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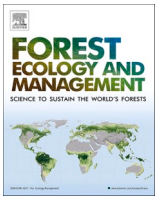

Genotype x environment interaction and climate sensitivity in growth and wood density of European larch

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ABSTRACT

European larch is an ecologically and economically important tree species planted across a wide range of environments. Understanding its response to the rapidly changing climate is essential to developing efficient gene resource management strategies in line with the assisted migration methodology. In this study, we quantified the genotype x environment interaction (GxE) of a larch provenance in a multi-environmental trial analysis using factor analytic (FA) modeling. We analyzed the mean annual height increment (MAI-H), the mean annual diameter increment (MAI-DBH), and wood density (PP). Additionally, we evaluated the effect of several environmental variables on these traits. The genetic correlations between sites varied from −0.53 to 0.99, −0.87 to 0.99, and −0.17 to 0.99 for MAI-H, MAI-DBH, and PP, respectively. This indicates the presence of low to high GxE. The growth traits showed more GxE signal than wood density. Narrow-sense heritability estimates were 0.41, 0.16, and 0.35 for MAI-H, MAI-DBH, and PP, respectively. The FA modeling of order 2 explained 77.4%, 67.9%, and 77.3% of the genetic variance for MAI-H, MAI-DBH, and PP, respectively. For MAI-H, the latent regression plots for the predicted site means indicate a significant positive correlation with the first factor loading. At the individual genotype level, the latent regression plots indicated high levels of GxE, especially for growth traits. Significant and relatively high correlations were found between several EVs and the factor loadings of the FA models, suggesting their possible influence on the genotypic performance across environments. Regarding MAI-H, elevation, averaged monthly mean temperature, precipitation seasonality, and stand age were correlated with the first factor loading. Annual temperature range with both the first and second factor loadings. For MAI-DBH, the mean diurnal range was correlated with the first factor loading. In the case of PP, we found that elevation was correlated with the second factor loading. Overall, this approach successfully modeled the GxE and identified environmental variables likely affecting it. Therefore, we conclude that this methodology is a valuable tool for selecting suitable genotypes adapted to specific environmental conditions.

1. Introduction

Boosting productivity in forest stands has been a constant target in the forest industry sector. Silviculture, since the 13th century, is the part of forestry that deals with regulating forest stands composition, growth, and quality to meet anthropogenic needs. Tree breeding is the part of silviculture that deals with modifying populations' genetic composition. Large-scale tree breeding activities have been implemented since the mid-20th century (White et al., 2007; Zobel and Talbert, 1984). Genetic tree improvement is characterized by the selection and breeding of superior individuals that will boost productivity and present favorable characteristics (Alan, 2020; Ruotsalainen, 2014). Tree breeding challenges include the following: (1) large experimental plots due to mature trees' size, (2) wide ranges of environments that represent the conditions of the planned reforestation sites as tree growth is highly influenced by environmental conditions (climate, slope steepness, soil composition, etc.), and (3) long time periods, as it takes many years for trees to reach sexual maturity, and because several economic traits can be measured only years after planting (e.g., wood quality) (El-Kassaby and Klapste, 2016). Additionally, forest field experimentation is susceptible to issues such as diseases, pests (e.g., grazing), and extreme events (e.g., wind, drought, flooding, etc.) over these long periods.

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In light of climate change (CC) (Lindner et al., 2010), forests and breeding programs are facing further challenges. The temperatures have already increased, and are predicted, by the end of the century, to globally increase by between 1 °C and 5.7 °C, depending on the underlying emissions scenario (IPCC 2021: Masson-Delmotte et al., 2021). Additionally, extreme events are also predicted to increase in frequency and intensity (Seidl et al., 2017).

Faced with changes in environmental conditions, to maintain their fitness and endure, natural tree populations can either persist (phenotypic plasticity), adapt (changes in allelic frequencies over generations), or migrate (during the pollination and seeds dissemination stages) (Aitken et al., 2008; Bussotti et al., 2015). However, many studies reported the likely inability of certain populations to cope with the ongoing rate of CC (Isaac-Renton et al., 2018; Matyas, 2021; Seidl et al., 2017), especially for some populations located at the warmest border of the species distribution (Schueler and Liesebach, 2014).

Currently, forest reproductive material (seeds or seedlings) for reforestation is mostly derived from local populations; however, with the predicted changes in climate, a growing part of the scientific community is considering assisted migration to mitigate its negative impact (Aitken and Bemmels, 2015; Browne et al., 2019; Williams and Dumroese, 2013). In forestry, assisted migration is the process of planting non-local forest reproductive material which is expected to be best adapted for the anticipated climate of the target plantation area. Nevertheless, artificial gene flow across large distances is not without risks (Montwé et al., 2018): if seeds are poorly selected, then it can lead to issues such as maladaptation and diebacks of the new populations, with poor economic, ecological, and/or social outputs.

European larch (*Larix decidua* Mill.) is a deciduous conifer native to the Alps and the Carpathian Mountains. It is adapted to a continental climate, with cold winters and hot summers. In its Alpine natural distribution, *L. decidua* is found on a wide range of elevations from 450 to more than 2,300 m a.s.l. (Saulnier et al., 2019). It is a fast-growing pioneer tree species. As it is light-demanding at all its life stages, larch performs well after disturbances, in open forests, and newly established plantations (Zeidler et al., 2022).

L. decidua is considered an important commercial species, due to its fast growth and adaptable properties, as well as its wood quality. With the right environmental conditions, it can produce high wood quality and quantity with an average annual increment rate of approximately 10 m^3/ha (Zeidler et al., 2022). In terms of volume production, larch is the seventh most important tree species in Europe (Danek and Danek, 2022). Due to its economic importance, it has been widely planted in central and northern Europe from foothills to mountainous areas (Zeidler et al., 2022).

