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Within and between population phenotypic variation in growth vigor and sensitivity to drought stress in five temperate tree species

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ABSTRACT

Within-population variation in individual tree growth and response to climate has an impact on forest dynamics, resilience and adaptation to environmental change.

Combining dendrochronological analyses with a process-based ecophysiological model simulating drought stress at the stand scale, we studied the phenotypic variation of two growth-related traits within 22 pure stands of five contrasted tree species sampled in the RENECOFOR network over a wide range of ecological conditions. First, we computed the annual stress level from soil, climate and stand inventory data. Second, we computed individual sensitivity as the quantitative growth response to drought stress level and individual vigor as the capacity to grow in favorable years relative to an average stand-level growth model. We analyzed within-population variation and covariation of individual vigor and sensitivity, their temporal changes during stand development, as well as the effect of environmental conditions on population-level means, variances and correlation.

Our results show that within-population variances in sensitivity and vigor exceed the between-population variances for all species. The populations located in more stressful environments, i.e., low summer precipitation and extractable soil water, showed lower mean and variance of sensitivity, suggesting possible multiscale adaptation at the population level and within populations. None of the environmental factors considered had an effect on the average population vigor or on the within-population variance of vigor. We found a general positive correlation between individual growth sensitivity and vigor in 17 out of 22 populations, potentially revealing a growth performance trade-off. The correlation was more pronounced in low extractable soil water environments, which may be related to a need for stressful conditions to reveal the trade-off or be the consequence of adaptive processes, i.e., acclimation and selection.

If high within-population stand phenotypic variation in growth traits contributes to the resilience and adaptive capacity of forests to climate change, a trade-off could represent a constraint on selection. We provide genetic and environmental arguments supporting the hypothesis of a trade-off, then we highlight the importance of integrating it into the management process, especially during selective thinning, to avoid indirectly increasing population sensitivity by selecting the most vigorous trees.

1. Introduction

Climate change is associated with increasing drought stress in all forest biomes around the world (Allen et al., 2010; Choat et al., 2012; Allen et al., 2015), with a potentially major impact on their role as carbon sinks (Ma et al., 2012; Anderegg et al., 2015). Drought stress reduces tree growth (Lempereur et al., 2015) and photosynthesis (Cornic & Massacci 1996), and when drought is intense and/or long, drought stress can cause hydraulic failures and lead to defoliation and tree death (Brodribb & Cochard 2009). Tree rings analysis is a widely recognized

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approach to assess the effect of climate on tree growth (Fritts, 1971, Cook, 1985, Giguère-Croteau et al., 2019) and detect early-warning signs of mortality (Cailleret et al., 2019). Dendroecological approaches proved successful in investigating the impact of drought stress on the average radial growth of stands or cohorts and highlighting important variations in this impact with life history traits (DeSoto et al., 2020), social status (Mérian & Lebourgeois, 2011), stand structure and geographical location within the species distribution range (Camarero 2021). Moreover, introducing the interindividual variability in tree-ring–climate relationships allows for a more in-depth assessment of the effect of climate on stand growth that could improve the quality of ecological inferences (Carrer et al., 2011).

Within-population interindividual phenotypic variation of growth results from the combination of extrinsic factors, such as resource availability and competition, and intrinsic factors, such as genotype, acclimation, microsite, age, size and social status (Aranda et al., 2010; Corcuera et al., 2011). In the context of climate change, two growth traits are useful to distinguish: the sensitivity to drought stress, i.e. the response of tree growth to stress level, and the growth potential, hereinafter referred to as vigor. Sensitivity and vigor both contribute to tree size and therefore to competitive and possibly reproductive performances. In comparison to the precisely defined drought sensitivity and its extensive use in ecophysiological and dendrometrical studies, vigor has been defined more loosely and mainly used in applied genetic studies with little consideration of stand dynamics effects. Within-population variation and covariation of individual vigor and sensitivity to drought are factors of resilience in the face of climate change. Phenotypic variations in drought tolerance may buffer the short-term impacts of drought on the ecological functions of forests (Bréda et al., 2006; Aitken et al., 2008; Grady et al., 2011; Alfaro et al., 2014). In the long term, within-population variance and correlations of growth traits determine their take on selection and the evolutionary potential of populations. On different time scales, acclimation and selection are likely to jointly influence the sensitivity and vigor of the populations as well as the phenotypic variation, with both processes being subject to local environmental constraints. Previous works revealed the genetic basis of within-population variation for sensitivity to climate (Liepe 2014; Bansal et al., 2015; Depardieu et al., 2020).

Among tree populations, a genetic trade-off between vigor and sensitivity to climate has been reported in multisite common garden experiments: those populations that grow better in favorable sites generally grow less than others in stressful conditions (e.g., *Pinus contorta* and *P. sylvestris* in Rehfeldt et al., 2001; 2002). The genetic component of this trade-off may result from a balancing selection process for contrasting ecological strategies, such as a water economy strategy in which plants maintain low growth rates and low rates of gas exchange during droughts or a water uptake strategy in which plants have more rapid instant growth through higher rates of gas exchange when water is available, allowing them to complete important biological functions before drought onset (Arntz & Delph 2001). At the within-population scale, a phenotypic trade-off between vigor and sensitivity was observed in *Abies alba* by Nourtier et al., (2014) and in *Cedrus atlantica* by Fallour-Rubio et al., (2009). In a *Fagus sylvatica* population facing summer droughts, Bontemps et al., (2017) observed phenotypic trade-offs in the phenology, growth dynamics and anatomy among trees related to vigor and sensitivity. This trade-off can be due to environmental variability: individuals with higher water resources are expected to be more vigorous but also more sensitive to drought stress (Nourtier et al., 2014; Cailleret et al., 2019). Within-population trade-offs may also be under genetic control, which could explain the changes in correlation observed between cohorts within a single *Cedrus atlantica* forest (Fallour-Rubio et al., 2009).

Ring width data provide repeated growth measures over time, i.e., under different climates, of the trees that survived competition and hazards until sampling. Hence, they are very valuable data for disentangling individuals from environmental effects on growth vigor and sensitivity *in situ*, which can be achieved by using an individual-based growth analysis model that explicitly considers the factors of tree age, size, social status, the overall site environment and an individual random effect that captures the genetic and microsite effects (Fallour-Rubio et al., 2009). Additionally, tree growth vigor and sensitivity to drought stress need to be considered dynamic phenotypic traits (Peltier & Ogle, 2020). Indeed, these traits are driven not only by static factors such as tree genotype or microsite conditions but also by dynamically changing factors such as tree age, size and social status (Cook, 1985; Trouvé et al., 2014; Perin et al., 2017; Forrester, 2019; Peltier & Ogle 2020; Mašek et al., 2021). These individual features may change drastically over the potential long lifespan of trees in relation to stand development and forest management. To our knowledge, however, no study to date has combined a growth analysis model at the tree scale with a dynamic perspective of vigor and sensitivity.

