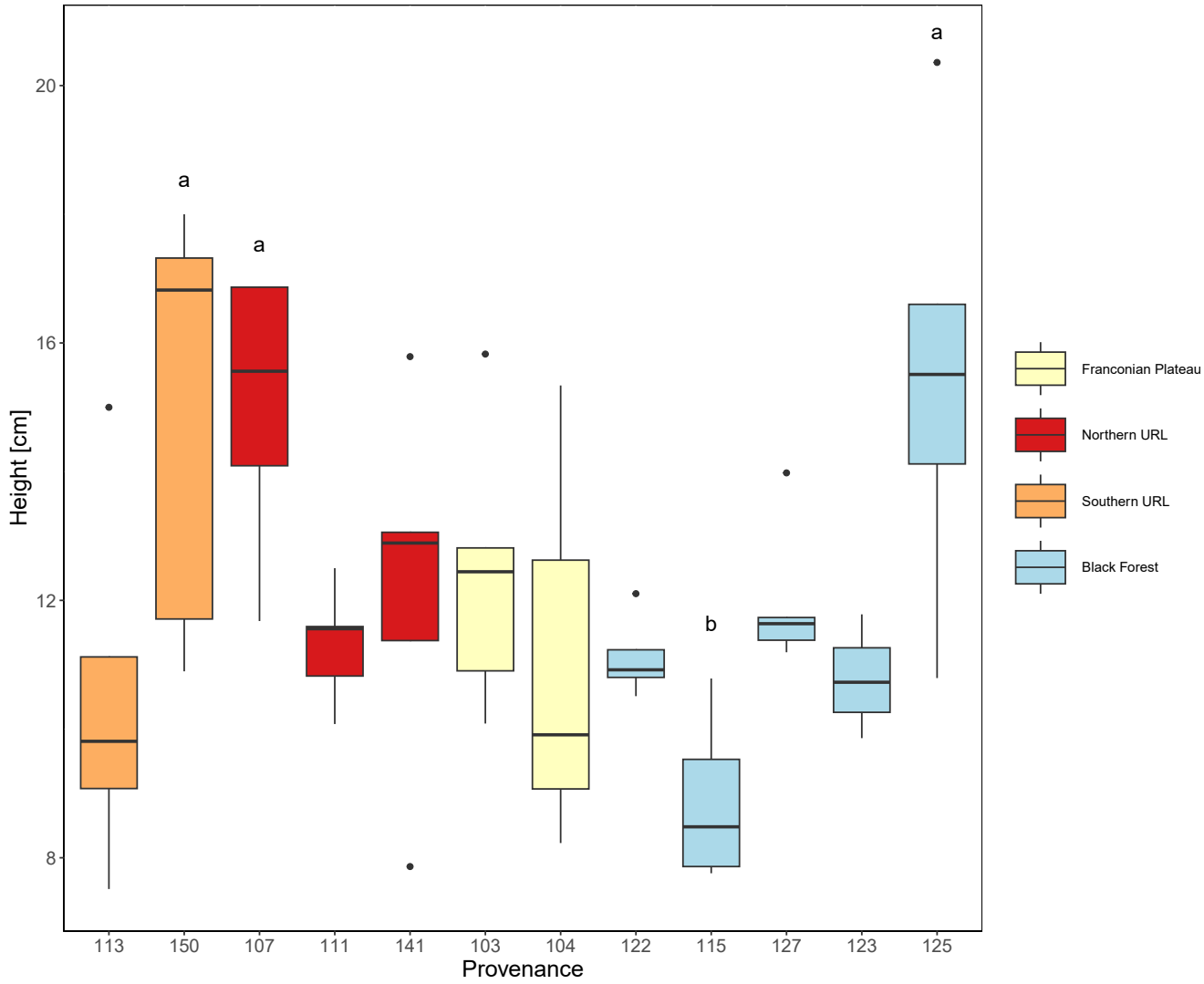

Figure 3
Height (in cm) of provenances consisting of separately kept open-pollinated progenies measured in 2021 at the end of the second growing season. Different letters indicate significant differences (see Table 1). Different colors represent provenance groups, with shading indicating relative temperature differences, ranging from cold (blue) to warm (red). The names of the provenances can be found in Table 1.