L. decidua has been described as showing high plasticity in terms of local adaptation to climate (Saulnier et al., 2019), and relatively robust response to climate stressors (Vacek et al., 2022) such as drought and frost (George et al., 2017; Obojes et al., 2022; Zeidler et al., 2022). Other studies have found that larch is highly negatively affected by droughts (Danek and Danek, 2022), low water availability (Swidrak et al., 2013), and high temperatures (Obojes et al., 2022). It has also been described as positively influenced by increasing temperatures (Danek and Danek, 2022; Foff et al., 2014), especially during the Spring months (Danek and Chuchro, 2019; Izworska et al., 2022). Regarding precipitations, it was found to be generally negatively affected by an increase in precipitation levels (Foff et al., 2014), even though studies indicate different monthly responses (positive in November and July but negative in September) (Izworska et al., 2022; Swidrak et al., 2013). Growth seems to be negatively affected by higher elevations (Foff et al., 2014; Li et al., 2003). Finally, larch has shown an augmentation of climate sensitivity with aging (Carrer and Urbinati, 2004).

In addition to the environmental factors, tree growth is influenced by the genetic makeup of the individuals (genotype) and its interaction with the environment (GxE). Most growth traits are polygenic, where a very large number of genes contribute to the traits' variation. For larch species, growth traits as well as wood density, have been described as relatively highly heritable with individual narrow-sense heritability estimates ranging from 0.30 to 0.35 for height, 0.24 to 0.30 for wood density, and with a value of 0.24 for diameter at breast height (Lstibůrek et al., 2020; Poupon et al., 2021; Ratcliffe et al., 2014).

GxE can be described as different genotypes responding to an environment in different ways. This means that if a set of genotypes is measured in only one site, their ranking is limited to this specific environment. Hence, to make quality decisions for tree selection, it is important to test genotypes across several environments. Some genotypes show a stable response across environments, which makes them valuable, as they can be planted more widely. With CC, those genotypes are also important if the environment changes during the trees' lifetimes. In addition, stable genotypes could reduce the risk of maladaptation by assisted migration.

Traditionally, breeding experiments estimate GxE by using complex linear mixed models. Those models rely on data from relatives growing in different environments (multi-environment trial, MET). GxE models typically consider a different variance for each environment and a specific genetic correlation between each pair of environments. For a large number of variance components to estimate, a typical model will have convergency and computational issues. One good approximation to this is the Factor Analytic (FA) structure (Smith et al., 2001b) that allows the estimation of loadings associated with underlying environmental covariables (Thompson et al., 2003). The FA structure has been widely used in agricultural crops (Beeck et al., 2010; Kelly et al., 2007; Smith et al., 2001b) and more recently, in tree breeding (Calleja-Rodriguez et al., 2019; Cullis et al., 2014; Ogut et al., 2014).

In this study, we aim to investigate European larch's response to its environment to facilitate germplasm resource management that will allow the species to withstand environmental changes such as different planting sites or CC. The specific objectives of this study are: (1) to fit a multi-environmental statistical model to quantify the magnitude of GxE for two growth traits and wood density, (2) to evaluate the impact of climate on European larch by fitting complex FA GxE models and associate their estimated loadings against key environmental covariables, and (3) to determine the dynamics of GxE responses of specific genotypes.

2. Materials and methods

2.1. Tree data

The material used in this study originates from a clonal seed orchard that was established in 1954 from a local European larch provenance in the North-Eastern Alps (North-East of Austria; from 14° 12′ 14.4″ to 16° 31′ 4.8″ and 47° 37′ 8.4″ to 48° 37′ 26.4″). The orchard consists of 53 phenotypically superior trees. Subsequently, open-pollinated seeds have been harvested and extensively used in regional reforestation activities over the last 60 years.

In 2018, data sampling and genetic analysis were performed by , and these data constituted the basis of this study. These authors selected 21 forest stands (sites) established for operational planting (random distribution of progenies), using the seeds from the above-mentioned orchard. The stands were selected based on a minimum of 200 trees, a composition including only or mostly European larch, a low level of environmental variation within sites, and similar soil compositions. These stands are geographically spread over a 110 km by 170 km area, with elevations ranging between 280 and 760 m. asl (see Fig. 1 in Poupon et al. (2021)), and with stand's ages ranging from 25 to 37 years. Across these stands, the authors measured over 4,000 individuals for height (m; using a hypsometer), diameter at breast height (cm; using a caliper), and wood density via Pilodyn penetration (PP) method (mm; using a 6 J Forest Pilodyn (Cown, 1978); a lower PP corresponds to a higher density). Damaged or ill-formed trees were not sampled.

In addition, 1,253 of the sampled individuals were also genotyped

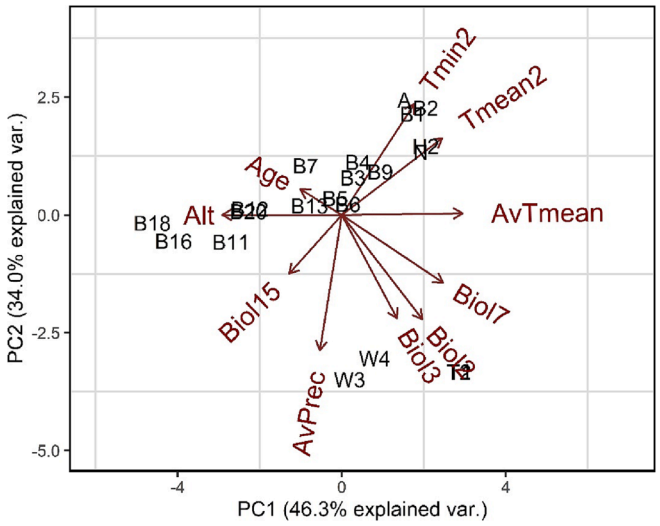

Fig. 1. Loading plot of the selected EVs. The x- and y-axis are the two first components of the PCA analysis. The sites' names are indicated in black and the EVs are in brown.