Another challenge when investigating tree growth sensitivity to environmental stress is to qualify and quantify the stress level. Some approaches, such as the resistance, recovery and resilience indices proposed by Lloret et al., (2011), bypass the quantitative level of stress and focus on the temporal sequence of growth variation. In this way, Depardieu et al., (2020) estimated within-population genetic variation in Lloret indices based on common garden experiments. However, in natural stands, this approach raises the question of comparability between individuals, sites and species, since the observed response is specific to a given water stress level in a given background stress, both of which are often not measured (Schwarz et al., 2020). Other dendroecological studies explicitly consider the individual pedoclimatic variables driving intra- and interannual variation in tree growth (e.g., Fritts, 1971, Mérian et al., 2011). As it can be challenging to generalize the relation between tree-ring widths and any single pedoclimatic variable, another related approach consists of using synthetic drought indices, such as the Palmer drought severity index or standardized precipitation evapotranspiration index (PDSI: Palmer, 1965; SPEI: Vicente-Serrano et al., 2010). Such indices precisely account for the environmental factors of stress but are irrespective of the physiological reaction of the plant and neglect the crucial importance of soil properties, stand density and species functional traits, which may either amplify or buffer drought stress. In other words, they may not appropriately inform the effective intensity and duration of drought stress (Zang et al., 2020).

In this study, we combined dendrochronological analyses with an ecophysiological process-based model assessing the drought stress level and an individual-based growth model to investigate the phenotypic variation in growth sensitivity and vigor. We took advantage of the RENECOFOR dataset, an extensive tree-ring dataset that includes 61 pure stands of five temperate tree species, i.e., *Fagus sylvatica*, *Pseudotsuga menziesii*, *Pinus pinaster*, *Quercus petraea* and *Quercus ro*bur, sampled over a wide range of ecological conditions, thus covering a broad range of climate–growth relationships that have been shown to vary among species, stands and social cohorts (Lebourgeois et al., 2005, Lebourgeois et al., 2010, Mérian et al., 2011; Mérian & Lebourgeois, 2011; Guillemot et al., 2015). More specifically, in this study, we sought (1) to quantify the variance of growth sensitivity and vigor within forest tree populations, (2) to assess the correlation between these traits and, in particular, test for a possible trade-off, (3) to characterize the temporal dynamics of variances and correlation within populations, and (4) to identify pedoclimatic environmental factors that explain differences in variances, correlation, and average values of growth sensitivity and vigor among populations.

Here, we defined individual vigor as the growth performance in favorable years, and sensitivity as the reaction norm of growth to stress level. For both traits, we sought to capture an individual effect independent of cofactors such as age or size. We hypothesize that genetic and micro-environmental factors may jointly contribute to the observed variation in sensitivity and vigor at the individual tree level. We consider that phenotypic variation and covariation of growth sensitivity to drought and vigor directly influence forest stand dynamics and forest management choices and, therefore, interfere with selection through size-dependent reproductive success (Greene & Johnson, 1994; Burczyk et al., 1996), growth and survival (Caspersen et al., 2011; Bennett et al., 2015).

2. Material and methods

2.1. Study area and species

Our study is based on the French permanent plot network for the monitoring of forest ecosystems (RENECOFOR, part of the ICP Forests Level II network, Lorenz 1995). We focused here on five contrasted species (i.e., contrasted autecology, gymnosperm *vs* angiosperm, shade tolerant *vs* intolerant, high *vs* low growth rate) sampled in 61 forest tree populations managed in pure and even-aged stands: *Fagus sylvatica L.* ($n = 20$ populations), *Pseudotsuga menziesii (Mirb.) Franco* ($n = 6$), *Pinus pinaster Aiton* ($n = 7$), *Quercus petraea (Matt.) Liebl.* ($n = 19$) and *Quercus ro*bur L. ($n = 9$). Together, the five temperate species represent 43 % of the French standing volume (IGN, 2021). The 61 populations were located between 41°45′08′’ and 50°10′16′’N and between 3°32′34′’ and 9°12′23′’W (Fig. 1) and covered a wide range of bioclimatic conditions: oceanic ($n = 15$ populations), semi-continental ($n = 35$), Mediterranean ($n = 2$) and mountainous ($n = 11$).

Over the 1959–1994 period, the mean annual precipitation varied from 647 to 1441 mm per year among populations. The mean minimum and the mean maximum temperature ranged from 4.2 °C to 10.1 °C and 9.6 °C to 17.3 °C, respectively. The elevation ranged from 5 to 1400 m above sea level, and the slope ranged from 0 to 55 %. The populations sampled above an altitude of 500 m ($n = 13$) were mainly *F. sylvatica* and *P. menziesii*. Conversely, *P. pinaster*, *Q. ro*bur, and *Q. petraea* were mostly sampled on plains. We computed the extractable soil water for trees (*ESW*) as follows:

$$ESW = D(1 - C)(\theta fc - \theta wilt) \quad (1)$$

where D is soil depth, C is the coarse element percentage, $\theta wilt$ is humidity at the wilting point and θfc is humidity at field capacity assessed using soil texture data (Baize & Jabiol 1995; Supp. Table 1). The *ESW* computed over the entire soil profile ranged from 19 to 351 mm among populations.

2.2. Selected trees, ring-width measurements and analysis

We used tree coring data obtained in 1995 by Lebourgeois et al., (1997). Briefly, within each population, 23 to 30 dominant and codominant trees were cored at breast height as close as possible to the pith with an increment borer. Ring widths were measured with a stereomicroscope connected to a microcomputer and the tree ring program SAISIE (Becker, 1989) to the nearest 0.01 mm. Then, the individual ring width series were cross-dated by detecting regional pointer years and checked for erroneous dating (Lebourgeois et al., 2005).

Tree-ring widths generally show a pronounced trend to change with tree size and age as well as with stand structure and competition (Trouvé et al., 2014; Perin et al., 2017). In this study, to disentangle the effect of climate on radial growth from the effect of other factors unrelated to climate, we standardized the individual radial growth series using a 30-year cubic smoothing spline with a 50 % frequency response cutoff (Cook & Peters, 1981; Mérian & Lebourgeois, 2011). The transformation from the original ring width to the ring width index (*RWI*) was as follows:

$$RWI = W_{original}/W_{trend} \quad (2)$$

where $W_{original}$ is the original tree ring width and W_{trend} is the ring width

