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RESEARCH

Selecting cork oak and holm oak trees for stable tolerance to combined drought and *Phytophthora cinnamomi* stress

Raul de la Mata[1,2] · **Francisco Alcaide**[1] · **Rubén González**[1] · **Beatriz Cuenca**[3] · **Raúl Tapias**[4] · **Felipe Pérez**[5] · **Alejandro Solla**[1]

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Abstract

Using trees tolerant to drought and *Phytophthora cinnamomi* (*Pc*) infection is the most promising approach to restore *Quercus suber* and *Q. ilex* forests under decline. Breeding programs require heritability estimates for tolerance to combined stress. Moreover, the genetic variation underlying genotype-by-environment ($G \times E$) interactions in oak tolerance to combined stress has not been explored. We evaluated life expectancy of approximately 10,400 seedlings from 87 *Q. suber* and 90 *Q. ilex* half-sib families from Spain under *Pc*, *Pc*+drought, and drought+*Pc* scenarios. Intraspecific variation in tolerance across scenarios, additive genetic variance, and $G \times E$ interactions were analyzed. To ensure optimal selection strategies, family genotypic stability was quantified. Under well-watered conditions, *Q. suber* showed higher tolerance than *Q. ilex* to *Pc*, but under the *Pc*+drought scenario, mortality was similar between species. Geographic variation was detected in cork oak, with populations from eastern Spain showing greater susceptibility. Both species exhibited significant additive genetic variation under the *Pc* and *Pc*+drought scenarios, and narrow-sense heritability estimates (h_i^2) ranged from 0.10 to 0.16, indicating potential for selective breeding. We report a relevant $G \times E$ interaction, primarily due to family rank changes across scenarios. Genotypic stability analyses enabled selection of families with increased and stable tolerance, and the *Pc*+drought scenario was deemed optimal for selection. A backward selection strategy targeting the 20% most tolerant parents would allow genetic gains of 18% in both oak species. This is the first time oaks have been screened for enhanced and stable tolerance to combined stress.

Keywords Mediterranean oaks · Oak decline · Tree susceptibility · Genotype by environment interaction · Phenotypic plasticity · Forest genetic improvement · Tree breeding

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✉ Raul de la Mata
raul.delamata@upm.es

✉ Alejandro Solla
asolla@unex.es

Francisco Alcaide
falcaider@unex.es

Rubén González
rubenglezglez@unex.es

Beatriz Cuenca
bcuenca@tragsa.es

Raúl Tapias
rtapias@dcaf.uhu.es

Felipe Pérez
fperez@miteco.es

[1] Faculty of Forestry, Institute of Dehesa Research (INDEHESA), Universidad de Extremadura, Avenida Virgen del Puerto 2, 10600 Plasencia, Spain

[2] Present address: School of Forest Engineering and Natural Resources, Universidad Politécnica de Madrid, 28040 Madrid, Spain

[3] TRAGSA, Maceda Nursery, Carretera de Maceda a Baldrei km 2, 32700 Maceda, Ourense, Spain

[4] Department of Agroforestry Science, University of Huelva, Avenida de las Fuerzas Armadas s/n, 21007 Huelva, Spain

[5] Spanish Ministry for the Ecological Transition and the Demographic Challenge (MITECO), Madrid, Spain

Abbreviations

Pc	*Phytophthora cinnamomi*
BLUPS	Best linear unbiased predictors
BLUE*s*	Best linear unbiased estimates
GCA	General combining ability
REML	Restricted maximum likelihood
RLL	Restricted log-likelihood
LSD	Least square differences
-2RLL	-2 Restricted log-likelihood
AIC	Akaike information criterion
BIC	Bayesian information criterion

Introduction

Mediterranean forests are facing escalating pressures from climate and biotic stressors (Herguido-Sevillano et al. 2017; Gea-Izquierdo et al. 2021; López-Ballesteros et al. 2023). In particular, *Quercus suber* L. (cork oak) and *Q. ilex* L. (holm oak) forests are increasingly vulnerable to prolonged drought, high temperatures, lack of natural regeneration, soil degradation, and invasive pathogens (Brasier 1996; Camilo-Alves et al. 2013; Mora-Sala et al. 2019; Serrano et al. 2022). *Phytophthora cinnamomi* Rands (*Pc*), a major driver of oak decline in Mediterranean forests since the 1980s, is a soil-borne pathogen that disrupts water uptake by killing fine roots, exacerbating drought effects and leading to severe physiological stress and tree mortality (Solla et al. 2009; Redondo et al. 2015; Ruiz-Gómez et al. 2018). The synergistic interaction between *Pc* infection and drought stress amplifies their combined impact, posing a significant threat to the sustainability of these Mediterranean forests (Gea-Izquierdo et al. 2021; Serrano et al. 2022).

In response to oak decline in the Iberian Peninsula, management interventions including soil amendment, chemical treatment, and pathogen containment have shown promise, although they are often resource-intensive and provide only short-term relief (Rodríguez-Molina et al. 2021; López-Sánchez et al. 2022; López-García et al. 2024; Dorado et al. 2025). These limitations underscore the need for long-term strategies, especially the deployment of plant materials with enhanced tolerance to drought and *Pc* infection (Moreira et al. 2018; Martínez et al. 2023). Leveraging genetic variation in oak species provides a valuable opportunity to address combined threats. Variation among populations of *Q. ilex* and *Q. suber* has been widely documented for tolerance to drought (Ramírez-Valiente et al. 2009; Gimeno et al. 2009) and *Pc* infection (Moreira et al. 2018; Rodríguez-Romero et al. 2022), in separate studies. However, heritability estimates for tolerance to these combined stressors are lacking in *Q. suber* and remain very limited in *Q. ilex* (but see de la Mata et al. 2025), hindering the development of effective breeding strategies. Quantifying intraspecific variability and estimating heritability in tolerance to combined drought and *Pc* infection are crucial for tree genetic improvement programs.

The interplay between drought and *Pc* infection varies depending on the timing and severity of both stressors, highlighting the complexity of oak decline dynamics (Camilo-Alves et al. 2013; Encinas-Valero et al. 2022). In tree-pathogen interactions, genetic and environmental factors interact to shape host tolerance (Stenlid and Oliva 2016). The impact of the pathogen depends on host stress levels and pathogen-favorable conditions, emphasizing the role of the environment in determining genetic variation in tree tolerance (Dukes et al. 2009). Consequently, the genetic basis of oak tolerance to *Pc* may be further modulated by genetic variation in abiotic stress tolerance, leading to different species- and genotype-specific responses under different environmental conditions (Atkinson and Urwin 2012). Although holm oak is generally more susceptible to *Pc* than cork oak (Robin et al. 2001; León et al. 2017), it exhibits greater drought tolerance due to xylem resistance to cavitation and enhanced leaf resistance to desiccation (Ramírez-Valiente et al. 2020). Drought following infection has been consistently identified as the most detrimental scenario for Mediterranean oaks, as *Pc*-induced root damage impairs water uptake, exacerbating water stress effects (Brasier 1996; Camilo-Alves et al. 2013; Corcobado et al. 2014). Consequently, although drought tolerance and susceptibility to *Pc* are greater in holm oak than cork oak, the level of tolerance to combined stress is similar in the two species (de la Mata et al. 2025).