via microsatellite analysis for pedigree reconstruction. Family relationships were reconstructed using the likelihood-based method of the Cervus software package (Marshall et al., 1998). The presence of 491 full-sib families was established, which corresponds to 35% of the possible specific parental combinations (families); the unknown paternal contribution, due to external pollen flow (contamination) was estimated at 8.4% in the genotyped offspring (Lstiburek et al., 2020). The detail of the progenies' representation in each site can be found in Table S1. Given the pedigree reconstruction, the respective forest sites can be considered as full-sib progeny trials.

In this study, to correct for the age effect in the subsequent modeling, both height and diameter were divided by the sites' stand ages, to obtain mean annual increments, and these are thereafter referred to as MAI-H and MAI-DBH, respectively.

2.2. Environmental variables

To understand the dynamics of the GxE interactions in the present study, a series of climate variables were considered. These were derived from the WorldClim dataset (Hijmans et al., 2005). The list contains a total of 67 climate variables, including an average of monthly minimum, mean, and maximum temperatures and precipitation, together with 19 biologically relevant indicators. These indicators were derived from the monthly temperature and precipitation data, and they were used to describe quarterly and annual variations (Biol1 = Mean annual temperature, Biol2 = Mean diurnal range, Biol3 = Isothermality, etc.; see Table S2 for further details).

Using these climate variables together with the test sites' elevations and ages, several Principal Component Analyses (PCAs) were performed to assist in the selection of a reduced subset of these variables (Fig. 1). These PCAs considered the use of correlation matrices. Pairwise Pearson's correlations between these environmental variables (EVs) were also considered for the variables' selection. These, and all other analyses, were implemented using the statistical software R version 4.0.0 (R Core Team, 2020).

Single column fitting.

2.3. Statistical analyses

Single-site and multiple-site mixed linear models were performed using the library ASReml-R v. 4.1 (Butler et al., 2018).

The single site models, with associated diagnostic plots, were used to investigate the data, by fitting the following model:

$$\boldsymbol{y} = \mathbf{1}_n\mu + \boldsymbol{Za} + \boldsymbol{e} \quad (1)$$

where $\boldsymbol{y}$ is the $(n \times 1)$ vector of the response variable to be evaluated; n is the number of observations; μ is the overall mean; $\boldsymbol{a}$ is the $(m \times 1)$ vector of random additive genetic effects of m genotypes, with $\boldsymbol{a} \sim N(0, \sigma_a^2 \boldsymbol{A})$, in which σ_a^2 is the additive genetic variance; and $\boldsymbol{e}$ is the random $(n \times 1)$ vector of residual effects, with $\boldsymbol{e} \sim N(0, \sigma_e^2 \boldsymbol{I}_n)$, where σ_e^2 is the error variance. $\boldsymbol{Z}$ is the incidence matrix for genotype effects; $\mathbf{1}_n$ denote a vector of ones; $\boldsymbol{A}$ is the $(m \times m)$ pedigree-based relationship matrix; and $\boldsymbol{I}_n$ represent the identity matrix for the number of observations. Outliers were removed and narrow-sense heritability estimates were calculated to assess the quality of the data from each site.

The fitting of the MET models, using the factor analytic structure (FA), was executed by fitting the following mixed linear model:

$$\boldsymbol{y} = \mathbf{1}_n\mu + \boldsymbol{Xs} + \boldsymbol{Za.s} + \boldsymbol{e} \quad (2)$$

where $\boldsymbol{y}$ is the $(N \times 1)$ vector of the response variable over s environment; N is the total number of observations across all s sites; μ is the overall mean; s is the $(s \times 1)$ vector of fixed effects of sites; $\boldsymbol{a.s}$ is the $(ms \times 1)$ vector of random additive genetic effects (breeding values) of m genotypes nested within s environments, with $\boldsymbol{a.s} \sim N(0, \boldsymbol{G} \otimes \boldsymbol{A})$; and $\boldsymbol{e}$ is the random $(N \times 1)$ vector of residual effects with $\boldsymbol{e} \sim N(0, \sigma_e^2 \boldsymbol{I}_N)$, where σ_e^2 is the error variance. $\boldsymbol{G}$ is the $(s \times s)$ variance–covariance matrix for the effect of genotypes nested within environments, modeled as a factor analytic of order k (details below); $\boldsymbol{X}$ is the incidence matrix for the effects of the environment; $\otimes$ is the Kronecker product; and the other terms were previously defined.

The factor analytic structure of order k (FA_k), in which k is the number of multiplicative components, was considered to model the $\boldsymbol{G}$ matrix and is defined as:

$$\boldsymbol{G} = (\Lambda\Lambda^{\mathrm{T}} + \psi) \quad (3)$$

where $\boldsymbol{\Lambda}$ is the $(s \times k)$ matrix of factor loadings $\{\lambda_{sk}\}$, in which λ_{sk} is the k^{th} factor loading $(k = 1, 2, \ldots, k)$ for the environment s; and $\boldsymbol{\psi}$ is a diagonal matrix $(s \times s)$ with specific variances for each environment. The significance of a model of order $k + 1$ was assessed against the model with an order k using a likelihood-ratio test. In addition, the percentage of explained variance by each model, the log-likelihood, and the Akaike information criteria (AIC) were also considered for model selection.