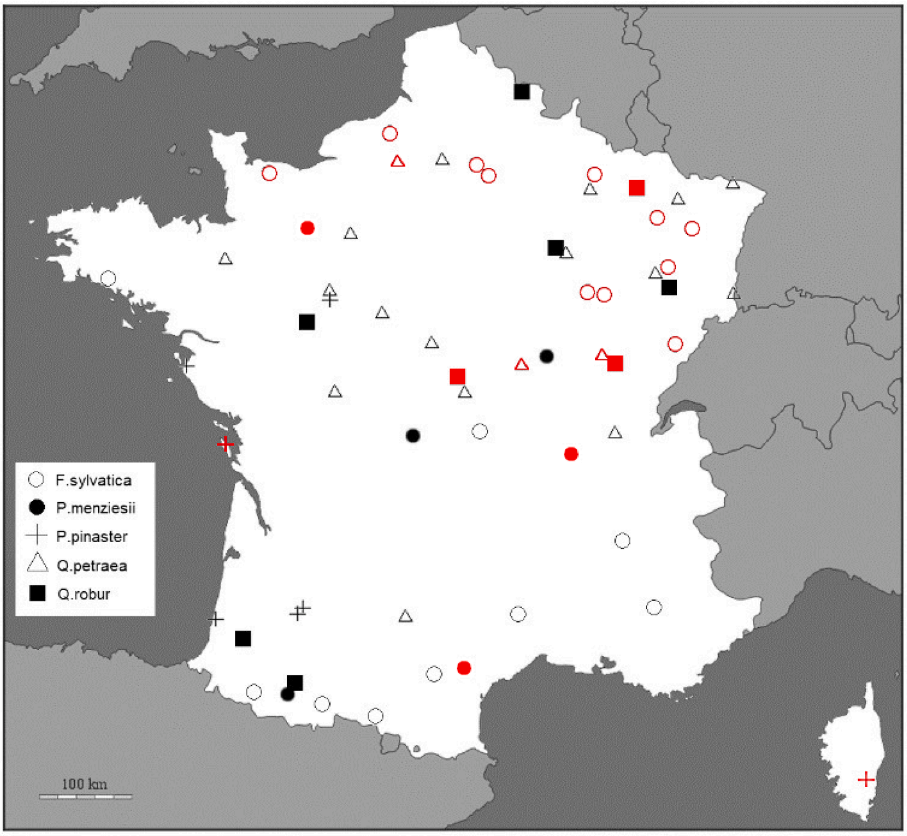

Fig. 1. Geographical position of the 61 forest tree populations in the RENECOFOR network (ICP Forests Level II network) for the five species studied. The 22 populations selected for analysis are in red (see 2.4. Selection of populations and temporal intervals for analyses).

trend unrelated to climate identified by the spline function. The standardized individual series were averaged using a bi-weighted robust mean to create stand tree-ring chronologies (Cook & Peters 1981).

All core data processing was undertaken using the Dendrochronology Program Library (dplR; Bunn, 2008) in R version 3.6.2 (R Development Core Team, 2019).

2.3. *Simulation of the edaphic drought stress level*

An appropriate approach to quantify water stress is key for any type of growth responses analysis as the drought index choice may strongly influence the results (Van Loon et al. 2016). Raw climate data, as well as the PDSI or SPEI index, are valuable indicators for the study of drought on large scales but do not capture the intensity and duration of site-specific soil water deficits (Zang et al. 2020). For these reasons, we opted for an ecophysiological approach and exhaustivity quantified water reserves and flux within each plot.

We used an ecophysiological process-based model (CASTANEA, Dufrêne et al., 2005; Davi & Cailleret 2017) to simulate the annual drought stress level relative to the soil water content experienced by trees (*StressLvl*). We set the soil forcing variables (soil depth, texture, coarse element percentage) using the plot soil values available in the RENECOFOR dataset. We extracted the daily local climatic variables (minimum, average and maximum temperatures; precipitation; wind speed; average relative humidity; global radiation) from the objective analysis module SAFRAN (Durand et al., 1993; Vidal et al., 2010) using the closest grid points to the sampled populations (8 km grid resolution, data available from 1959 to 2019). We initialized the dendrometric variables, i.e., the number of trees per hectare (*Nha*) and the mean diameter at breast height (*DBH*), using the stand dendrometric values available in the RENECOFOR dataset. The parameters used for the simulations and their values are given per species in Supplementary Table 2.

We computed daily soil water content based on supply and demand dynamics applied to soil moisture and as a function of soil forcing variables. Campbell's soil water retention equation (Campbell, 1974) was used to predict the soil water potential (Ψ_{soil}) at a given volumetric water content (θ) anchored at the saturated volumetric water content (θ_{sat}) as:

$$\Psi_{soil} = \Psi_e \left(\frac{\theta}{\theta_{sat}}\right)^{-b} \tag{3}$$

where Ψ_e is the air-entry matric potential and b is the soil water retention parameter. Ψ_e, b and θ_{sat} are strongly dependent on soil texture, and we assessed their local values using soil texture data (Bonan, 2019; Supp. Table 1).

Then, we used CASTANEA to integrate the annual soil water balance (Dufrêne et al., 2005) in the form of a drought stress level indicator (*StressLvl*) computed as a Palmer index measured in MPa (Palmer, 1965):

$$StressLvl = \sum_{d=1}^{365} \Psi_{soil} \tag{4}$$

where Ψ_{soil} is the daily soil water potential of day d.

Thus, *StressLvl* integrates both the duration and intensity of the annual water deficit. Subsequently, we used the *StressLvl* time series simulated with CASTANEA to characterize the interannual variation in drought stress in each studied population.

2.4. *Selection of populations and temporal intervals for analyses*

To study the temporal dynamics of growth sensitivity and vigor, we defined 21-year moving intervals slipped by one year. The 21-year period represented a compromise between the temporal resolution required to reveal variations in growth performance and the minimum number of years required to observe sufficient annual variation in *StressLvl* and growth. Here, we eliminated populations whose tree-ring time series was less than the interval length of 21 years. The youngest selected populations show only a few temporal intervals.

The growth response to drought stress may be masked by other biotic, abiotic or anthropogenic disturbance factors. These factors may differ among species and populations, making it difficult to disentangle and quantify *a posteriori* (Galván et al., 2014). For these reasons, we carried out a double selection of populations and temporal intervals and retained only populations and intervals for which the growth response to drought stress was directly observable. To do so, we selected populations with a significant simple correlation between stand tree-ring chronology and *StressLvl* over the whole period of observation ($p < 0.05$) and the temporal intervals of these populations with a significant simple correlation between stand tree-ring chronology and *StressLvl* ($p < 0.05$). For some populations ($n = 14$), the correlation between *RWI* and *StressLvl* was not significant overall but significant for some temporal intervals; we still eliminated them. This selection process also led us to discard populations and intervals with low interannual drought stress variability or for which water was not a factor limiting growth.

Among the 61 initial populations, 22 met the selection criteria and were used for the analyses (Fig. 1): 11*F. sylvatica* populations (55 %), 3*P. menziesii* (50 %), 2*P. pinaster* (29 %), 3 *Q. robur* (33 %) and 3 *Q. petraea* (16 %). The geographical position of the 22 selected populations is highlighted in Fig. 1. The climatic and pedological ranges of the selected populations were close to those of the initial group: mean annual rainfall ranged from 686 to 1422 mm among selected populations; mean minimum and mean maximum temperature ranged from 5.6 °C to 10.1 °C and 11.9 °C to 16.4 °C, respectively; and extractable soil water for trees ranged from 19 to 275 mm (Supp. Table 3). The average population age in the selected temporal intervals varied between 13 and 183 (Supp. Table 3), which provided a contrasting population panel to analyze the variation of the studied traits.