Similarly, genotypes within species that show tolerance in one environment may become more susceptible in another, reinforcing the significance of $G \times E$ interactions. The potential presence of $G \times E$ interaction in tolerance to oak decline could complicate selection of forest reproductive materials for reforestation, as the tolerance of selected genotypes may vary across different environmental conditions. Previous studies documented significant population × site interactions for survival in *Q. suber* and *Q. ilex* under stressful Mediterranean field conditions (Ramírez-Valiente et al. 2021 and references therein), highlighting relevant genetic variation in the plasticity of tolerance to environmental stress at population level. However, no studies on these species have explored the importance of $G \times E$ interactions for selecting forest reproductive materials tolerant to the combined stress of drought and *Pc* infection.

Investigating genetic variation in tolerance of holm oak and cork oak to decline under diverse combination of drought and *Pc* infection is therefore essential when implementing tree breeding programs. In this study, we evaluated approximately 10,400 seedlings from 87 *Q. suber* and 90 *Q.*

ilex half-sib families collected across the distribution range of the species in Spain, under three scenarios of combined drought and *Pc* infection. Our objectives were to assess (i) seedling tolerance under *Pc*, drought + *Pc* and *Pc* + drought scenarios; (ii) geographic variation in tolerance to individual and combined stress across the distribution range of the species in Spain and environmental drivers at the seed source; (iii) additive genetic variation and heritability of tolerance; (iv) occurrence and causes of $G \times E$ interactions in oak tolerance across scenarios; (v) phenotypic plasticity of tolerance at the family level across scenarios; and (vi) the possibility of selecting genetic materials with stable tolerance across scenarios. We hypothesize that (1) different combinations of drought and *Pc* infection impact tolerance of *Q. suber* and *Q. ilex* seedlings differently; (2) intraspecific variation in tolerance to combined stress occurs at the population level and (3) at the family level; and (4) genetic variation in phenotypic plasticity among families influences their tolerance to different stress combinations, potentially enabling selection of *Q. suber* and *Q. ilex* trees with increased stable tolerance across stress combinations.

Material and methods

Genetic material

To explore patterns of inter- and intra-specific variation in tolerance to different scenarios of drought and *Phytophthora cinnamomi* (*Pc*) infection combinations, acorns were collected from nine *Quercus suber* and nine *Q. ilex* populations across their natural distribution in Spain (Fig. 1, Table S1). The cork oak populations were from nine different provenance regions and the holm oak populations were from eight (Díaz-Fernández et al. 1995; Jiménez et al. 1996). Climate at the origin of populations ranged from 10.8–17.7 °C mean annual temperature, 371–871 mm mean annual precipitation and 67–331 mm mean summer (May to September) precipitation (Table S1).

In fall 2019, acorns were collected from seven to 11 (average of 10; see Table S2) open-pollinated, asymptomatic and unrelated mature wild mother trees per population. Collected seeds were divided into three batches and sent to the three locations where the experiment was conducted (see Sect. "Experimental design, treatments and assessments"). Each batch was handled and sown in mid-January 2020, following the same protocol (see Methods S1a). Germinated plants were kept in natural daylight under greenhouse shade that reduced solar radiation by 50%, and watered to field capacity at least once a week until they were properly established.

Experimental design, treatments and assessments

The experiment was conducted in three greenhouses in Maceda (NW Spain; 42.276º N, 7.624º W, 540 m a.s.l.), Huelva (SW Spain; 37.273º N, 6.924º W, 19 m a.s.l.) and Plasencia (W Spain; 40.035º N, 6.083º W, 375 m a.s.l.) (Fig. 1). In Maceda, open pollinated seeds from 87 *Q. suber* and 90 *Q. ilex* mother trees (half-sib families) were arranged in a randomized complete block design replicated in 50 blocks. In each block, the two species were intermixed

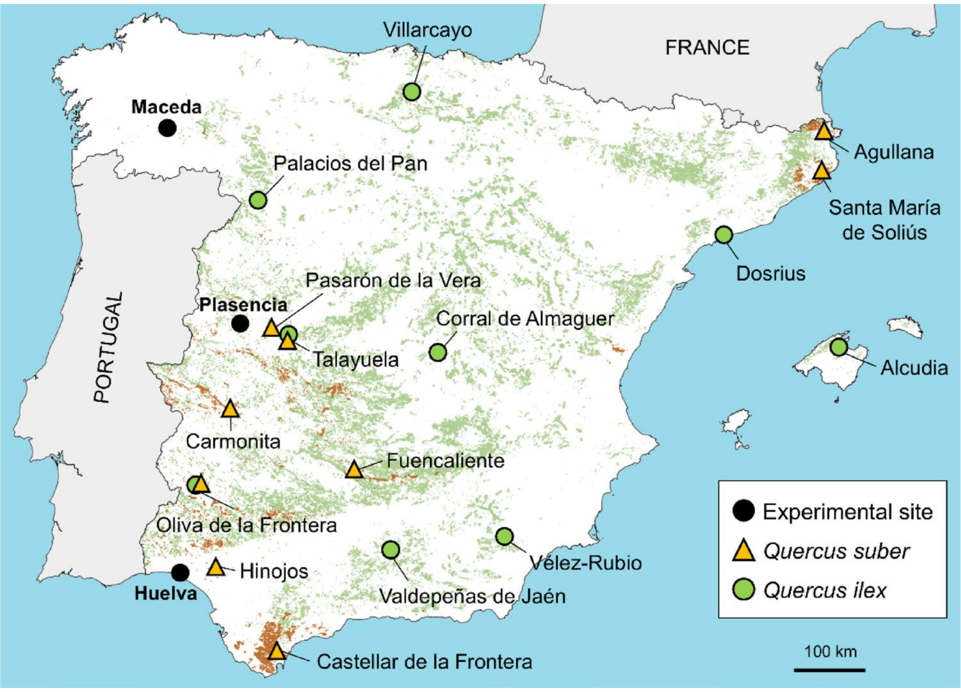


Fig. 1 Distribution of *Quercus suber* (brown areas) and *Q. ilex* (green areas) in Spain and location of the experimental sites and 18 study populations (brown triangles for *Q. suber* and green circles for *Q. ilex*). Scenarios of drought and *Phytophthora cinnamomi* (*Pc*) infection under greenhouse conditions were applied in Maceda (*Pc*), Huelva (drought + *Pc*) and Plasencia (*Pc* + drought)

and one seed per family (177 seeds/block) was placed at random. Each root trainer comprised 48 cells, such that four root trainers were required to complete one block. In Huelva and Plasencia, seeds from a subsample of 70 *Q. suber* and 73 *Q. ilex* mother trees were arranged in a randomized complete block design replicated in 25 blocks. Again, species were intermixed and one seed per family (143 seeds/block) was placed at random. Thus, three 48-cell root trainers were needed to complete one block. The total number of emerged seedlings was 6072 in Maceda, 2120 in Huelva and 2139 in Plasencia. Each family was represented by an average of 32 *Q. suber* and 37 *Q. ilex* seedlings in Maceda, and 14 *Q. suber* and 16 *Q. ilex* seedlings in Huelva and Plasencia (Table S2).