Site-to-site additive genetic correlations were calculated to evaluate the presence or absence of GxE as described by Oliveira et al. (2020), as highly correlated sites indicate a low GxE, and vice versa.

Based on the selected model, the averaged narrow-sense heritability ($\overline{h^2}$) was calculated for each trait using the following equation:

$$\overline{h^2} = \overline{\sigma_a^2}/(\overline{\sigma_a^2} + \sigma_e^2) \quad (4)$$

where $\overline{\sigma_a^2}$ is the averaged additive genetic variance, and σ_e^2 is the error variance. Then, the overall unbiased narrow-sense heritability (h_u^2), that corrects for GxE, was estimated using the following expression:

$$h_u^2 = \overline{h^2} \times \overline{\rho_a} \quad (5)$$

where $\overline{\rho_a}$ is the mean site-to-site additive genetic correlation.

To understand the relationship between genotypic expression and the environment represented by the factor loadings, for each trait, both the predicted site means and the estimated individual breeding values were plotted against the rotated loadings (rotation performed via the Varimax function; referred to only as loadings subsequently), to build latent regression plots (Cullis et al., 2014, 2010; Thompson et al., 2003).

Finally, to identify which EVs might influence the genotypic performances across environments (GxE), Pearson's correlations between the loadings and the selected EVs were calculated, along with their significance levels following the approach of Oliveira et al. (2020).

3. Results

3.1. Environmental variables

The two first principal components from the final PCA analysis explained 46.3% and 34.0% of the variance, respectively. A subset of 10 EVs was selected: averaged monthly precipitation (AvPrec), averaged monthly mean temperature (AvTmean), mean temperature of February (Tmean2), minimum temperature of February (Tmin2), precipitation seasonality (Biol15), mean diurnal range (Biol2), isothermality (Biol3), temperature annual range (Biol7), elevation (Elevation) and stand age (Age). The correlations among those variables have a mean of 0.41 with values ranging from 0.00 to 0.97.

The influence of the EVs on the two first components is visible from the biplot (merged loading and score plot) presented in Fig. 1. Elevation, and AvTmean are strongly influencing PC1, while AvPrec is strongly influencing PC2. The other EVs have different levels of relevance for both the first and second components. The PCA scores of the sites are clustered into three groups. Sites T1, T2, W3, and W4 are scoring negatively with PC2 and are distributed on the positive side of PC1. Sites A, B1, B2, H2, and N are grouped on the higher right section of the plot. The rest of the sites are distributed along the PC1, especially on the negative side.

3.2. Genetic parameters

The linear mixed models fitted using the FA structure indicated that the variance explained from the factors 1 to 4 (FA1 to FA4) varied, for MAI-H, MAI-DBH, and PP, from 64.8% to 91.0%, 56.0% to 94.4%, and 65.9% to 92.2%, respectively (Table 1). The log-likelihood values showed, as expected, a systematic increase with the number of factors used in the models, indicating better fits, while AIC indicated that the FA1 models were the preferred fit. According to the likelihood ratio test, for MAI-H and PP, the FA2 models were a statistically significant improvement over the FA1 models ($P = 0.022$ and $P = 0.094$, respectively). None of the higher-order models showed a significant improvement. Therefore, models of order $k = 2$ were selected for the subsequent analyses.

Based on the FA2 models' outputs, the overall unbiased narrow-sense heritability estimates for MAI-H, MAI-DBH, and PP across all sites were 0.41, 0.16, and 0.35, respectively. Individual sites' narrow-sense heritability estimates are listed in Table S3.

Genetic correlations for each trait are presented in Fig. 2, S1, and S2. For MAI-H, these correlations ranged from −0.53 to 0.99 (mean = 0.53). Several sites, such as A, B1, B2, B11, and B13, showed strong levels of similarities with correlations close to 1. Other sites, such as B16, B18, B5, B9, and T2, showed mild similarities with almost null correlations. A few negative correlations were found (6.2% of the total correlation values) with site N. For MAI-DBH, genetic correlation ranged from −0.87 to 0.99 (mean = 0.25), the differences among sites were more pronounced, with a relatively high proportion of negative values (32.8%) that were found especially at sites N, H2, B6, B9, B5, B4, and B20. For PP, the correlations ranged from −0.17 to 0.99 (mean = 0.56) with a low proportion of negative correlations (4.3%). Many correlations among sites were moderate to high. The sites B20 and H2 showed the lowest correlation values.

1,5 column fitting.

The latent regression plots with the predicted sites means for MAI-H (Fig. 3) show that the means are significantly positively correlated with the first loading ($R^2 = 0.34$, $P = 0.003$). However, with the second loading, the correlation coefficient is almost null ($R^2 < 0.01$, $P = 0.563$). In the case of MAI-DBH and PP (Figs. S3 and S4), correlation coefficients were lower with values ranging from < 0.01 to 0.11 (Table 2).

Table 1
Summary statistics of the FA models of orders 1 to 4, for MAI-H, MAI-DBH, and PP. *Model* is designating the order of the models, *VE* is the cumulative variance explained, *LogL* is the loglikelihood, *AIC* is the Akaike's Information Criteria, *P* represents the significance of the model k + 1 over the model k based on a significance level of 0.10, and *VC* is the number of variance components estimated by the respective models.