2.5. *Growth sensitivity to drought stress and vigor*

We first estimated individual growth sensitivity and vigor within each selected temporal interval and then computed mean values over the selected intervals both at the individual tree level within each population and at the population level.

2.5.1. *Sensitivity estimation*

For each tree of each population and at each selected temporal interval T, we computed the regression coefficient between the ring width index (*RWI*) and *StressLvl* simulated with CASTANEA as a quantitative estimate of individual growth sensitivity to drought stress. We used the following linear model to estimate individual sensitivity within each selected temporal interval T (*TSensi*):

$$RWI_{i,n} = \beta + TSensi_i \times StressLvl_n + \varepsilon_{i,n} \tag{5}$$

where β is the intercept, *TSensi* is the temporal growth sensitivity to drought stress, *StressLvl* is the annual drought stress simulated by the process-based model, and ε is the between-year growth residual. Subscripts i and n denote the individual and the year considered, respectively.

2.5.2. *Vigor estimation*

We computed individual vigor on a subset of the data corresponding to the three years of lowest *StressLvl* within each selected 21-years interval, as follows.

For pure even-aged stands, growth models, in which annual growth is a function of DBH, had been developed for *F. sylvatica* (Dhôte 1991; Dhôte & Le Moguedec 2012), *Quercus* sp. (Dhôte & Le Moguedec 2012; Trouvé et al., 2014), *P. menziesii* (Deleuze et al., 2004; Trouvé et al., 2014; Perin et al., 2017) and *P. pinaster* (Najar et al., 1999). In these empirical models, the relationship between DBH and radial growth dynamically evolves with stand structure. Here, for each of the three years, we assumed a linear relation of radial growth to DBH, and we defined individual vigor as the deviation from this average growth model, so vigor is independent of initial tree size. The populations of the RENECOFOR network are, for the most part, managed in even-aged stands (Mérian & Lebourgeois, 2011). However, few ones are likely to deviate from even-aged structure. Therefore, we systematically added age as an explanatory factor in the model. Thus, we analyzed the 3-year subdataset within each interval with the following model:

$$Woriginal_{i,n} = \beta + \tau_n + DBH + \tau_n : DBH + Age_i + TVig_i + \varepsilon_{i,n} \quad (6)$$

where $Woriginal_{i,n}$ is the original ring width of tree *i* in year *n*, β is the intercept, τ_n is the effect of year *n* on growth, *DBH* is the effect of DBH, $\tau_n : DBH$ is the interaction between DBH and year, Age_i is the average age of tree *i* in the considered interval, $TVig_i$ is the temporal vigor of tree *i* in the considered interval, and $\varepsilon_{i,n}$ is the residual variation for the *i*th tree in the *n*th year. We used individual overbark DBH of year *n* (see Perin et al., 2017), computed from the cumulative ring widths from the inside out until year *n*. For the few populations deviating from even-aged, collinearity is possible between *DBH* and *Age*, but it does not affect the estimation of vigor.

2.5.3. Sensitivity and vigor: From dynamic variables to intrinsic individual and average population values

To characterize each individual by unique values, we computed the individual intrinsic growth sensitivity (*ISensi*) and vigor (*IVig*) for each individual of each population as the mean of its sensitivity and vigor values over the selected intervals. We computed the average population sensitivity (*μSensi*) by averaging the intrinsic sensitivity of individuals and the average population vigor (*μVig*) by averaging individual growth in favorable years. In addition, based on the average population sensitivity and vigor, we computed the between-population variances for each species and over all species as references to which we compared the within-population variances. Finally, to quantify the correlation between growth sensitivity and vigor, we computed the Pearson correlation coefficient between intrinsic vigor (*IVig*) and sensitivity (*ISensi*) for each population and between temporal dynamic growth sensitivity (*TSensi*) and vigor (*TVig*) for each interval. Table 1 lists all the growth variables and their associated variances and correlations.

2.6. Statistical analysis between populations

We used mixed models to study the overall effects of local environmental conditions (climate and soil) and average population age across species and sites on population means, variances and correlations between growth sensitivity and vigor. For each of these variables, we built a model with 1959–1994 average summer precipitation and maximum temperature (in June, July, and August), extractable soil water and average population age in the selected intervals as explanatory variables. We added the species as a random cofactor in the model. The retained models were:

$$Y_p = \beta + Pr_p + Tmax_p + ESW_p + age_p + sp_p + \varepsilon_p \quad (7)$$

where *Y* successively corresponds to *μSensi*, *var (ISensi)*, *var (IVig)* and *r (IVig, ISensi)*; β is the intercept; *Pr* and *Tmax* are the 1959–1994 average summer precipitation and maximum temperature, respectively; *ESW* is the extractable soil water; *age* is the average population age in the selected intervals; *sp* is the species random cofactor; and ε is the between-population *Y* residual. Subscript *p* denotes the population. Specifically, for the average population vigor (*μVig*), we added tree density (*Nha*, a proxy for competition; Supp. Table 3) as explanatory variables since growth is largely dependent on competition level:

$$\mu Vig_p = \beta + Pr_p + Tmax_p + ESW_p + Nha_p + age_p + sp_p + \varepsilon_p \quad (8)$$

We performed all statistical analyses using R version 3.6.2 (R Development Core Team, 2019).

Table 1
Glossary of the growth variables and associated variances and covariances analyzed in this study.

Full Name	Code	Unit	Description
Temporal vigor	*TVig*	cm	A temporal dynamic variable quantifying the specific ability of a tree to grow in favorable years relative to an average growth model
Intrinsic vigor	*IVig*	cm	The averaged value of *TVig* over temporal intervals
Average population vigor	*μVig*	cm	The average growth of populations during favorable years
Variance of temporal vigor	*var (TVig)*	cm^2	The variance of temporal vigor
Within-population variance of vigor	*var (IVig)*	cm^2	The variance of intrinsic vigor
Within-species between-population variance of vigor	*var (μVig| sp)*	cm^2	The within-species variance of average population vigor
Between-population variance of vigor	*var (μVig)*	cm^2	The total variance of average population vigor over all species
Temporal sensitivity	*TSensi*	MPa^{-1}	A temporal dynamic variable quantifying the specific response of a tree's growth to drought stress level
Intrinsic sensitivity	*ISensi*	MPa^{-1}	The averaged value of *TSensi* over temporal intervals
Average population sensitivity	*μSensi*	MPa^{-1}	The average population sensitivity obtained by averaging the individual intrinsic sensitivities
Variance of temporal sensitivity	*var (TSensi)*	MPa^{-2}	The variance of temporal sensitivity
Within-population variance of sensitivity	*var (ISensi)*	MPa^{-2}	The variance of intrinsic sensitivity
Within-species between-population variance of sensitivity	*var (μSensi| sp)*	MPa^{-2}	The within-species variance of average population sensitivity
Between-population variance of sensitivity	*var (μSensi)*	MPa^{-2}	The total variance of average population sensitivity over all species
Correlation between temporal sensitivity and vigor	*r (TVig, TSensi)*	–	The Pearson correlation coefficient between temporal vigor and temporal sensitivity
Within-population correlation between sensitivity and vigor	*r (IVig, ISensi)*	–	The Pearson correlation coefficient between intrinsic vigor and intrinsic sensitivity