In each greenhouse, seedlings were subjected to a different treatment of drought and *Pc* infection combination. A single stress scenario of *Pc* was applied in Maceda, as the presence of the pathogen in this location is typically associated with summer rainfall. On 2 July 2020, seedlings in Maceda were soil infested with a highly virulent *Pc* strain (San-Eufrasio et al. 2021; see Methods S1b for further details). After inoculation, trays were flooded for three days to promote sporangia production and zoospore release, and inoculated plants were waterlogged three more times in summer to stimulate the effect of *Pc*. Apart from the four waterlogging periods, seedlings were periodically watered to field capacity to avoid drought stress. The same treatment was applied again in the following growing season. A combined *Pc* + drought scenario was applied in Plasencia, due to the extremely dry summers in this region. On 2 July 2020, seedlings were soil infested with *Pc* and trays were flooded for three days after inoculation. Trays were waterlogged three times in summer and watered to field capacity only once a month until the end of October. This treatment simulated a typical dry summer scenario. The same treatment was applied again in the following growing season. A combined drought + *Pc* scenario was implemented in Huelva, as the influence of the Atlantic Ocean in this region often leads to dry springs followed by mild summers. On 1 June 2020, irrigation was stopped for one month at this location, simulating a typical dry spring. On 2 July 2020, seedlings were soil infested with *Pc*. Trays were flooded for three days after inoculation and waterlogged three times in summer, following the same protocol as for the *Pc* scenario. The same treatment was applied again in the following growing season. Seedlings were kept under natural light and optimal growing conditions, and therefore no other source of mortality was expected. The experiment lasted two growing seasons and ended on 20 November 2021.

In forest tree species, tolerance to pests and diseases generally displays a continuous phenotypic distribution, ranging from tolerant to susceptible individuals (Sniezko et al. 2023). A prior study on holm oak tolerance to *Pc* supports a quantitative rather than qualitative genetic basis (de la Mata et al. 2025). Hence, to determine differences in tolerance among species, populations, and families across the three scenarios, plant mortality was recorded weekly during the first growing season and every two weeks in the second growing season. Plant mortality was parameterized as 0 and 1, if the plant survived or not, and time to death of plants (life expectancy in days) was calculated from the date of death. To confirm plant infection, *Pc* was successfully re-isolated in September 2021 from necrotic and non-necrotic fine roots in a subset of plant samples under each scenario (results not shown).

Statistical analyses

All analyses were performed in SAS 9.4 (SAS-Institute 2013), using time to death for quantitative genetic estimations as a proxy of plant tolerance. Time to death of seedlings was used instead of mortality because it was continuous and normally distributed. Furthermore, overall mortality exceeded 80% after two growing seasons in most scenarios (see Fig. S1), making it less informative for detecting genetic variation in tolerance (Falconer 1989).

Differences among species and scenarios

To determine differences in tolerance among species and scenarios, we fitted the following linear mixed model:

$$\begin{aligned} Y_{ijklmn} = {} & \mu + S_i + I_j + B\left(I\right)_{k(j)} \\ & + P\left(S\right)_{l(i)} + F\left(P\left(S\right)\right)_{m(l(i))} \\ & + S \times I_{ij} + P\left(S\right) \times I_{jl(i)} \\ & + F\left(P\left(S\right)\right) \times I_{jm(l(i))} + \varepsilon_{ijklmn} \end{aligned} \tag{1}$$

where Y_{ijklmn} is the time to death observed in the $ijklmn^{\text{th}}$ seedling; μ is the overall mean; S_i is the fixed effect of the species i; I_j is the fixed effect of the scenario j; $B(I)_{k(j)}$ is the fixed effect of the block k within the scenario j; $P(S)_{l(i)}$ is the fixed effect of the population l within species i; $F(P(S))_{m(l(i))}$ is the random effect of the family m within population l and species i; $S \times I_{ij}$ is the fixed interaction between species i and scenario j; $P(S) \times I_{jl(i)}$ is the fixed interaction between population l within species i and scenario j; $F(P(S)) \times I_{jm(l(i))}$ is the random interaction between family m within population l and species i and scenario j; and ε_{ijklmn} is the random effect of the $ijklmn^{\text{th}}$ seedling or error term. The interactions of block with population and family were dropped from the model to facilitate convergence, as they were not significant in preliminary analyses. Because the dependent variable met the assumptions of normal distribution, the model was fitted using the SAS MIXED procedure (Littell et al. 2006), and variance components were estimated using the restricted maximum likelihood (REML) method. Significance of family and family × scenario interaction random effects were tested using log-likelihood ratio tests by comparing the restricted log-likelihoods (RLL) of the full model with the respective reduced models, excluding the effect to be tested (Yang 2002). Degrees of freedom were calculated using the Satterthwaite approximation. Adjusted means for species × scenario combinations were estimated using the LSMEANS statement of the MIXED procedure. Post-hoc comparisons among fixed effect levels were performed using the conservative Tukey–Kramer method for species and scenario combinations.

Within-species geographic variation and its environmental drivers

To quantify population variation in tolerance within species, the model shown in Eq. 1 was fitted for cork oak and holm oak separately across the three scenarios. Mixed models were also fitted for each individual scenario. Adjusted means for populations of each species were estimated using the LSMEANS statement of the MIXED procedure. Post-hoc comparisons among populations were performed using the less conservative Least Square Differences (LSD) method to detect any difference.

We tested whether geographic and climate factors at the seed source accounted for variation in tolerance among populations. When statistical differences among populations were detected, we estimated Pearson's correlations among LSMEANS of time to death for each population across the three scenarios and the main geographic and climate parameters at the origin of each seed source (Table S1). Bonferroni's correction was used to reduce the possibility of obtaining false-positive results (type I errors) when multiple pairwise tests are performed on a single set of data (Dunn 1961). The geographic features tested were the latitude and longitude coordinates. Climate at the seed source location was characterized using six basic parameters with relevant effects on biological processes and broader data availability (see Table S1 for a description of the climate variables selected). Climate data for the normal series (1961–1990) was generated with the ClimateEU v4.63 software package (Marchi et al. 2020; Table S1) for each seed source location. This software locally downscales historical climate data layers into scale-free point estimates of climate values.

Additive genetic variation, relevance of family × scenario interaction, and heritability

To quantify family (additive genetic) variation and the family × scenario ($G \times E$) interaction, we used the same model as for the geographic variation, similarly fitted for cork oak and holm oak separately across the three scenarios. Mixed models were also fitted for each individual scenario. Significance of family and family × scenario interaction random effects were tested using log-likelihood ratio tests, and their relevance was estimated as the percentage of the total variance accounted for by each variance component. Best linear unbiased predictors ($\mathrm{BLUP_S}$) of the family effect (general combining ability, *GCA*) were estimated using the REML method. Genetic correlations for time to death between pairs of scenarios were calculated through Pearson's *r* coefficients among family BLUPS predicted under each scenario. Only families tested under the three scenarios were included (Table S2).

Narrow sense individual heritabilities (h_i^2) were estimated as the ratio of additive genetic variance to total phenotypic variance. To correct the additive genetic variance estimates assuming average selfing rates of 1–3% (Ortego et al. 2010; Soto et al. 2007), a kinship coefficient (*r*) of 0.27 was used. We calculated individual heritabilities following the formula:

$$h_i^2 = \frac{\left(\frac{1}{r} \times \sigma_f^2\right)}{\sigma_f^2 + \sigma_{f\times i}^2 + \sigma_e^2} \tag{2}$$

where σ^2_f is the family variance; $\sigma^2_{f\times i}$ is the family × scenario interaction variance; r is the kinship coefficient; and σ^2_e is the residual variance. For single scenario heritabilities, $\sigma^2_{f\times i}$ was dropped from Eq. 2. Given that the variance components were estimated through a model with population as a fixed effect, the individual heritabilities estimated are suitable for within population selection. To estimate across-population heritabilities, the population effect should have been considered as random, applying the formula described in Hamann et al. (2002). However, because within- and across-population heritabilities were almost the same (estimates across populations showed an increase of only 1–2%), for simplicity we have shown only within-population estimations. The standard error of heritability was estimated following the Delta method, based on asymptotic estimates of the variances and covariances of the variance components of the mixed models (Lynch and Walsh 1998).