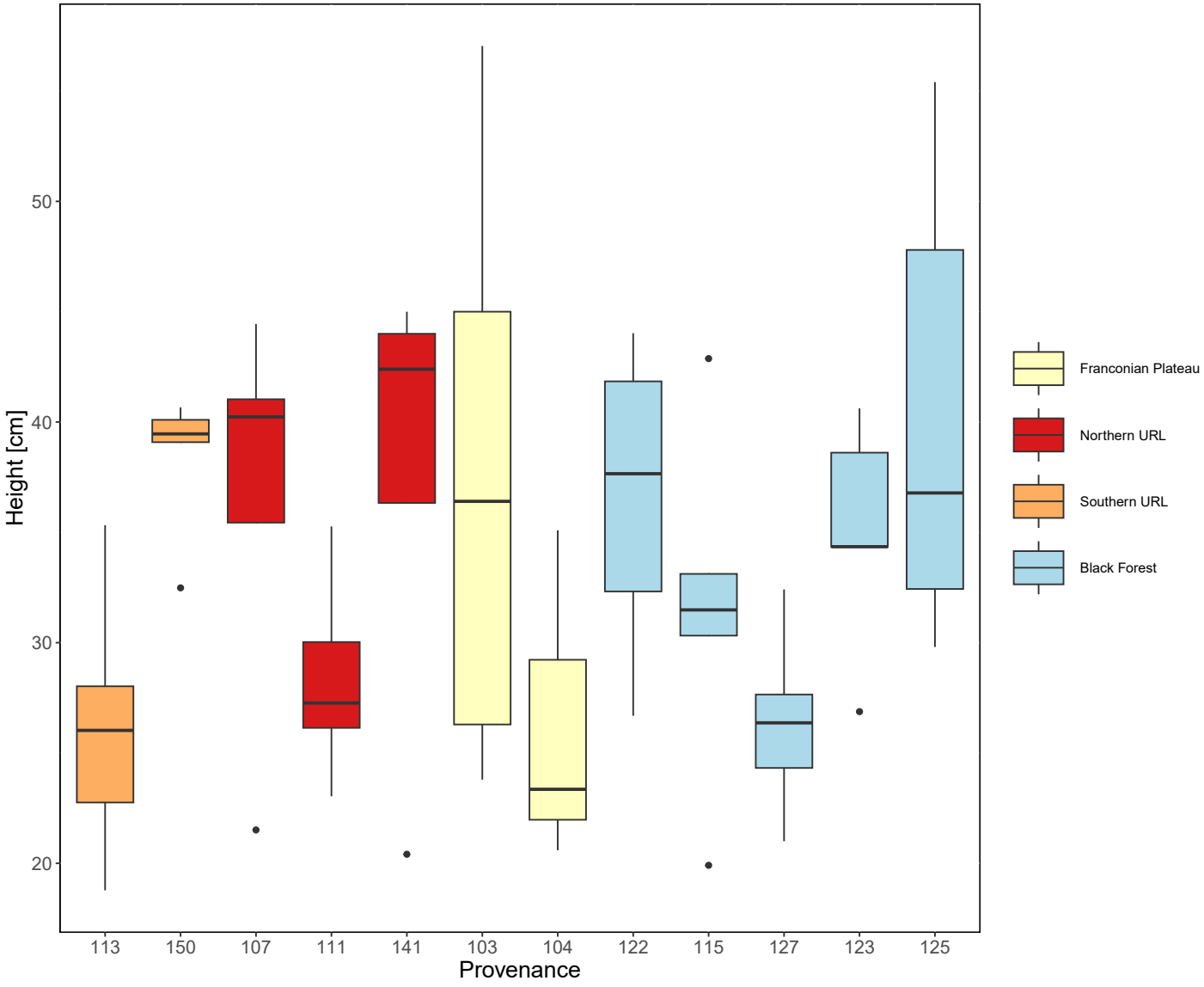

Figure 4
Height (in cm) of provenances consisting of separately kept open-pollinated progenies measured in 2022 at the end of the second growing season. Different colors represent provenance groups, with shading indicating relative temperature differences, ranging from cold (blue) to warm (red). The names of the provenances can be found in Table 1.

The germination rate averaged 28 % overall, with a significant variation observed among the progenies of different provenances. We did not observe a correlation between seed weight and germination rate (τ = 0.008, p = 0.932), but found a significant correlation between seed weight and height in 2021 (τ = 0.209, p = 0.025) and 2022 (τ = 0.212, p = 0.023).

Phenological observations in relation to geographic locations and growth performance

Budburst onset was delayed significantly with increasing elevation (pairwise correlation test using Kendall's rank correlation τ; τ = 0.184, p = 0.037, Figure 5) but was not related to the latitude of provenance (τ = -0.006, p = 0.949). Neither the altitude, nor the latitude exhibited significant correlation with the onset of senescence (τ = 0.053, p = 0.549 for altitude; τ = 0.021, p = 0.807 for latitude).