	Model	VE	LogL	AIC	P	VC
MAI-H	FA1	64.8	−2828.87	**5727.74**		42
	FA2	77.4	−2812.84	5731.67	**0.022***	63
	FA3	87.4	−2804.38	5742.75	0.260	84
	FA4	91.0	**−2797.95**	5761.90	0.684	105
MAI-DBH	FA1	56.0	−3816.69	**7703.37**		42
	FA2	67.9	−3807.39	7718.78	0.352	63
	FA3	89.3	−3798.33	7730.66	0.257	84
	FA4	94.4	**−3789.54**	7743.07	0.285	105
PP	FA1	65.9	−1093.41	**2258.82**		42
	FA2	77.3	−1082.10	2268.20	**0.094***	63
	FA3	85.6	−1074.60	2285.20	0.590	84
	FA4	92.2	**−1065.65**	2297.31	0.268	105

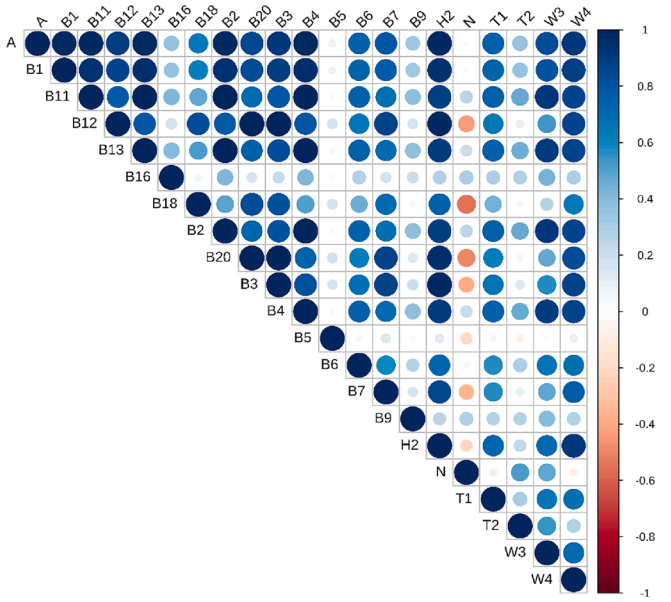

Fig. 2. Additive site-to-site genetic correlations of the FA2-MAI-H model. The size of the circles and their colors represent the amplitude of the correlations. The blue color signifies positive correlations and the red color negative ones.

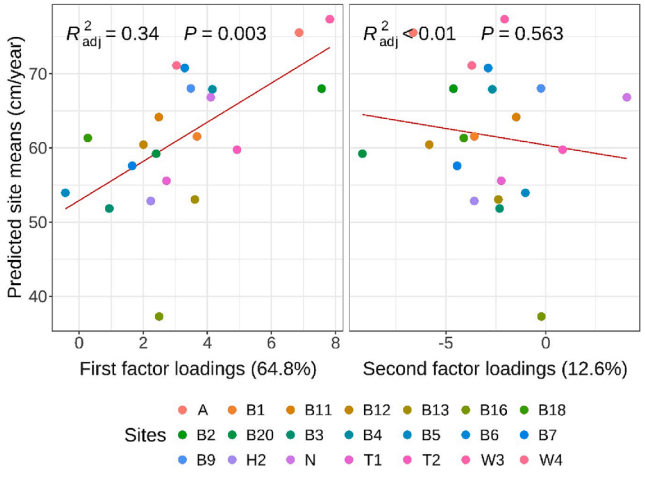

Fig. 3. Latent regression plots with the predicted site means of the FA2-MAI-H model. The linear regressions are represented by the red lines. R^2_{adj} is the adjusted coefficient of determination of the linear regression, and *P* represents the significance of the correlations.

Table 2
Summary statistics of the latent regression plots between the predicted site means and the loadings of the factors 1 and 2 of the FA2 models for MAI-H, MAI-DBH, and PP. R^2_{adj} is the adjusted coefficient of determination of the linear regression, and *P* represents the significance of the correlations based on a significance level of 0.10.

	Factor 1		Factor 2	
	R^2_{adj}	P	R^2_{adj}	P
MAI-H	0.34	**0.003**	0.01	0.563
MAI-DBH	0.06	0.146	0.11	**0.082**
PP	0.02	0.262	0.01	0.365

Noticeably, for both MAI-H and MAI-DBH, site B16 is clearly showing lower mean values (see Table S4); however, this site does not stand out for PP.

3.3. Single column fitting

For the model FA2-MAI-H, the latent regression plots with individual genotypes for the eight most represented genotypes are presented in Fig. 4. Several types of responses are observable. Some genotypes are showing a relatively constant expression along the loadings. For example, we can see this with the genotypes L1 and *L*10 (A). However, interestingly, these genotypes differ in terms of overall predicted mean: genotype L1 (61.14 ± 1.16; not shown) presents a better performance, with less variability around the mean than genotype *L*10 (58.57 ± 1.36; not shown). Other genotypes, such as L17 and L8 (A and B), are showing a more sensitive response along the loadings. Noticeably, however, genotype L17 presents breeding values that are mostly positive while, in contrast, they are mostly negative for genotype L8. For MAI-DBH and PP, equivalent patterns were found (see Figs. S5 and S6).

Pearson correlation coefficients between the selected EVs and the loadings of the FA2 models are presented in Table 3, Table S5, and Table S6, for MAI-H, MAI-DBH, and PP, respectively. Several statistically significant correlations were found and are described below. For MAI-H, Biol7, and AvTmean are positively correlated; while Elevation, Age, and Biol15 are negatively correlated with the first loading. The correlations' absolute values range from 0.40 to 0.50. Biol7 is also positively correlated (0.38) with the second loading. Regarding MAI-DBH (Table S5), Biol2 is positively correlated with the first loading (0.41). Finally, for PP, a positive correlation between the second loading and Elevation (0.40) was observed.