Causes of family × scenario interaction

To interpret family × scenario interaction (i.e., variation in phenotypic plasticity among families) of tolerance, we followed the likelihood framework proposed by Yang (2002) for each species separately. Under this framework, various reduced models constraining different components of the family variance—covariance (VCOV) structure were fitted. Hypothesis testing regarding the constraints imposed on the VCOV structure was performed by restricted likelihood ratio tests (Fry 2004). We tested for (H1) heterogeneity of family variances across scenarios (scale effect), (H2) heterogeneity of scenario-to-scenario family correlations across pairs of scenarios, and (H3) deviations from perfect correlations between all scenario pairs (cross-over interaction (COI); see details in Methods S2).

Quantifying family variation in phenotypic plasticity of tolerance: correlation with average tolerance

We assessed the extent to which the families studied varied in phenotypic plasticity of tolerance across scenarios, and quantified family sensitivity to the variation in the stresses imposed across scenarios. Family stability is the inverse of phenotypic plasticity, and is important when selecting genotypes for use in varying conditions of tree decline. Phenotypic plasticity estimates (λ-scores) across scenarios for each family were obtained following the methodology of Denis et al. (1997), also used in pine species (de la Mata et al. 2012). Classical models of phenotypic plasticity can be integrated into a mixed model framework (Denis et al. 1997; Piepho 1999), allowing flexible modeling of the family × scenario interaction. To describe the family × scenario effect, classical stability approaches were applied using appropriate variance–covariance (VCOV) structures (see Methods S3). An additive mixed-effects model was fitted, assuming no family differences in stability, alongside four different stability models to account for variation in stability among families (Methods S3). Performance of the VCOV-based models was compared using -2 restricted log-likelihood (-2RLL), Akaike's information criterion (AIC), and Bayesian information criterion (BIC), all of which follow a smaller-is-better approach.

To determine whether stability was influenced by tolerance of families, we calculated Pearson's correlations between family phenotypic plasticity scores (λ-scores) and family BLUPS of time to death, considering both pooled and individual scenarios. Negative correlations would indicate that families with longer life expectancy exhibited higher stability and lower phenotypic plasticity across scenarios.

Breeding values of tolerance and genetic gains

Our first operational step to breed cork oak and holm oak tolerant to decline was based on backward selection of the most tolerant parents, for future replication in a seed orchard. We therefore estimated the half-sib family adjusted breeding values for time to death in each species upon the mixed model estimates across scenarios and under each scenario, using the following equation (Isik et al. 2017; White et al. 2007):

$$Adj.BV_{HS} = Grandmean + BLUE_{population} + (2 \times GCA) \tag{3}$$

where $Adj.BV_{HS}$ is the half-sib family adjusted breeding values; the *Grand mean* is calculated from the solution of the fixed factor estimates; $\text{BLUE}_{population}$ is the best linear unbiased estimate of the population; and *GCA* is the general combining ability of the parent or best linear unbiased predictor (BLUP_s) of the random family effect.

Based on a backward selection strategy for the 20% most tolerant parents as a proof of concept, we estimated expected genetic gains following:

$$\Delta G = \frac{MeanAdj.BV_{HS} - Grandmean}{Grandmean} \times 100 \tag{4}$$

where ΔG is the expected genetic gain (%), and *Mean Adj.* BV_{HS} is the mean of the half-sib family adjusted breeding values for the 20% most tolerant parents.

The relevance of the family × scenario interaction for the 20% most tolerant parents was also quantified.

Results

Differences in tolerance between species and among scenarios

Life expectancy was significantly different depending on the species, the scenario, and their interaction ($p < 0.001$; Table 1). Under the combined *Pc* + drought scenario, seedlings showed the shortest life expectancy (249 days), although no significant differences between species were detected (Fig. 2). Under the *Pc* scenario, seedlings showed the longest life expectancy (351 days), with cork oak living longer than holm oak. Under the combined drought + *Pc* scenario, plants showed intermediate life expectancy (314 days), with *Q. suber* living longer than *Q. ilex*. For *Q. suber*, under the *Pc* + drought scenario seedlings showed the shortest life expectancy, whereas under the *Pc* and drought + *Pc* scenarios they showed the longest life expectancy, with no significant differences between the two

Table 1 Summary of the mixed model analysis [Eq. 1] for time to death (days) of *Quercus ilex* and *Q. suber* seedlings analyzed jointly across three scenarios of drought and *Phytophthora cinnamomi* (*Pc*) infection (*Pc*, drought + *Pc*, and *Pc* + drought)

Fixed effects	DF (NumDF, DenDF)	*F*-ratio	$p>F$
Species	1, 182	41.31	<0.001 ***
Scenario	2, 376	207.38	<0.001 ***
Population (species)	16, 167	3.22	<0.001 ***
Block (scenario)	78, 9896	4.67	<0.001 ***
Species × scenario	2, 376	93.81	<0.001 ***
Population (species) × scenario	32, 335	1.76	<0.008 **
Random effects	**VC ± s.e**	**VC (%)**	$p>\chi^{2\,(1)}$
Family (population)	210.8 ± 115.3	0.8	0.043 *
Family (population) × scenario	521.5 ± 150.0	2.0	<0.001 ***
Residual	25639.0 ± 366.1	–	–

(1) Denotes the significance level associated with the chi-square value given by the difference in two times the log likelihood of the specific random factor included in vs. excluded from the mixed model. Because variance components are constrained to be positive, test of variance components are one-tailed (Fry 2004)

For the species, scenario, population (nested within species) and block (nested within scenario) fixed effects and their interactions, degrees of freedom (DF), *F*-ratio and associated significance level (* $p<0.05$; ** $p < 0.01$; *** $p < 0.001$) are shown. For the family (nested within population), family-by-scenario interaction and residual random effects, variance component estimates ± standard errors (VC ± s.e.), corresponding variance percentage (%) and associated significance levels of the log-likelihood ratio tests $^{(1)}$ for significance of each variance component are shown