3. Results

3.1. Within-population variations in growth sensitivity and vigor

Within each species, within-population variance of sensitivity (resp. vigor) represents on average 520 % (resp. 376 %) of the between-population variance. Considering all species together, the mean within-population variance of sensitivity (resp. vigor) represents 47 % (resp. 17 %) of the between-population variance over all populations from all species (detailed variances are given in Supp. Table 4). These results indicate that most of the phenotypic variation in vigor and sensitivity to drought stress is within populations.

Among the twenty-two populations, the correlation between intrinsic sensitivity and vigor was significantly positive in ten populations at threshold $p < 0.05$ and in three populations at threshold $p < 0.1$, which included 7*F. sylvatica* populations (64 %), 2*P. menziesii* (67 %), 1*P. pinaster* (50 %), 2 *Q. robur* (67 %), and 1 *Q. petraea* (33 %) (Fig. 2 for *P. menziesii* and Supp. Fig. 1 for the other species). In these 13 populations, individual trees with better vigor showed higher growth sensitivity to drought stress. No significant negative correlation was observed. It should be noted that some trees, for the most part the less

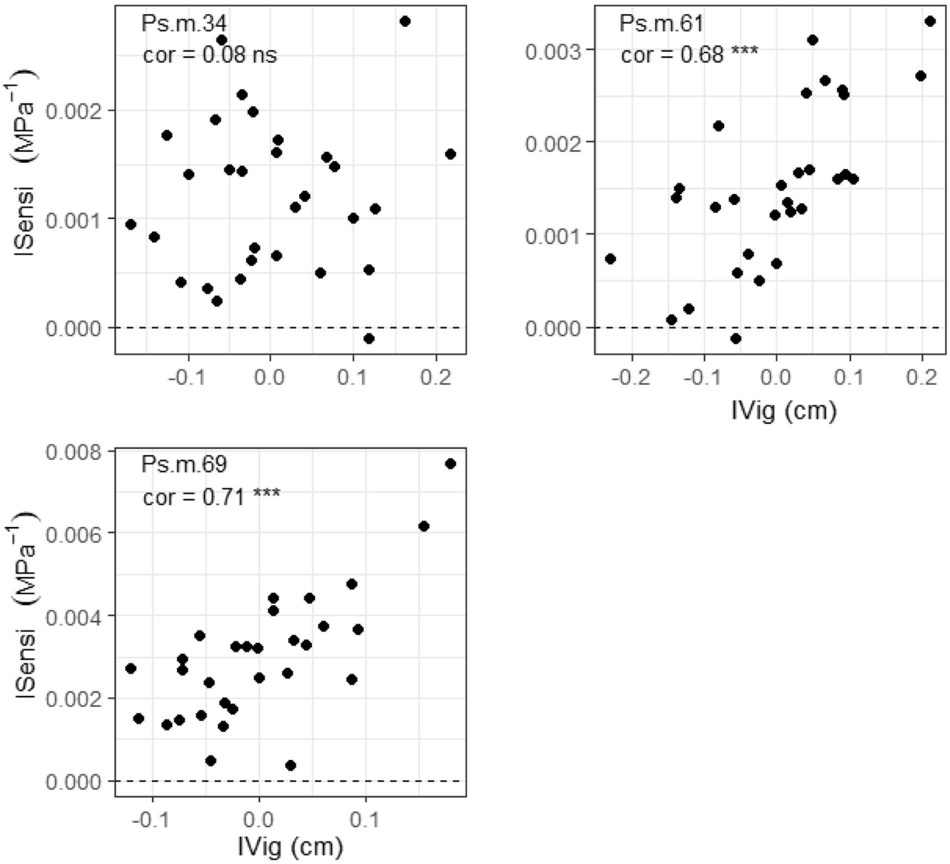

Fig. 2. Correlation between intrinsic sensitivity (*ISensi*) and intrinsic vigor (*IVig*) in the three *P. menziesii* populations (Ps.m 34, Ps.m 61 and Ps.m 69). Each point represents an individual tree. The correlation was significantly positive in two of the three populations (Ps.m 61 and Ps.m 69). The significance level is indicated on the graphs by '***' at $p < 0.001$, '**' at $p < 0.01$, '*' at $p < 0.05$, '.' at $p < 0.1$ and 'ns' above. The dotted lines indicate zero sensitivity. Note that some trees were insensitive, i.e., $ISensi \leq 0$.

vigorous ones, were insensitive to drought stress, i.e., $ISensi \leq 0$.

We observed a temporal variation in the variance of sensitivity and vigor: the temporal variations within populations did not overcome the largest differences between contrasted populations and did not show a clear common pattern among populations or species (Fig. 3a,b for *P. menziesii* and Supp. Fig. 2 for the other species). The value and significance of the correlation coefficients between growth sensitivity (*TSensi*) and vigor (*TVig*) also varied among temporal intervals without a clear pattern (Fig. 3c). Nevertheless, the correlation was positive for most populations and intervals (Fig. 3c for *P. menziesii* and Supp. Fig. 2 for the other species). We found at least one significant positive correlation between temporal sensitivity and vigor within 17 of the 22 selected populations and no significant negative correlation. We observed this correlation in populations at the juvenile stage (e.g., <15 years in Ps.m 69) as well as in largely mature populations (e.g., >180 years in Q.r 55).

3.2. Effect of environmental conditions of the populations on the variations in sensitivity and vigor

Over the entire period from 1959 to 1994, the different populations showed high contrasts in the environmental factors driving water deficits: average summer precipitation (*Pr*) ranged from 116 to 347 mm, average summer maximum temperature (*Tmax*) ranged from 19 to 24 °C, and extractable soil water ranged (*ESW*) from 19 to 275 mm (Supp. Table 3). It should be noted that the range of water conditions varied between species with some overlap: *ESW* varied significantly between species unlike *Pr* and *Tmax*.

Regarding sensitivity to drought stress, summer precipitation (*Pr*; $p < 0.001$) and extractable soil water (*ESW*; $p = 0.009$) had a positive effect on the average population sensitivity ($\mu Sensi$), while maximum summer temperature (*Tmax*) and average population age (*age*) had no significant effect (Table 2a; Supp. Fig. 3a,b). The overall model had a marginal R^2 value of 0.56. In addition, summer precipitation (*Pr*; $p < 0.001$) had a positive effect on within-population variance of sensitivity (*var (ISensi)*), while extractable soil water (*ESW*), maximum summer temperature (*Tmax*) and average population age (*age*) had no significant effect (Table 2b; Supp. Fig. 3c). The overall model had a marginal R^2 value of 0.56. To summarize, the average population value and the within-population variance of sensitivity to drought stress decreased with greater water constraints.