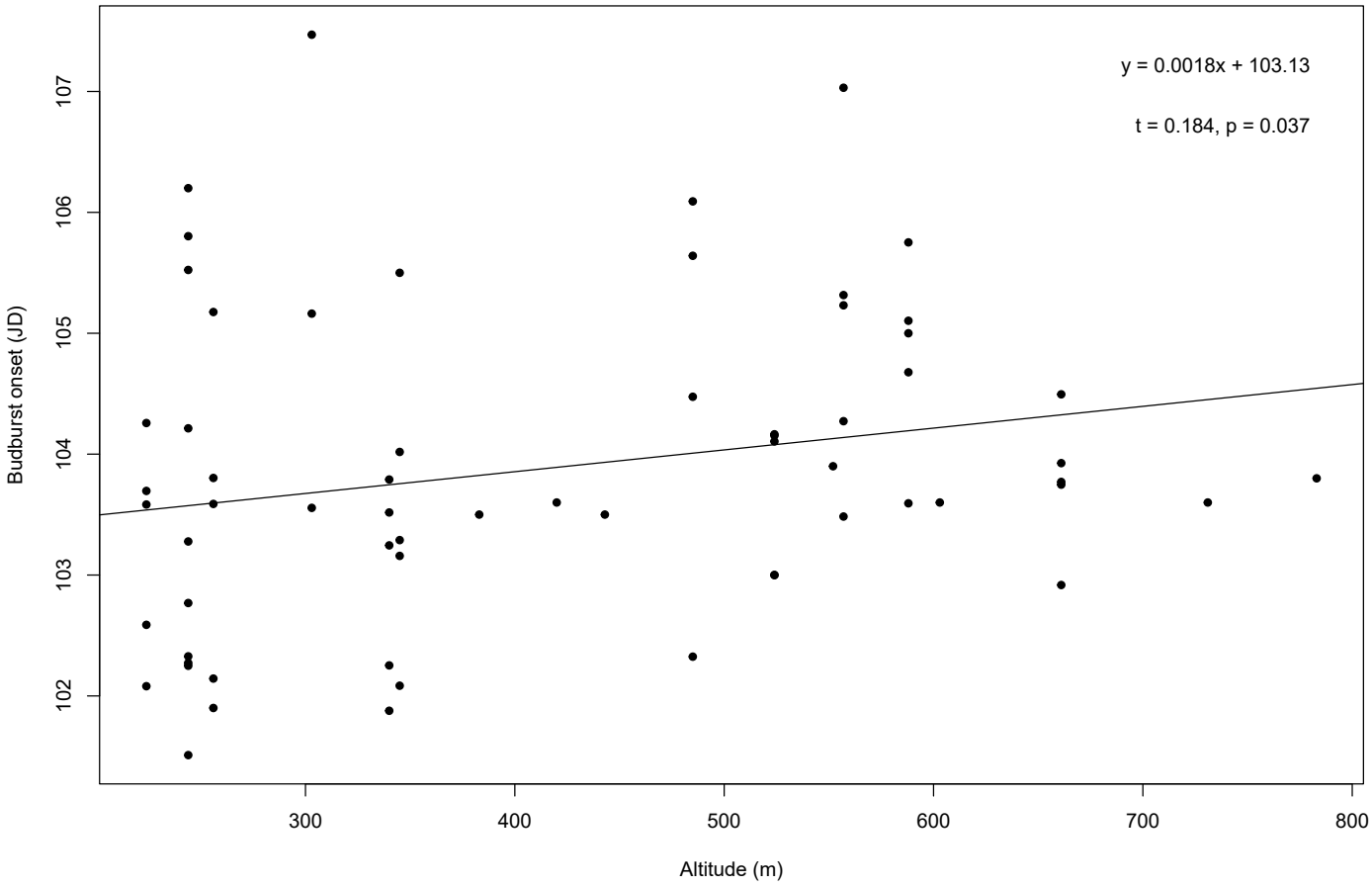

Figure 5
Significant correlation between altitude (in m above sea level) and budburst onset date (in Julian days; JD). Every dot illustrates the progeny of one mother tree or population (with bulked seeds).

Our analysis did not reveal a significant correlation between the duration of the vegetation period and total height in 2022 ($\tau = 0.063$, $p = 0.462$). Likewise, when considering height growth in 2022 (i.e. the difference between height in 2022 and 2021), no significant correlation was observed ($\tau = 0.061$, $p = 0.480$).

Discussion

Clinal variation for budburst

The onset of budburst among provenances was significantly correlated with the elevation of the origin. The progenies from low-altitude provenances displayed an earlier budburst compared to those from higher altitudes (224 m-783 m a.s.l.). The mean budburst onset varied between Julian Day 102 and 105 depending on the provenance (April 12th and 15th, respectively). These findings support our hypothesis that delayed budburst is a result of cold adaptation and align with previous research along two altitudinal gradients in the French Pyrenees (Alberto et al., 2011; Vitasse et al. 2009). Among provenances from that area, budburst onset was delayed by 0.47-0.69 days per 100 m of origin altitude difference (Alberto et al., 2011). Although the maximum pairwise difference we found here between the provenances was 3.1 days, the average delay in budburst by 100 m of elevation in our study was 0.18 days, which is somewhat lower than in the two Pyrenean valleys. This could be because our study area included different biogeographic regions with additional characteristics influencing the phenological behavior of the oaks. Notably, the Franconian Plateau features a more continental climate with significantly colder winters compared to the other areas. Although our provenances from that area occur at low altitudes, they flushed relatively late. This might be the result of adaptation to a colder climate with late frosts and natural selection favoring late flushing individuals. Nevertheless, with a difference of up to 437 m (refers to the 12 provenances used in ANOVA), the elevation span in our study was wide enough to demonstrate the earlier budburst of low-altitude provenances. On the other hand, a maximum difference of two degrees of geographical latitude was probably not enough to capture latitudinal clinal variation of budburst.