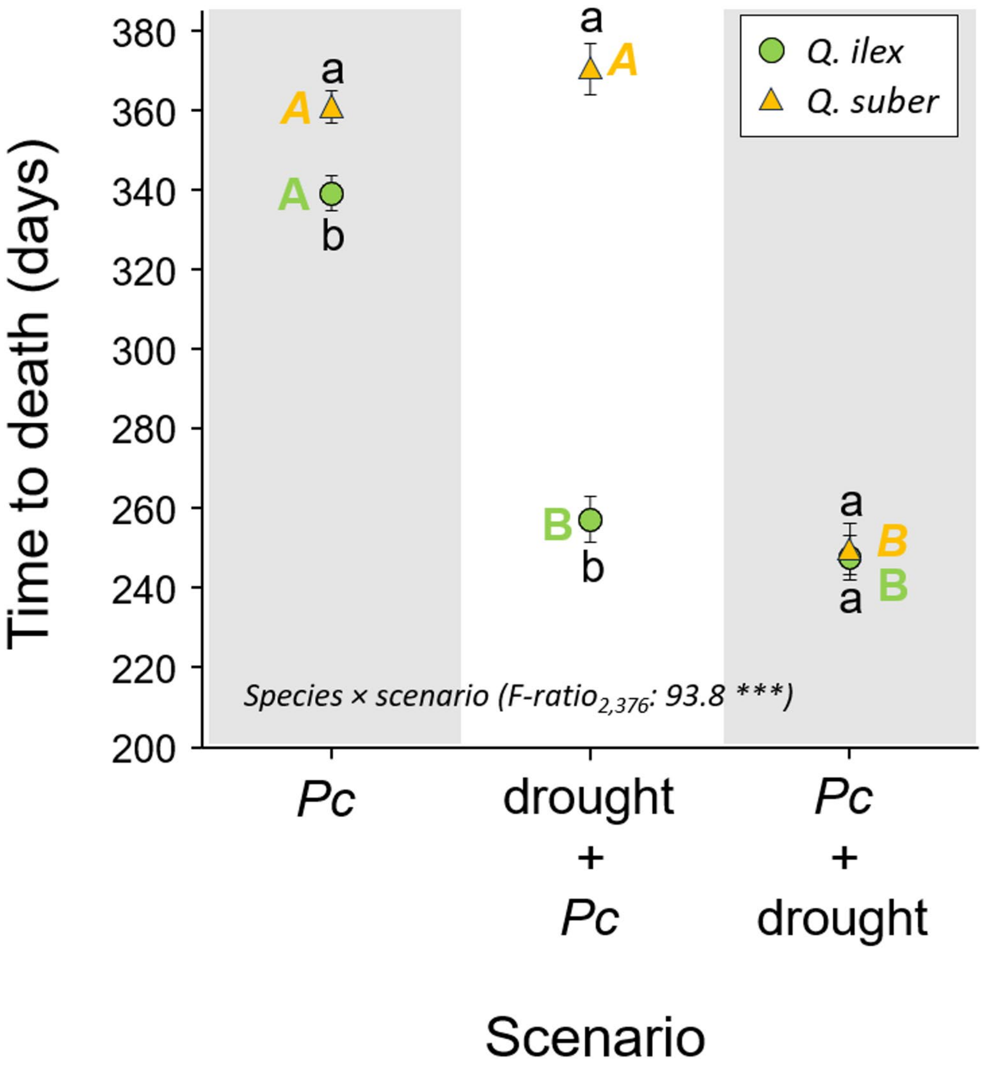


Fig. 2 Time to death of Quercus ilex (green dots) and Q. suber (orange triangles) seedlings under Phytophthora cinnamomi (Pc) infection, drought+Pc, and Pc+drought scenarios. Dots and triangles show LSMEANS ± s.e., and different lowercase letters in black indicate significant differences (p<0.05) between species within each scenario. Different capital letters in green and orange indicate significant differences (p<0.05) among scenarios in Q. ilex and Q. suber, respectively. All post-hoc comparisons among LSMEANS were implemented using the conservative Tukey-Kramer method

scenarios (Fig. 2). For *Q. ilex*, there were no significant differences in time to death between the *Pc*+drought and drought+*Pc* scenarios, while under the *Pc* scenario, plants showed the longest life expectancy (Fig. 2).

Geographic variation in tolerance to drought and *Pc* infection in *Q. suber* and *Q. ilex*

Results from the mixed models (Table 2) showed a highly significant population within species effect on time to death for *Q. suber* ($p < 0.001$) but not for *Q. ilex* ($p = 0.230$), indicating geographic variation in tolerance to drought and *Pc* infection only for cork oak. The lack of variation among populations in holm oak was confirmed by analyzing individual scenarios separately (Table 3). In contrast, significant differences were observed among cork oak populations, except under the drought+*Pc* scenario (Table 3).

Cork oak seedlings from Carmonita, in west-central Spain, showed the highest life expectancy across scenarios (Figs. 1 and 3), while populations in eastern Spain (Santa María de Soliús and Agullana) were the least tolerant (Fig. 3). A negative correlation between tolerance and longitude was found in cork oak (Fig. 4), as the most tolerant populations were located in western Spain.

Additive genetic variance, relevance of family × scenario interaction, and heritability

The family within population effect for time to death was significant in *Q. ilex* ($\chi^2 = 0.014$) but not in *Q. suber* ($\chi^2 = 0.357$), based on the results of the mixed models across scenarios (Table 2). The family × scenario ($G \times E$) interaction effect was highly significant ($\chi^2 < 0.01$) for both species, with its variance component exceeding that of the family variance component sixfold in cork oak and 1.5-fold in holm oak (Table 2). The narrow sense heritability estimates for time to death for *Q. suber* (0.01 ± 0.02) and *Q. ilex* (0.04 ± 0.02) across scenarios were low.

Results from the mixed models for each scenario showed significant family effects on time to death ($p < 0.05$) for both species under the *Pc* and *Pc*+drought scenarios, but not under the drought+*Pc* scenario (Table 3). In *Q. suber*, narrow sense heritabilities under the *Pc* and *Pc*+drought scenarios were 0.10 ± 0.03 and 0.16 ± 0.08, respectively, while in *Q. ilex*, heritabilities were 0.11 ± 0.03 and 0.12 ± 0.06, respectively (Table 3). These results indicate significant additive genetic variation under the *Pc* and *Pc*+drought scenarios in both species.

Causes of family × scenario interaction

To explore the causes of the family × scenario ($G \times E$) interaction of seedling tolerance (Table 2), results of the

Table 2 Summary of the mixed model analyses for time to death (days) of *Quercus ilex* and *Q. suber* seedlings across three scenarios of drought and *Phytophthora cinnamomi* infection (scenario; *Pc*, drought+*Pc*, and *Pc*+drought)

Species	Fixed effects	DF (NumDF, DenDF)	*F*-ratio	$p > F$
Quercus ilex	Scenario	2, 155.0	218.89	<0.001 ***
	Population	8, 81.3	1.35	0.230 ns
	Block (scenario)	78, 5367.0	3.90	<0.001 ***
	Population × scenario	16, 313.3	1.41	0.140 ns
	Random effects	VC ± s.e	VC (%)	$p > \chi^{2\,(1)}$
	Family (population)	304.6 ± 164.5	1.21	0.014 *
	Family (population) × scenario	466.2 ± 194.6	1.86	0.008 **
	Residual	24,329.0 ± 471.3	–	–
Species	Fixed effects	DF (NumDF, DenDF)	*F*-ratio	$p > F$
Quercus suber	Scenario	2, 217.0	98.65	<0.001 ***
	Population	8, 86.4	5.56	<0.001 ***
	Block (scenario)	78, 4449.0	2.76	<0.001 ***
	Population × scenario	16, 181.0	2.04	0.013 *
	Random effects	VC ± s.e	VC (%)	$p > \chi^{2\,(1)}$
	Family (population)	100.2 ± 160.5	0.36	0.357 ns
	Family (population) × scenario	593.7 ± 232.4	2.16	<0.001 ***
	Residual	26,815.0 ± 571.8	–	–

(1) Denotes the significance level associated with the chi-square value given by the difference in two times the log likelihood of the specific random factor included in versus excluded from the mixed model. Because variance components are constrained to be positive, test of variance components are one-tailed (Fry 2004)