4. Discussion

According to the PCA analysis, due to the relative position of the variables along the first and second components (explaining 46,3% and 34.0% of the variability, respectively), Elevation and temperature-related variables are the main drivers of the difference between sites over precipitation-related variables. Considering that the selected sites have a relatively steep elevational gradient (about 500 m) and that elevation and temperature variables are usually negatively associated, these results are consistent. Additionally, the geographical area of the study does not exceed 170 km wide; hence, a low precipitation gradient is expected. Age is represented by a small vector, indicating that it explains less variability among the sites than the other variables, but it is still relevant. There is a large number of variables that present very high absolute correlations among themselves and therefore, the selected set seemed reasonable to describe the process.

The overall unbiased narrow-sense heritability estimates for MAI-H, MAI-DBH, and PP across all sites are 0.41, 0.16, and 0.35, respectively. These results are similar to the heritability estimates previously reported by Ratcliffe et al. (2014) and Lstibůrek et al. (2020).

Interesting genetic correlations were found, ranging from −0.87 to 0.99, with some sites having positive strong correlations (greater than0.6), others lower, and finally some negative ones. The former type of interaction is indicating a strong agreement in terms of genotype ranking among sites, the second is indicating a high GxE, while the latter is indicating a strong agreement in ranking but in opposite directions. The latter could be explained by genotypes showing some maladaptation to specific conditions; or, it could also be due to poor data quality on some sites. Both growth traits indicated the presence of mild to strong GxE among several sites, however, MAI-DBH also exhibited a high proportion of negative correlations (32.8%). One possible explanation could be that the negative values are connected to inter-tree competition that introduced additional noise into the model. Indeed, tree diameter is known to be strongly correlated to the surrounding tree density (Ledermann, 2010). For PP, most of the genetic correlations were high. These results are coherent since wood density is usually found less sensitive to GxE (Fukatsu et al., 2010; Škorpík et al., 2018; Wielinga et al., 2009).

The latent regression plots with the predicted site means were used to get insight into the relationship between the provenance and the environments represented by the loadings. A mild but significant correlation of the predictions with the first loading may be observed in MAI-H (Fig. 3A). This indicates that the genotypes have a similar expression along the environments clustered in the first loading, with moderate to low GxE. In contrast, a less clear pattern is visible along the second loading as well as in MAI-DBH and PP (Figs. S3 and S4). Interestingly, site B16 is showing, in a consistent way, the lowest values in terms of min, max, and mean values per site and in terms of predictions (Fig. 3, and S3; Table S4) in both MAI-H and MAI-DBH, indicating poor growing conditions for that specific site.

The latent regression plots with individual genotypes (Figs. 4, S5, and S6) are a useful tool to interpret patterns of genotypic expressions (GxE) for each trait. A wide range of responses are visible, and they indicate different adaptability levels. Interestingly, some genotypes are showing relatively constant breeding values across the studied environments indicating a stable performance. This is an important element to consider for making good breeding decisions. Indeed, stable genotypes associated with high breeding values are preferably selected in the forest industry, as planted superior seeds are expected to perform well across a wide range of environments/conditions.

In the presented methodology, based on FA to identify which EVs influence the genotypic performances across environments, it was necessary to correlate them against the loadings. For a better understanding of this methodology, when an EV is positively correlated with a loading, and this loading is positively correlated with the population predictions or a specific genotype, it is likely to be positively correlated with the population/genotype. However, if the EV is negatively correlated to the loading, then it is likely to be negatively correlated with the population/genotype. Similar reasoning is valid for other possible combinations.

For each trait, one or more loadings were found to be significantly and moderately to highly correlated with the environmental variables. For MAI-H, five EVs were correlated with the first loading. AvTmean and Biol7 (temperature annual range) were found to be positively correlated, indicating that temperature may influence MAI-H. As the first loading is positively correlated with the site means (Fig. 3), it suggests that an increase in temperature has a positive effect on growth. This result is congruent as it has already been widely reported in the literature (Carrer and Urbinati, 2006), though dendroclimatic analysis also revealed that seasonal temperature variation, such as high summer temperatures coupled with droughts, might have negative effects on radial growth (George et al., 2017; Koprowski, 2012) and might similarly affect height development. At the genotypic level however, we can see that a majority of individuals are more or less positively affected by temperature, while few of them revealed a decreasing trend (Fig. 4). This can be explained in several ways, for example, previous studies revealed significant genetic variation of drought reaction among as well as within larch populations (George et al., 2017; Schueler et al., 2021). Therefore, single