No significant differences among provenances for senescence

The onset of senescence varied between Julian days 274 and 328 with a high variation within provenances, but no significant differences among provenances, in contrast to our hypothesis of early leaf

senescence due to cold adaptation. For different oak populations at similar latitudes and elevations in Romania, the onset of senescence was observed within a shorter time frame between Julian days 281 and 313 (Gafenco et al., 2022). The definition of senescence varies between different studies. Sometimes the onset of senescence is defined as the time point when 50 % of the leaves are no longer green (Morin et al., 2010), while elsewhere, it is defined as the time point when 50 % of the leaves are brown or have fallen off (Vitasse et al., 2009). These events can be weeks apart (Gallinat et al., 2015), making comparisons of senescence with other publications challenging.

We observed remarkable senescence differences among open-pollinated progenies within provenances. For example, in population 113 – Freiburg, the difference between the progeny with the earliest vs. the one with the latest senescence was 47 days. In order to account for differences among progenies (within provenances), individual seedling measurements would be required (as in Jensen & Hansen, 2008; Morin et al., 2010; Torres-Ruiz et al., 2019). For practical reasons, we decided to only count saplings per phenological phase within a progeny for each mother tree, without individual-level tracking. The observed variation in senescence among progenies along with a non-significant variation among provenances implies low selection pressure for this trait, which results in the maintenance of a high trait variation within populations. Repeated observations over several years (as in Gafenco et al., 2022; Jensen & Hansen, 2008; Morin et al., 2010; Vitasse et al., 2009) would allow testing whether observed variations in phenology are under genetic control, showing whether the rank of phenological scores among progenies remains stable.

Our comparison among provenances revealed that neither the effect of the origin on the onset of leaf senescence by itself, nor its correlation with altitude or latitude were significant. Provenances of sessile oaks from high-altitude in the French Pyrenees exhibited delayed senescence in a common garden experiment compared to those from lower-altitude origins (Vitasse et al., 2009). These provenances were sampled from a range of elevations between 200 and 1,600 meters above sea level, while the common garden was located at 23 meters, significantly lower than the high-altitude provenances (Vitasse et al., 2009). This suggests that montane provenances require lower temperatures for leaf senescence due to their adaptation. Thus, a relatively late autumn cooling at the experimental site may explain the late senescence of high-altitude provenances. On the contrary, other progenies of the closely related pedunculate oak (*Quercus robur*) from the French Pyrenees, including some originating from the same populations, exhibited the opposite pattern - senescence onset occurred earlier for higher-altitude provenances compared to lower-altitude provenances (Le Provost et al., 2023). The relationship between the elevation of the origin populations and leaf senescence is often not straightforward (Firmat et al., 2017; Gafenco et al., 2022; Torres-Ruiz et al., 2019). In a study with provenances of sessile oak from a wider latitudinal range in northern Europe (grown in a greenhouse), senescence began earlier for the provenances from higher latitudes than for those from lower latitudes. This correlation was explained by differences in photoperiod (Jensen & Hansen, 2008). In our study, the lack of clinal variation for this trait may be attributed to the limited latitudinal and altitudinal range of our area.

Significant correlation between seed weight and juvenile growth suggests maternal effects

We found that seed weight was significantly correlated with height both in the first (2021) and the second year (2022) in agreement with our hypothesis. A larger nutrient reserve in seeds can enable stronger pre-photosynthetic growth, contributing to higher survival rates and enhanced seedling growth, argue Harper & Obeid (1967) and Stanton (1984). Johnson et al. (2019) shows that acorn size in oaks may remain correlated with the height of the resulting plant over several years. Furthermore, Ramírez-Valiente et al. (2009) state that variation of seed weight among mother trees of cork oak (*Quercus suber*) shows maternal effects resulting from the environmental conditions of a site during the year of acorn maturation. Such an effect could explain the significant differences of seed weight among provenances observed in our study. Other studies on various oak species indicated that larger acorns are positively associated with higher survival rates and faster seedling growth (Tripathi & Khan, 1990). A higher seed mass may also positively affect other fitness related traits like germination and survival at the juvenile stage (Ramírez-Valiente et al., 2009). Therefore, we suggest that the positive correlation between seed weight and juvenile growth in our study reflects maternal effects.