For fixed effects, degrees of freedom (DF), *F-ratio* and associated significance level (ns: not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$) are shown. For random effects, variance component estimates ± standard errors (VC ± s.e.), corresponding variance percentage (%) and associated significance levels of the log-likelihood ratio tests $^{(1)}$ for significance of each variance component are shown

Table 3 Summary of the mixed model analysis for time to death (days) of *Quercus ilex* and *Q. suber* seedlings under each scenario of drought and *Phytophthora cinnamomi* (*Pc*) infection (*Pc*, drought + *Pc*, and *Pc* + drought)

	Quercus ilex			*Quercus suber*		
Scenario / fixed effects	DF (NumDF, DenDF)	*F*-ratio	$p > F$	DF (NumDF, DenDF)	*F*-ratio	$p > F$
Pc						
Population	8, 78.6	1.75	0.100 ^{ns}	8, 77.6	5.28	< 0.001***
Block	41, 3172.0	3.05	< 0.001***	41, 2669.0	3.11	< 0.001***
drought + Pc						
Population	8, 56.0	1.49	0.181 ^{ns}	8, 66.8	1.41	0.209 ^{ns}
Block	19, 1083.0	3.66	< 0.001 ***	19, 901.0	1.62	0.045*
Pc + drought						
Population	8, 62.9	0.90	0.524 ns	8, 59.4	4.04	< 0.001***
Block	18, 1109.0	5.23	< 0.001***	18, 872.0	3.43	< 0.001***
Scenario / random effects	VC ± s.e	$p > \chi^{2\,(1)}$	h_i^2 ± s.e	VC ± s.e	$p > \chi^{2\,(1)}$	h_i^2 ± s.e
Pc						
Family (population)	675.6 ± 201.3	< 0.001***	**0.11 ± 0.03**	689.8 ± 245.0	< 0.001***	**0.10 ± 0.03**
Residual	21,367.0 ± 537.3	–		26,103.0 ± 716.8	–	
drought + Pc						
Family (population)	441.6 ± 397.4	0.199 ^{ns}	0.06 ± 0.06	332.3 ± 448.1	0.411 ns	0.04 ± 0.05
Residual	26,301.0 ± 1140.3	–		31,997.0 ± 1522.9	–	
Pc + drought						
Family (population)	1,026.3 ± 526.0	0.011*	**0.12 ± 0.06**	1,037.7 ± 519.0	0.007 **	**0.16 ± 0.08**
Residual	30,874.0 ± 1317.6	–		23,685.0 ± 1145.3	–	

(1) Denotes the significance level associated with the chi-square value given by the difference in two times the log likelihood of the specific random factor included in vs. excluded from the mixed model. Because variance components are constrained to be positive, test of variance components are one-tailed (Fry 2004)

For fixed effects, degrees of freedom (DF), *F-ratio* and associated significance levels (ns: not significant; * $p < 0.05$; *** $p < 0.001$) are shown. For random effects, variance component estimates ± standard errors (VC ± s.e.), associated significance levels of the log-likelihood ratio tests (1) for significance of each variance component, and narrow sense individual heritabilities (h_i^2) and associated standard errors are shown (significant heritabilities are shown in bold)

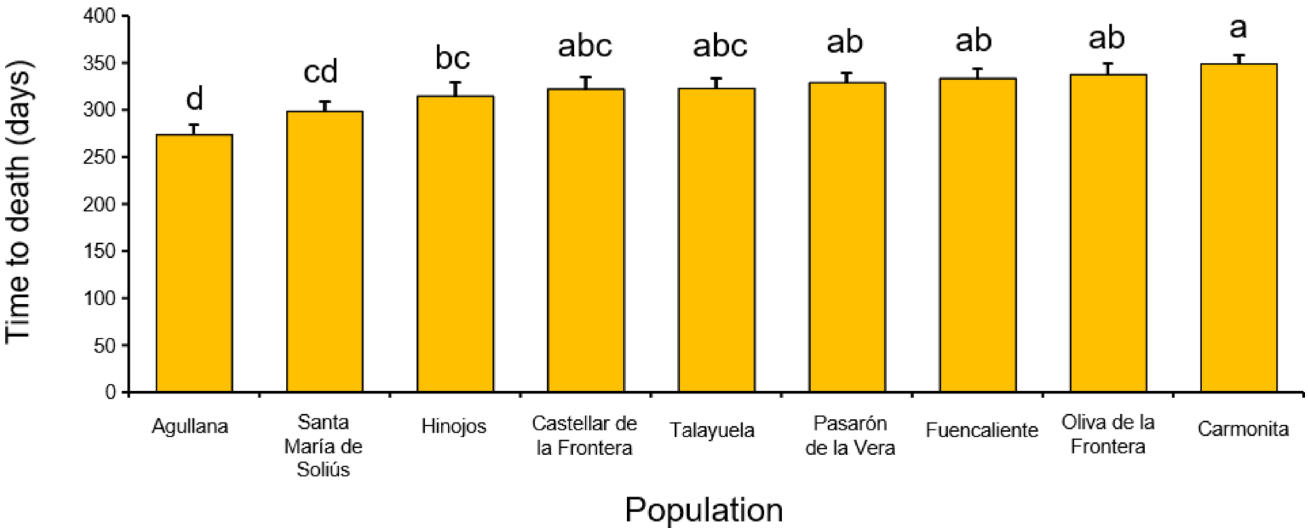
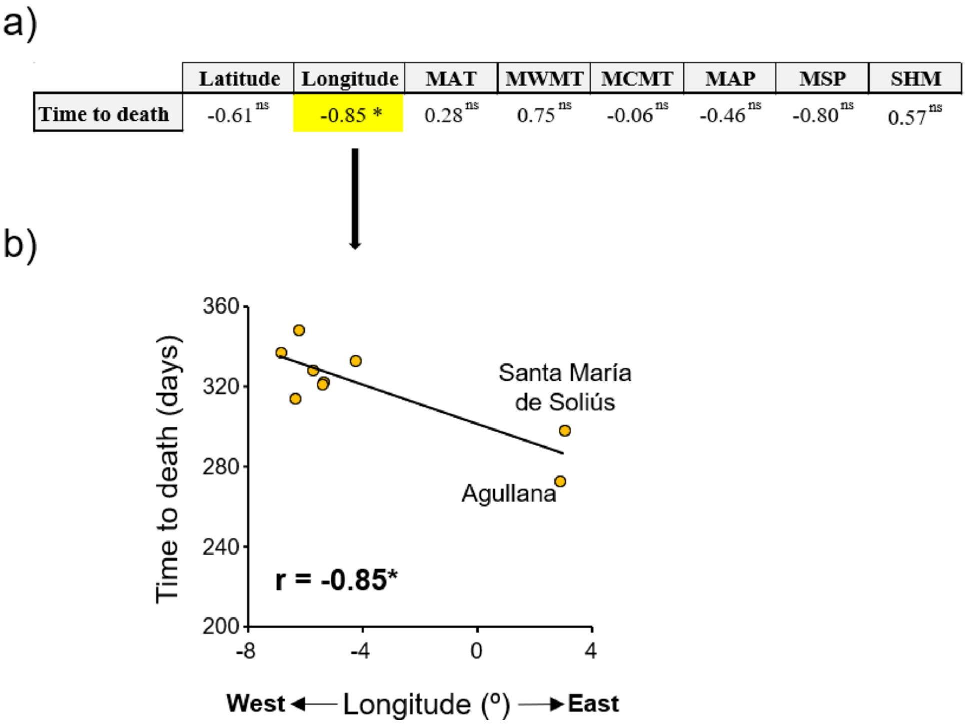