Regarding vigor, no factor had a significant effect on either average population vigor (μVig) or on the within-population variance of vigor (*var (IVig)*) (Table 2c,d).

Regarding the sensitivity–vigor correlation, extractable soil water (*ESW*; $p = 0.012$) had a negative effect on the within-population correlation between sensitivity and vigor (*r (IVig, ISensi)*), while maximum summer precipitation (*Pr*), summer temperature (*Tmax*) and average population age had no significant effects (Fig. 4; Table 2e). The overall model had a marginal R^2 value of 0.24. These results indicate that environmental factors were a major determinant of the correlation between growth sensitivity to drought stress and vigor within populations.

4. Discussion

In this study, we quantified the variation and covariation of vigor and sensitivity to drought, as well as their temporal dynamics, both within and between 22 populations of five contrasting temperate species. We defined two growth variables at the individual tree level as a framework to disentangle the components of tree growth performance in environments with varying drought stress levels. We argue that these two individual growth variables can be considered new tree-ring based phenotypic traits (Housset et al., 2018).

Our results are based on a subset of the RENECOFOR dataset for

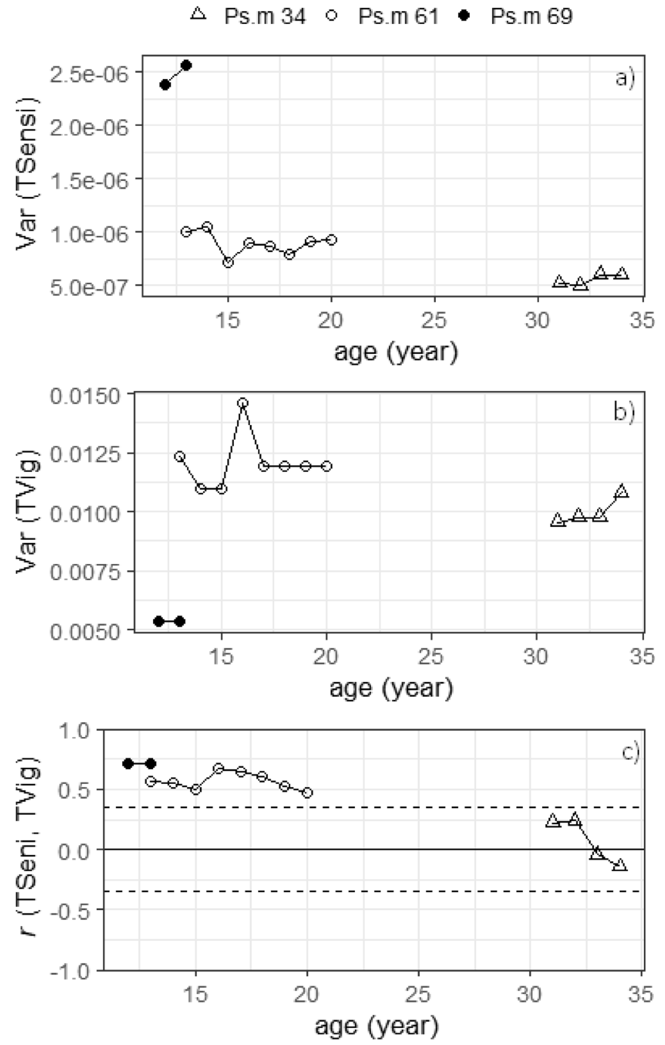

Fig. 3. Variances (a, b) and correlation (c) of temporal sensitivity (*TSensi*) and temporal vigor (*TVig*) for each interval T of the three *P. menziesii* populations (Ps.m 34, Ps.m 61 and Ps.m 69). Each point represents an interval T characterized by the average age of the trees (*age*). On the graph c, the dashed lines represent the values beyond which correlation coefficients are significant at $p < 0.05$ computed for a sample size of $n = 30$ individuals.

Table 2
Results of the mixed models on all the selected populations ($n = 22$ populations) of average population sensitivity (a), within-population variance of sensitivity (b), average population vigor (c), within-population variance of vigor (d), and within-population correlation between sensitivity and vigor (e) according to average summer precipitation (*Pr*), average maximum summer temperature (*Tmax*), extractable soil water (*ESW*), species (*sp*), stand density (*Nha*) and average population age (*age*). Significant results are shown in bold with the significance level indicated by '***' at $p < 0.001$, '**' at $p < 0.01$, '*' at $p < 0.05$ and '.' at $p < 0.1$.

Source		Estimate	Chisq.	Df	p-Value
a) *μSensi*					
	(Intercept)	6.14×10^{-3}	0.95	1	0.329
	Pr	2.78×10^{-5}	16.87	1	**<0.001*****
	Tmax	-4.65×10^{-4}	2.56	1	0.110
	ESW	1.23×10^{-5}	6.73	1	**0.009****
	age	2.69×10^{-6}	0.14	1	0.712
b) *var (ISensi)*					
	(Intercept)	-2.75×10^{-6}	0.16	1	0.687
	Pr	3.50×10^{-8}	22.87	1	**<0.001*****
	Tmax	-1.27×10^{-7}	0.16	1	0.688
	ESW	8.33×10^{-9}	2.58	1	0.108
	age	-5.55×10^{-9}	0.48	1	0.488
c) *μVig*					
	(Intercept)	1.66×10^{-1}	0.27	1	0.602
	Pr	4.35×10^{-4}	1.15	1	0.284
	Tmax	1.07×10^{-2}	0.49	1	0.483
	ESW	-2.00×10^{-4}	0.36	1	0.548
	age	-1.19×10^{-3}	3.24	1	0.072
	Nha	-5.37×10^{-5}	0.36	1	0.550
d) *var (IVig)*					
	(Intercept)	2.79×10^{-3}	0.12	1	0.730
	Pr	-1.23×10^{-5}	2.08	1	0.150
	Tmax	5.91×10^{-5}	0.03	1	0.871
	ESW	1.24×10^{-5}	2.68	1	0.102
	age	3.245×10^{-6}	0.09	1	0.761
e) *r (IVig, ISensi)*					
	(Intercept)	-0.29×10^{-1}	0.10	1	0.753
	Pr	7.08×10^{-4}	0.53	1	0.468
	Tmax	3.36×10^{-2}	0.64	1	0.422
	ESW	-1.70×10^{-3}	6.25	1	**0.012***
	age	-3.12×10^{-4}	0.09	1	0.766