In contrast to the aforementioned result, there was no correlation between germination rate and seed weight. Variable seed quality among families and stands could have accounted for this. For certain stands, a relatively high proportion of acorns were infested with weevils, which might have damaged the embryos resulting in germination failure. A further possibility is that seed weight does not have an effect on germination rate. Interestingly, Landergott et al. (2012) found out that seed weight had no effect on the germination rate of open-pollinated families of *Q. petraea, Q. robur* and *Q. pubescens* whereas it was positively correlated with first-year seedling growth, in agreement with our findings.

No effect of phenology on growth performance

We hypothesized that an extended vegetation period, resulting in increased sunlight exposure and enhanced photosynthesis, would lead to a higher seedling growth compared to those experiencing a shorter vegetation period. However, our study did not reveal any significant impact of the vegetation period on growth performance. This is in contrast to other studies showing that phenological traits determining the vegetation period are linked to growth characteristics (Kleinschmit, 1993). For example, a clinal variation in tree height at the age of 22 years was reported for pedunculate oak from the same study area as ours. In particular, provenances from lower altitudes exhibited a higher growth performance, which was attributed to their adaptation to a longer vegetation period (Wunderlich et al., 2017). Other studies, too, have linked such differences in growth performance to photosynthetic performance (Modrow et al., 2020) as well as various climate factors, such as temperature and precipitation (Campelo et al., 2023; Gil-Pelegrín et al., 2017).

One possible explanation for the lack of a significant relationship between the vegetation period and growth performance could be the difference between juvenile and mature growth. We measured tree height at the age of one and two years and found a significant effect of seed weight on juvenile growth likely reflecting maternal effects which are expected to weaken with increasing age (Baliuckas & Pliura, 2003; González-Rodríguez et al., 2011). Rank changes in growth performance between different ages are common in similar common-garden trials with oak species (Adams et al., 2007; Grotehusmann & Schönfelder, 2011; Jensen, 2000). We could also observe rank shifts in height between 2021 and 2022 in our study. Phenological traits like budburst show a generally high heritability in oaks (Alberto et al., 2011). On the

other hand, juvenile growth in our experiment seems to be influenced by maternal effects. Therefore, it could be that an effect of phenology (i.e. length of vegetation period) on growth performance (as this was observed e.g. in Wunderlich et al., 2017) will be established with increasing age and decreasing maternal effects.

Conclusions

Evidence on the genetic variation of adaptive traits in forest tree species provides a valuable basis to inform seed sourcing. In our case, we identified a clinal variation in budburst of sessile oak along an altitudinal gradient. Population genetic studies based on molecular markers report autochthony of our study populations (Neophytou et al., 2024). This is in line with the hypothesis that oaks could adapt to their local environments for many generations, giving rise to the observed patterns of variation in budburst. Thus, our results support that high-elevation provenances of sessile oaks are adapted to colder climates with late frosts. This adaptation is rather of local importance, given the current global warming and an upward shift of climatic zones. With increasing temperatures and under the assumption of adaptation to altitude, assisted gene flow should take place from lower to higher altitudes and not vice versa. However, the risk of late frosts can be particularly high when transferring reproductive material upwards (Sang et al., 2021). Therefore, a prudent strategy for assisted gene flow in our study species would be not to exceed 200-400 m of altitudinal difference between seed source and plantation site and combine local seed sources with the transferred reproductive material. The establishment of three field trial plots along an environmental gradient with our saplings in early 2023 will enable the long-term monitoring of provenance and progeny growth performance. As the oaks grow, more economically important traits like volume growth and stem form can be quantified, genotype by environment interactions can be addressed and more detailed recommendations can be made.

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Data availability

The original data used for the analysis are available at the Dryad digital repository, https://doi.org/10.5061/dryad.cfxpnvxjq. The analysis script and the used data tables are provided in the appendix.

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