Fig. 3 Time to death of *Quercus suber* seedlings from nine populations in Spain grown under three scenarios of drought and *Phytophthora cinnamomi* infection. Location of populations is shown in Fig. 1. Bars are LSMEANS ± s.e. of values obtained under the three scenarios tested, and different letters indicate significant differences ($p < 0.05$) after using the less conservative Least Square Differences (LSD) method



	Latitude	Longitude	MAT	MWMT	MCMT	MAP	MSP	SHM
Time to death	-0.61^{ns}	-0.85 *	0.28^{ns}	0.75^{ns}	-0.06^{ns}	-0.46^{ns}	-0.80^{ns}	0.57^{ns}

Fig. 4 Correlations between LSMEANS of time to death of *Quercus suber* seedlings from nine populations grown under three scenarios of drought and *Phytophthora cinnamomi* infection and geographic and climate parameters at the seed source (latitude (°), longitude (°), MAT (mean annual temperature, °C), MTWM (mean temperature of the warmest month, °C), MTCM (mean temperature of the coldest month, °C), MAP (mean annual precipitation, mm), MSP (mean summer, May to September) precipitation, mm) and SHM (summer heat-moisture index, (MTWM)/(MSP/1000)). Pearson *r* coefficients (**a**), population values (dots) and regression lines for the only significant correlation (**b**) are shown. Bonferroni's correction for multiple comparisons was applied by dividing the critical *P-value* ($\alpha = 0.05$) by the number of comparisons made (n = 8). Significant correlation estimates (*) at $p < 0.006$ are equivalent to a Pearson *r* coefficient ≥ 0.82

likelihood-based analysis of the family × scenario interaction were summarized in Table 4. In both species, the hypothesis of perfect family correlation (H3) is rejected, but the hypothesis of homogeneous family variances (H1) cannot be rejected. Thus, the lack of perfect family correlation between scenario pairs (crossover interaction, COI), rather than the heterogeneity of family variance across scenarios (interaction due to a scale effect), was the main cause of the interaction. The interaction was therefore due to changes in family rankings (COI), the important source of the $G \times E$ interaction for breeding purposes. Similarly, the hypothesis of homogeneity of family covariance across scenarios (H2) cannot be rejected (Table 4), indicating that family rank changes are equally distributed among all pairs of scenarios, and no single scenario or pair of scenarios is responsible for the crossover interaction. The pairwise correlations of family BLUPS for seedling life expectancy were significant (but low) between the drought + *Pc* and *Pc* + drought scenarios in both species, but not between these scenarios and the *Pc* scenario (Table S4).

Phenotypic plasticity of tolerance

The best fitting model for family plasticity (the opposite of family stability) of time to death across scenarios based on the lowest -2 restricted log-likelihood, AIC and BIC values was the Eberhart-Russell model, for both species (Table S5). Using this model, estimates of phenotypic plasticity (λ-scores) varied significantly among families (Table S6), ranging from −10.0 to 195.3 (21.5-fold range) in *Q. suber* and −4.3 to 134.7 (33-fold range) in *Q. ilex*.

In *Q. ilex*, estimates of family plasticity of tolerance correlated negatively with family BLUPS of time to death under the three pooled scenarios ($r = -0.26$; $p < 0.05$), drought + *Pc* ($r = -0.54$; $p < 0.001$) and *Pc* + drought ($r = -0.67$; $p < 0.001$) and correlated positively ($r = 0.57$; $p < 0.001$) under the *Pc* scenario (Fig. 5). In *Q. suber*, plasticity estimates and family BLUPS under the pooled and *Pc* scenarios did not correlate, although they correlated under the drought + *Pc* ($r = 0.38$; $p < 0.001$) and *Pc* + drought ($r = -0.66$; $p < 0.001$) scenarios (Fig. 6). Negative correlations indicated that families with longer life expectancy exhibited higher stability (lower plasticity) across scenarios, while positive correlations indicated the opposite. The results showed that high family

Table 4 Likelihood ratios after testing hypotheses (H1, H2 and H3) on the causes of the interaction between family and scenarios of drought and *Phytophthora cinnamomi* infection ($G \times E$ interaction) for time to death in *Quercus ilex* and *Q. suber*

	# Parms	Structure type	χ^2	*Df*	$p>\chi2$
Quercus ilex					
Full Model$^+$	9	UNR			
H1: Homogeneity of family variance across scenarios	5	CS*	0.78	2	0.677
H2: Homogeneity of family covariance across scenario pairs	7	CSH	1.79	2	0.408
H3: Perfect family correlation between all scenario pairs	6	UNR^{++}	8.17	3	0.042
Quercus suber					
Full Model$^+$	9	UNR			
H1: Homogeneity of family variance across scenarios	5	CS*	0.90	2	0.638
H2: Homogeneity of family covariance across scenario pairs	7	CSH	4.53	2	0.103
H3: Perfect family correlation between all scenario pairs	6	UNR^{++}	12.40	3	0.006

$^{(+)}$ The full model is described in Sect. "Causes of family × scenario interaction" *#Parms* are the number of random parameters in each model. *Structure type* relates to the structure of the variance–covariance matrix (UNR: Unstructured Correlations (full model); CS: Compound Symmetry; CSH: Heterogeneous Compound Symmetry). $^{(*)}$ To test hypothesis 1 (H1), the CS model was compared with the CSH model. $^{(++)}$ Shows additional restrictions fixing correlations between all scenario pairs to a value of '1'. The chi-squared values (χ^2) shown are the differences in two times the log-likelihood of the full model and different simplified constrained models. Degrees of freedom (*Df*) associated with the chi-squared values result from the difference between the number of covariance parameters specifying the full and the constrained models

Analyses were performed by comparing the full model (characterized by unrestricted genetic variances and covariances across scenarios) with simplified models where different parameters of variance and covariance were restricted. $p < 0.05$ indicates that the simplified model fits significantly worse than the full model, and therefore the hypothesis associated with the imposed restriction should be rejected (see Sect. "Causes of family × scenario interaction")

tolerance and stability across scenarios occurred simultaneously under the *Pc* + drought scenario for both species, and under the drought + *Pc* scenario for holm oak.

Selection of the most tolerant stable families

Based on these results, only the *Pc* + drought scenario showed significant heritabilities, as well as a positive correlation between seedling tolerance and stability. Adjusted breeding values for time to death of the 70 *Q. suber* and 73 *Q. ilex* half-sib families subjected to *Pc* + drought are shown in Fig. 7a and b, respectively. Based on a backward selection strategy of the 20% most tolerant parents (14 for cork oak and 15 for holm oak), the estimated expected genetic gains (ΔG) for time to death were 18% for both species after one cycle of backward selection, indicating a gain of 45 days of life expectancy. Selecting the 20% most tolerant *Q. ilex* parents under the *Pc* + drought scenario reduced the relative importance of the family × scenario ($G \times E$) interaction variance by 27% compared to family variance (Fig. 7c).

Discussion

We evaluated approximately 10,400 seedlings from 87 *Q. suber* and 90 *Q. ilex* half-sib families, collected across the distribution range of the species in Spain, under three different scenarios combining drought and *Pc* infection. The objective was to elucidate the genetic basis of plastic responses in tree tolerance to inform effective strategies of forest genetic improvement.