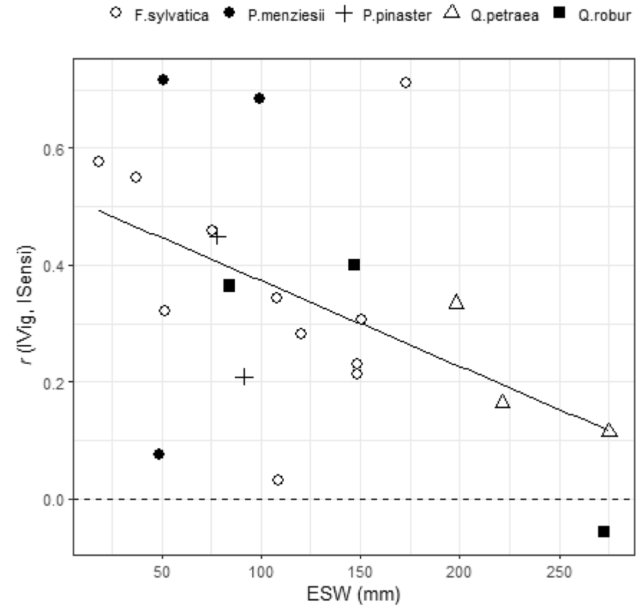

Fig. 4. Effect of extractable soil water (*ESW*) on the correlation between sensitivity and vigor (*r (IVig, ISensi)*). Each point represents a population. The correlation increases with lower *ESW*. The line shown is the simple regression coefficients on all the selected populations ($n = 22$): $r\ (IVig, ISensi) = 0.52 – 1.47 \times 10^{-3}\ ESW$ ($R^2 = 0.24$).

which growth response to stress was present (selection of populations and intervals). The pedoclimatic range of all the populations and that of the selected subset were equivalent. We hypothesized that the populations and intervals removed from the analyses experienced insufficient drought stress to observe a growth response and/or were impacted by other disturbance factors masking the relationship between growth and drought stress. Nevertheless, species-specific seasonal growth dynamics may also affect the response to drought. First, the formation of earlywood in ring porous wood species, such as *Quercus* sp., largely depends on remobilization from reserves accumulated in previous years and starts before budburst (Michelot et al., 2012). In these species, tree rings of similar widths can have very different proportions of latewood (Lebourgeois, 1999). Therefore, wood density can differ considerably from year to year, buffering the variation of ring width in response to environmental conditions over the overall growing period (Schwarz et al., 2020). In this study, we attribute the small proportion of *Quercus* sp. populations selected for analyses (21 % compared to 49 % for other species) to these physiological and anatomical characteristics and to the fact that the *Quercus* sp. populations are preferentially on the best site conditions in the RENECOFOR network (Lebourgeois, 1999; Mérian et al., 2011). Second, there may be a certain time lag between the growth period and the water stress period, e.g., drought in autumn could deepen the annual water deficit while annual growth would not be affected. The intra-annual analysis of radial growth can help to define the growing season over which to integrate the stress (Olivar et al., 2014). The growing season varies greatly depending on the site and the species (Michelot et al., 2012). Pine species show active growth in October and late regrowth until November (*P. pinaster*, Vieira et al., 2009; *P. halepensis,* Olivar et al., 2014). In oak, growth usually stops at the first events of water deficit, during the months of June-July (*Q. petraea*, Bréda & Granier, 1996). For the sake of comparability between sites and species, we have integrated stress at the scale of the entire year. Thus, our selection of intervals would exclude autumn drought events having no impact on the annual growth. However, in the temperate region, most of the water stress occurs in July and August, and therefore a moderate impact on the results is expected.

4.1. A notable within-population variation in sensitivity and vigor

Our results reveal high levels of within-population phenotypic variation in growth sensitivity and vigor. On average for all species and for both traits, the within-population variance was higher than the variance of population mean values, even though the different populations of each species were sampled in different geographic areas and different environmental conditions. This suggests both genetic and environmental contributions to between-population variance. We had no information on microenvironmental heterogeneity within each population that could help disentangle the genetic and microenvironmental components of within-population variance, but the environmental characterization at the population level provides a clue on this issue, as follows.

The average population sensitivity was mainly driven by two environmental factors, summer precipitation and extractable soil water (ESW). Summer precipitation also had a positive effect on within-population variance in sensitivity. As a parsimonious interpretation, we can assume that the positive impact of summer precipitation on within-population variance simply results from a scale effect, thus contributing to the environmental component of the variance of sensitivity. In contrast, ESW only drove the average population sensitivity but neither the within-population variance nor the average population vigor. Thus, ESW is likely to explain part of the between-population variance that is not a scale effect, whereby lower sensitivity in populations of lower ESW effectively indicates a lower response to stress. Although we cannot properly test for local adaptation based on our dataset, this cline in sensitivity along the ESW gradient suggests past adaptation to drought stress regimes. Furthermore, it has been shown that microgeographic variation in soil conditions within populations may contribute to interindividual variation in the response to drought (Nourtier et al., 2014) and there is increasing empirical evidence of microenvironmental adaptation within forest tree populations (Audigeos et al., 2013; Heer et al., 2018; Brousseau et al., 2021). Therefore, we also hypothesize that part of the within-population variance in sensitivity, which is higher than between-population variance, is partly under genetic control.

The average population vigor was not affected by any environmental factors. In particular, the lack of effect of summer precipitation indicates that our selection of the most favorable years for computing vigor effectively excluded water-limiting years. None of the environmental factors tested showed an effect on the within-population variance in vigor, indicating in particular that within-population phenotypic variation in vigor was unrelated to drought conditions.

In this study, we considered temporal variations in growth vigor and sensitivity to drought during stand development. For growth-related traits, temporal changes in population means and variances during a rotation cycle result from dynamic environmental factors (e.g., trends in climate change), evolution of stand structure, tree age, and long-term memory of past events (e.g., acclimation). For both studied traits, the dynamics of within-population variances differed among species and populations with no clear pattern. The temporal variations in within-population variances were sometimes important but did not exceed the largest between-population differences of average values. Thus, averaging over temporal intervals, as we did here, provides more robust estimates of within-population variance of growth-related traits. Moreover, stand age had no effect on either trait (mean population values and variances), suggesting that we indeed captured an individual effect independent of cofactors such as tree age or size.

4.2. A growth vigor-sensitivity trade-off within populations facing drought stress

We observed a positive correlation between vigor and sensitivity to drought stress within 17 of 22 populations (77 %) in both juvenile and largely mature stands. Vigorous trees showed higher sensitivity to drought stress episodes. Conversely, trees with higher sensitivity showed a higher capacity to benefit from favorable years. These correlations can originate from different and non-mutually exclusive environmental and genetic causes.