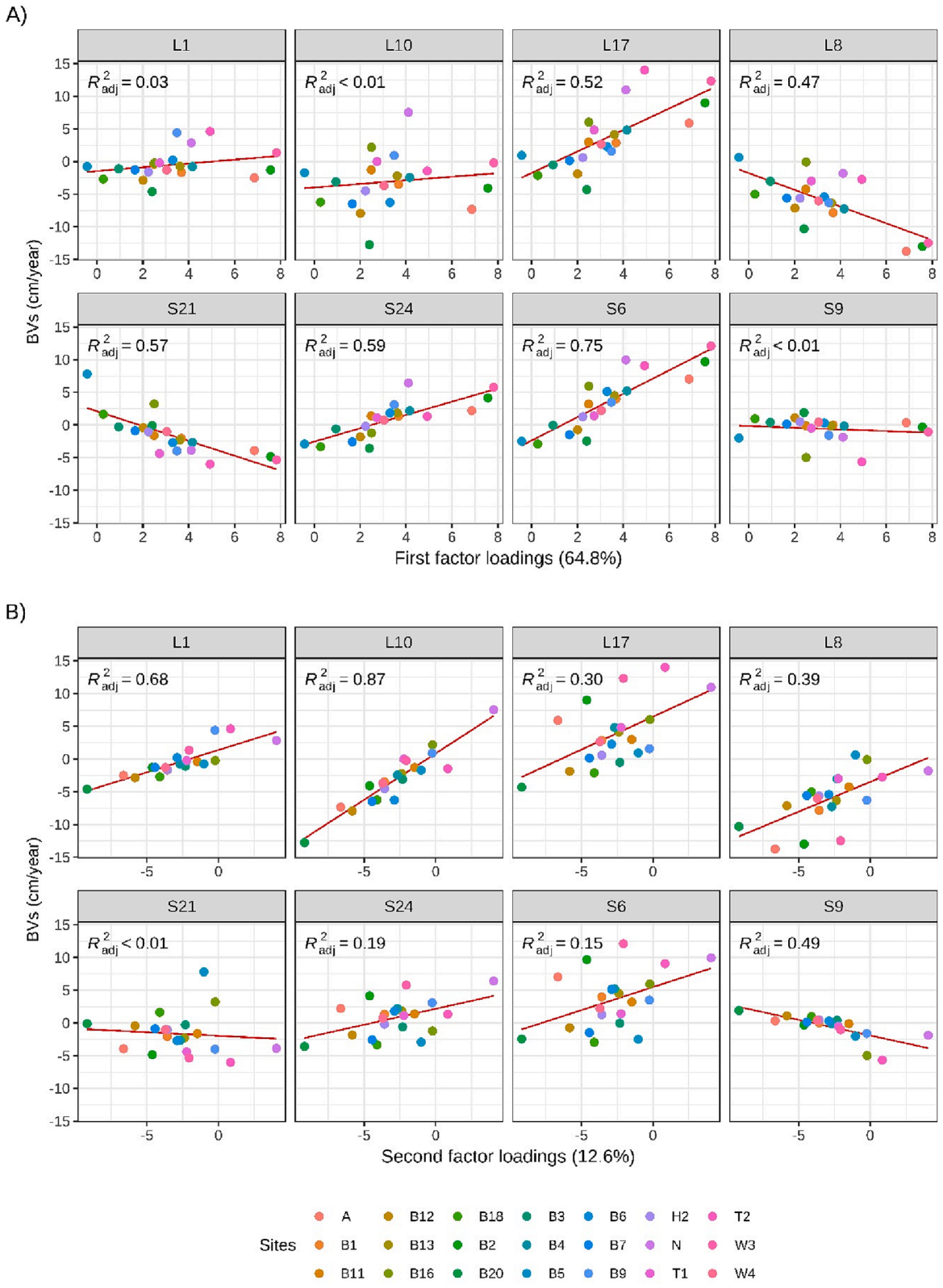

Fig. 4. Latent regression plots of the first (A) and second (B) factors of the FA2-MAI-H model with the breeding values of the eight parents with the most progenies. The linear regressions are represented by the red lines. R^2_{adj} is the adjusted coefficient of determination of the linear regression.

genotypes might show low resistance to higher temperatures, which are more likely connected to drought. Moreover, also genotype-specific differences in the phenological course of needle enfolding, early- and late-wood growth, and growth cessation might cause interactions with temperature or other EVs (George et al., 2019). Elevation is negatively correlated with the loading, however, as mentioned above, an increase in elevation is generally accompanied by a decrease in temperature indicating consistent results. The precipitation seasonality Bio15, which is calculated as the coefficient of variation of monthly precipitation revealed to be negatively correlated to the first loading. Therefore, a

Table 3
Pearson's correlation coefficients between the loadings of the first and second factors (*L1* and *L2*) of the FA2-MAI-H model and the EVs. *P* represents the significance of the correlation based on a significance level of 0.10.

EVs	L1	P	L2	P
Elevation	−0.48	**0.029**	−0.20	0.386
Age	−0.50	**0.022**	−0.03	0.891
Biol2	0.31	0.178	0.31	0.173
Biol3	0.11	0.649	0.30	0.193
Biol7	0.40	**0.071**	0.38	**0.091**
Biol15	−0.41	**0.064**	0.36	0.112
Tmean2	0.30	0.194	0.16	0.480
Tmin2	0.21	0.368	0.05	0.816
AvPrec	0.01	0.970	0.08	0.721
AvTmean	0.45	**0.043**	0.26	0.256

more unequal precipitation distribution around the year, including possible drought spells, might have a negative effect on growth. Noticeably, no correlations were found with AvPrec. Age is negatively correlated, and at the population level, it seems to indicate a negative correlation with tree height. This is quite interesting since age was accounted for by considering mean annual increment instead of cumulative height. However, the annual growth rate is known to reduce over time, and this was not corrected for in the model, so this could explain the relevance of age in these results.

For MAI-DBH (Table S5), only Biol2 is positively correlated with the first loading. It is a temperature-related variable that indicates the amplitude of the difference between the maximum and the minimum temperatures for each month. Its value increases with a greater amplitude.

In the case of the PP (Table S6), Elevation is positively correlated with the second loading. However, it is important to notice that the second loading explains only about 12% of the variability in the dataset so this correlation is not strongly supported by our results. Nonetheless, correlations between wood density and elevation have already been reported for many species (Chave et al., 2006; Topaloğlu et al., 2016; Zhang et al., 2022).

In contrast with Poupon et al. (2021), in this study, we used a complex modeling approach to provide further insight into this data. There is substantial documentation in the literature recognizing the superiority of FA modeling over traditional linear models for MET analysis (Beeck et al., 2010; Smith et al., 2001a, 2001b, 2015). Its flexible, yet complex structure, allowed for a powerful analysis of this messy and unbalanced dataset. Two factors explained, on average, 74% of the variability for each trait, and together with the narrow-sense heritability estimates, it indicates a successful description of the GxE dynamics for this population. Moreover, the latent regression plots (Figs. 4, S5, and S6) showed contrasting, yet strong, correlations between the loadings and the genotypes, emphasizing its explanatory power for GxE modeling and interpretation.

Understanding GxE in tree breeding is fundamental, as tree selection generally aims at reforestation activities across a wide range of landscapes and environmental conditions. Indeed, a high GxE, represented by genetic correlation values approaching zero, indicates an unstable ranking of genotypes across environments. Thus, a rigorous GxE analysis in MET enables increased accuracy and enhanced ability for optimal genotype selection. Additionally, in the event of future additional testing, sites sharing high correlations (for example the sites A, B1, B2, B11, and B13 for MAI-H) can be clustered together into a single breeding zone requiring less sampling and reduced testing effort. This, in turn, will enable to divert and optimize resources to, for example, obtain more data per site, or sample new sites, aiming at increasing the predictive power of the GxE modeling and selection.

As previously mentioned, stability across environments is an important factor in tree selection for breeding. However, in the context of climate change, the ability of trees to cope with different climatic conditions is becoming critical. We hypothesize that stable genotypes, and also genotypes performing increasingly well with conditions that are predicted to develop in the future, are more likely to show resistance (the ability of trees to resist external stress) and resilience (the ability of trees to rapidly return to their original state). However, both factors should be further investigated.

The use of the reconstructed pedigree in this study resulted in reasonable heritability estimates for the studied traits. Additionally, the analysis of the data, based on these additive relationships, successfully revealed clear and detailed response patterns at the genotypic level. Therefore, we recommend this, or similar, methodologies of pedigree reconstruction to be implemented in observational studies based on a sample of trees from several forest stands. The pedigree reconstruction used in this study has the additional advantage to facilitate the selection of outstanding genotypes in tree breeding. This has the potential to be financially superior and faster than the conventional forest breeding approach (Lstiburek et al., 2020).

The present study, due to a steep elevational gradient along the Northern Alps foothills, covers an interesting range of environments situated at the species' lowest elevations. Regarding CC, many studies have stated that the warmest parts of a species' distributional range are those more likely at greater risk to be negatively impacted (Schueler and Liesebach, 2014), highlighting the strength of this study. Nonetheless, it remains geographically limited as it covers only a small portion of the European larch range. We believe that identifying and sampling more distant sites, afforested using the same orchard, would be a good approach to extending the applicability of this study.

Concerning the data collection, the use of mature trees is an excellent source of information that seedlings from new sites cannot always provide. Furthermore, obtaining mature tree data of known parentage in a controlled study is a long and expensive process. The methodology used here allowed the use of standard reforestation material, originating from a typical seed orchard, which highly reduced the time and financial resources required. One disadvantage of this methodology is the unbalanced nature of the data and the lack of an experimental design, and while the flexible nature of the factor analytic structure provided interesting results, a reduction of the unbalance would likely provide more confidence in the results and increased precision. We expect that a larger number of stands and trees sampled from each stand would alleviate this issue.

Understanding the impact of EVs on the data was, in our opinion, quite successful. In this study, we had the opportunity to analyze the potential influence of multiple temperature and precipitation variables, as well as elevation, at the same time. Several of them were found to be significantly (moderately to highly) correlated with the different traits under study. However, one way to increase our understanding of the dataset in further analysis would be to include other types of variables and indicators, such as soil composition and structure, sun exposition levels, slope, aspect and steepness, and homogeneity of the stands, to name a few (Manzanedo et al., 2018; Soong et al., 2020; Van Sundert et al., 2018).

In the framework of CC, we believe that this approach can be a useful tool for assisted migration as it can help understand the GxE within a population of interest and infer which EVs are influencing the genotypes' response and how. Additionally, we believe that it is possible to hypothesize how a genotype will behave across the environments clustered in the factor loadings beyond the studied range of environments. This can facilitate the selection of specific genotypes that are adapted to a current environment and its predicted future climate or that show reasonable plasticity to perform well in a range of conditions. Considering that commercial forest stands are traditionally established within the same seed zone (White et al., 2007), to study and exploit assisted migration in the future, we emphasize the need to select stands situated at the edge of the predicted future environmental conditions. It is also possible to perform the FA analysis described here using data from traditional breeding trials or studies established specifically to evaluate

assisted migration.

5. Conclusion

In this study, we aimed to understand the dynamics of European Larch's response to a range of environmental conditions. We used data from 1253 trees planted across 21 sites that were afforested using the seeds of a seed orchard that was established using a single seed zone. The trees' height, diameter at breast height, and wood density, together with their previously reconstructed pedigree, were used to perform multi-environmental trial analyses fitting a factor analytical structure. For each trait, our results indicated typical heritability estimates for European larch. Varying genetic correlations between sites were found, with growth traits generally showing stronger GxE than wood density. Additionally, our results showed that height is positively influenced by higher average monthly mean temperatures, temperature annual range, and balanced yearly precipitation while being negatively affected by elevation. For diameter at breast height and wood density, our conclusions are more limited, nonetheless, our results indicated that the mean diurnal range for the former and elevation for the latter explain a good portion of the variability. Interestingly, highly variable responses to the environment were found between the genotypes for each trait. Based on our results, we believe that this kind of study can be used to successfully understand tree species' complex response to their environment and to aid tree breeding programs for the selection of suitable genotypes adapted to specific conditions. The selected genotypes can be used within traditional reforestation projects, but also, in the framework of a changing climate, for assisted migration.

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CRediT authorship contribution statement

Valérie Poupon: Investigation, Formal analysis, Writing – original draft, Visualization. **Salvador A. Gezan:** Conceptualization, Methodology, Validation, Investigation, Writing – review & editing, Formal analysis, Supervision. **Silvio Schueler:** Investigation, Writing – review & editing, Resources. **Milan Lstibůrek:** Investigation, Writing – review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2023.121259.

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