The observed positive correlation between vigor and sensitivity could first result from the acclimation of trees to the spatially heterogeneous microenvironmental conditions within stands. In microsites with low available water (e.g., low ESW) and/or high evapotranspiration (e.g., high density of trees, high LAI), individual trees may experience higher drought stress than expected on average and respond adaptively through shifts in allocation to foliage, sapwood, and roots at the expense of vigor. Adaptive responses include short-term reductions in leaf area through early senescence (Ciais et al., 2005; Bréda et al., 2006), resource-intensive adaptations in hydraulic architecture and wood density induced by longer-term growth (Ruiz Diaz Britez et al., 2014), and lasting global physiological, morphological and architectural changes (e.g., tree height, number and longevity of stems, leaves and roots; Nicotra et al., 2010). Conversely, under favorable microsites (e.g., higher ESW, better fertility), the accumulation of aboveground biomass due to growth may increase the sensitivity to drought events, since these morphological investments in stems and leaves induce substantial maintenance costs in water and carbohydrates during dry periods (McDowell et al., 2011; Cailleret et al., 2019). Changes in the heterogeneity of stand structure (e.g., LAI, tree crown volume, clumping) through forest dynamics and silvicultural interventions are expected to lead to temporal variations in the vigor–sensitivity correlation, as observed. The pronounced spatial heterogeneity often associated with shallow soils could lead to a higher correlation between sensitivity and vigor, as we observed in lower ESW environments (Nourtier et al. 2014).

The vigor–sensitivity correlation could also be of genetic origin, whereby selection for vigor entails a functional cost in terms of sensitivity and *vice versa*, potentially resulting in the coexistence of different genotypes within the population. Stomatal control determines the reduction in assimilation during water deficit periods. Therefore, genotypes characterized by maximum transpiration and assimilation rates under favorable conditions, and thus by high vigor, are expected to show stronger stomatal control during dry episodes, reducing carbon assimilation accordingly (Roussel et al., 2009a,b; Martínez-Vilalta et al., 2012). Vigor can be associated with a larger leaf area, which implies more photosynthesis and thus more growth but also more water loss through evapotranspiration and thus greater sensitivity (Marron et al., 2003). Lower sensitivity can be associated with increased root development, with the allocation of resources to the roots resulting in a substantial cost in terms of aboveground growth (Aranda et al., 2010). Wood density, a trait implicated in resistance to cavitation, is related to slower growth and longer life (Chave et al., 2009). Although universal, this relationship is not systematically found at the intraspecific level (Fajardo et al., 2022). The coexistence of different adaptive combinations of growth, phenology and anatomy traits, i.e., trait syndromes, was observed in a water-stressed population of *F. sylvatica* (Bontemps et al., 2017). Here, we observed a weaker correlation between vigor and sensitivity in higher extractable soil water environments, i.e., lower drought stress environments, which suggests a low selection pressure on sensitivity leading to the persistence of genotypes *a priori* unfavorable, that is to say not so vigorous but sensitive. The effect of ESW on the correlation between vigor and sensitivity is also consistent with the lack of a significant relationship between drought stress and growth for plots with low stress level. Thus, environmental conditions favoring drought stress, such as low extractable soil water, might be necessary to reveal the trade-off between growth sensitivity and vigor.

4.3. Implications for population adaptation and management under climate change

Forest dynamics tends to progressively lower the social rank of trees with lower growth and then, in particular for shade-intolerant species, to eliminate them through asymmetric competition (Hülsmann et al., 2018). Both vigor and sensitivity are components of tree growth, and we can expect different selection intensities for sensitivity and vigor depending on the local drought regime. When drought is rare or absent, the selection will operate only on vigor, which is likely to indirectly induce the selection of sensitive trees through the trade-off or, at least, to maintain sensitive trees at a dominant social rank. In contrast, the more intense and/or regular the drought events, the greater the selection will operate against sensitivity, which is likely to indirectly select for less vigorous trees. In the context of climate change, we expect such local shifts in drought regimes through increasingly frequent and severe dry conditions. Despite the strong interindividual variations observed, a genetic correlation could restrain the response to selection and contribute to maintaining within-population genetic variation for both sensitivity and vigor (Pujol et al., 2018). Regarding the evolution of forest functions under climate change, selection for lower sensitivity may correlate with selection for reduced growth potential. Depending on the underlying genetic determinism, this is likely to lead to changes in population growth performance over generations.

Forest management modifies the composition, structure, environment, and therefore evolutionary processes of forest tree populations (Jactel et al., 2009; Lefèvre et al., 2014). When silvicultural operations consist of controlling competition by removing trees on the basis of their phenotype, one issue is that current selection criteria may not necessarily correlate with future adaptedness (Lefèvre, 2012). Indeed, our results suggest that systematically favoring fast-growing trees could be unsafe if water conditions deteriorate because this risks indirectly selecting sensitive trees and, therefore, affects future growth performance. Furthermore, choosing the fastest growing trees among those that remain as seed trees may possibly increase the growth sensitivity in the following generations depending on the underlying genetic basis. When silvicultural practices are used to buffer the intensity and therefore the impact of drought stress (e.g., reduction in stand density and LAI, Giuggiola et al., 2013; Schmitt et al., 2020), attention must be given to avoid over-selection of vigorous and sensitive genotypes and to avoid too much counter-action of acclimation processes. It is expected that the later these practices are applied, i.e., at a mature stand stage, the less the impact on selection for sensitivity will be, since much of the selection will have already taken place before (Lefèvre et al., 2014). One strategy could then be to maintain a significant drought stress level in the juvenile stage to favor adaptation and acclimation before reducing it through thinning or pruning. Ideally, this reflection should address multiple stressors rather than just one, and not just traits associated with growth. In addition, microsite heterogeneity within populations deserves attention in forest management strategies because it provides a variety of conditions with multiple benefits, in terms of resilience of the whole population and in terms of within-population genetic diversity (Scotti et al, 2016; Gauzere et al, 2020).

Only a modeling approach seems to be able to explicitly account for the complexity of the underlying interactions between demography, ecology, management and evolution (Oddou-Muratorio et al., 2020). Such models should consider all demographic performances, i.e., survival and reproduction in addition to growth, and the potential trade-offs between them as well as the underlying genetic basis for questions on a multigenerational scale.

5. Conclusions

We assessed within-population variation and covariation for growth performances, considered as dynamic phenotypic traits. We focused on two growth traits: vigor and sensitivity to drought stress. The phenotypic variation in vigor and growth sensitivity was considerable in all studied forest tree populations, and we observed a general trade-off between individual tree vigor and sensitivity to drought. The phenotypic variation within populations can be related to better resilience and evolvability, whereas the trade-off represents a potential constraint on adaptation. Overall, the phenotypic variation observed is expected to influence evolutionary trajectory and forest stand dynamics, forest management being impacted by and having an impact on this variation. In particular, selective thinning aimed at favoring fast-growing trees could indirectly: (i) increase population sensitivity to water stress, (ii) harm the process of acclimation, and consequently (iii) affect future growth performance under climate change. Here, management practices supporting the conservation of both slow-growing and fast-growing trees within populations could be considered as a possible strategy to mitigate the negative effects of droughts and increase population resilience.

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.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2022.120754.

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