Differences in tolerance between *Q. suber* and *Q. ilex* across scenarios of drought and *Pc* infection

In line with previous findings (Camilo-Alves et al. 2013; León et al. 2017; de la Mata et al. 2025), *Q. suber* exhibited higher tolerance than *Q. ilex* to *Pc* when plants were kept under well-watered conditions (see Fig. 1). The occurrence of drought stress after *Pc* infection resulted in significantly shorter life expectancy for both cork oak and holm oak, suggesting a synergistic effect that exacerbates tree susceptibility (San-Eufrasio et al. 2021). When drought followed infection, no significant differences were detected in tolerance between species, indicating that episodes of drought in infected oak forests will homogenize tolerance levels of species, as shown by de la Mata et al. (2025). In contrast, when drought preceded infection, increased susceptibility was observed only in *Q. ilex* (Serrano et al. 2021). Therefore, although prior drought may predispose holm oak to heightened susceptibility to the pathogen (as noted by Corcobado et al. 2014), this predisposing factor was not observed in cork oak, in agreement with González et al. (2020).

These results demonstrate significant and divergent plastic responses of tolerance in cork oak and holm oak seedlings to variable stress scenarios. The different responses of *Q. suber* and *Q. ilex* to *Pc* infection under varying drought timing underscore the complexity of plant-pathogen interactions under variable abiotic stress conditions (Ennos 2015; Gomes Marques et al. 2022). This highlights the need for better understanding of the interactions between drought and pathogen susceptibility and indicates the importance

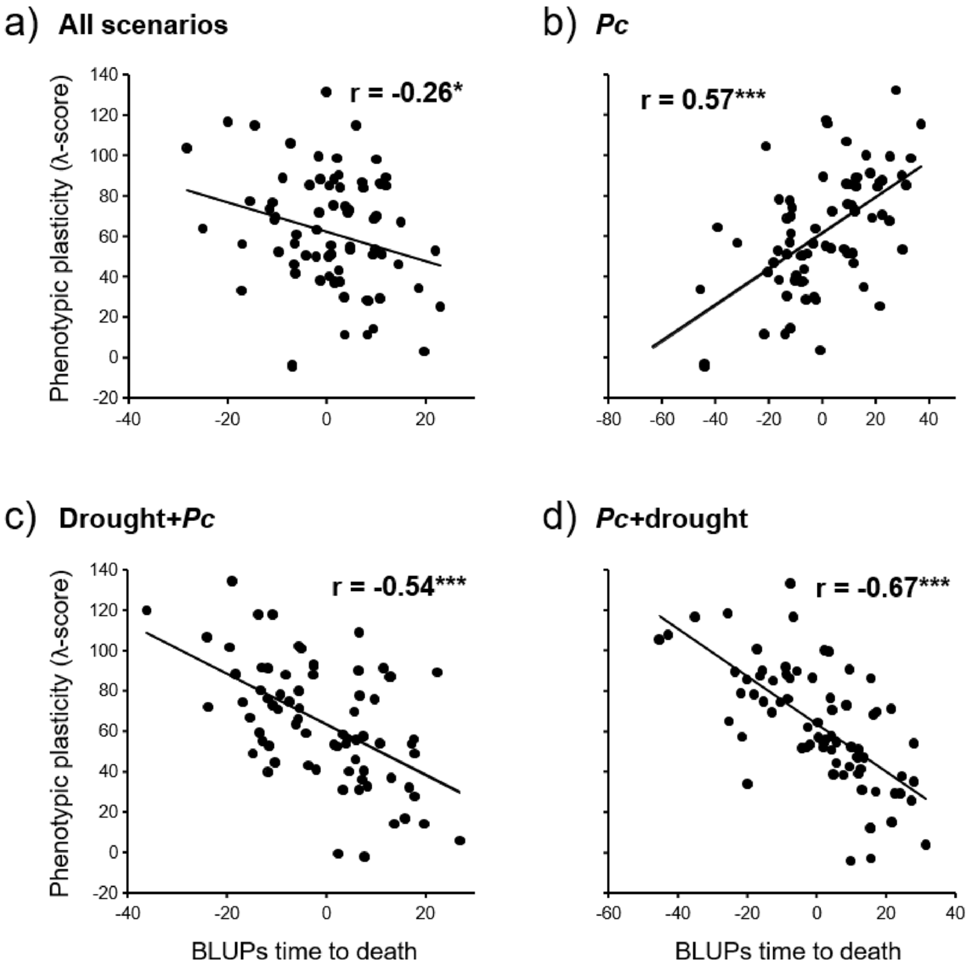


Fig. 5 Relation between phenotypic plasticity (λ-score; y-axis) and 'best linear unbiased predictors' (BLUPs) of time to death (x-axis) in all scenarios of drought and *Phytophthora cinnamomi* infection (**a**); and under the *Pc* (**b**); drought + *Pc* (**c**) and *Pc* + drought (d) scenarios for 73 *Quercus ilex* families (dots). Regression lines and Pearson *r* coefficients are shown. Asterisks indicate significant *P-values* (* $p < 0.05$; *** $p < 0.001$). Negative correlations indicate that families with longer life expectancy showed lower plasticity and thus higher stability

of selection strategies tailored to the unique ecological and physiological characteristics of each species.

East–west gradient for tolerance in *Q. suber* and lack of geographic variation in *Q. ilex*

The analysis combining all drought and *Pc* infection scenarios showed geographic variation in tolerance for *Q. suber* across its distribution range in Spain, compared to a lack of variation for *Q. ilex*, even though both species were sampled across a similar spatial range (see Fig. 1). Scenario-specific analyses supported this finding for *Q. ilex*, but for *Q. suber* under the drought + *Pc* scenario, where mortality was particularly low (Fig. S1), a lack of geographic variation was also observed. Interestingly, variation in cork oak tolerance was associated with longitude, forming an east-to-west gradient, with populations from the eastern range in Spain (i.e., Catalonia) displaying greater susceptibility.

Previous provenance trials of cork oak under stressful Mediterranean field conditions revealed significant variation among seed sources in survival (Ramírez-Valiente et al. 2010; Sampaio et al. 2016). Studies under field and greenhouse conditions identified population variation in susceptibility to *Pc* infection (Moreira et al. 2018; Martínez et al. 2023). Importantly, various functional traits associated with stress resistance in cork oak showed significant associations with longitude in earlier studies (Gandour et al. 2007; Ramírez-Valiente et al. 2014; Sampaio et al. 2016, 2019), consistent with the gradient observed here. The longitudinal trends observed in functional traits agree with the neutral genetic structure of cork oak and phylogeographic research conducted on this species (Jiménez et al. 2004; Lumaret et al. 2005; Magri et al. 2007; Pina-Martins et al. 2019). Research has repeatedly demonstrated that eastern and western cork oak populations followed different evolutionary paths, influenced by long-term historical processes. These distinct trajectories likely explain the geographic pattern of tolerance observed in our study.

Our results indicate no significant population-level variation in holm oak responses to drought and *Pc* stress, aligning with other research demonstrating limited population differentiation in drought-related functional traits (Sánchez-Vilas and Retuerto 2007; Gimeno et al. 2009) and *Pc* tolerance (de la Mata et al. 2025). However, this finding

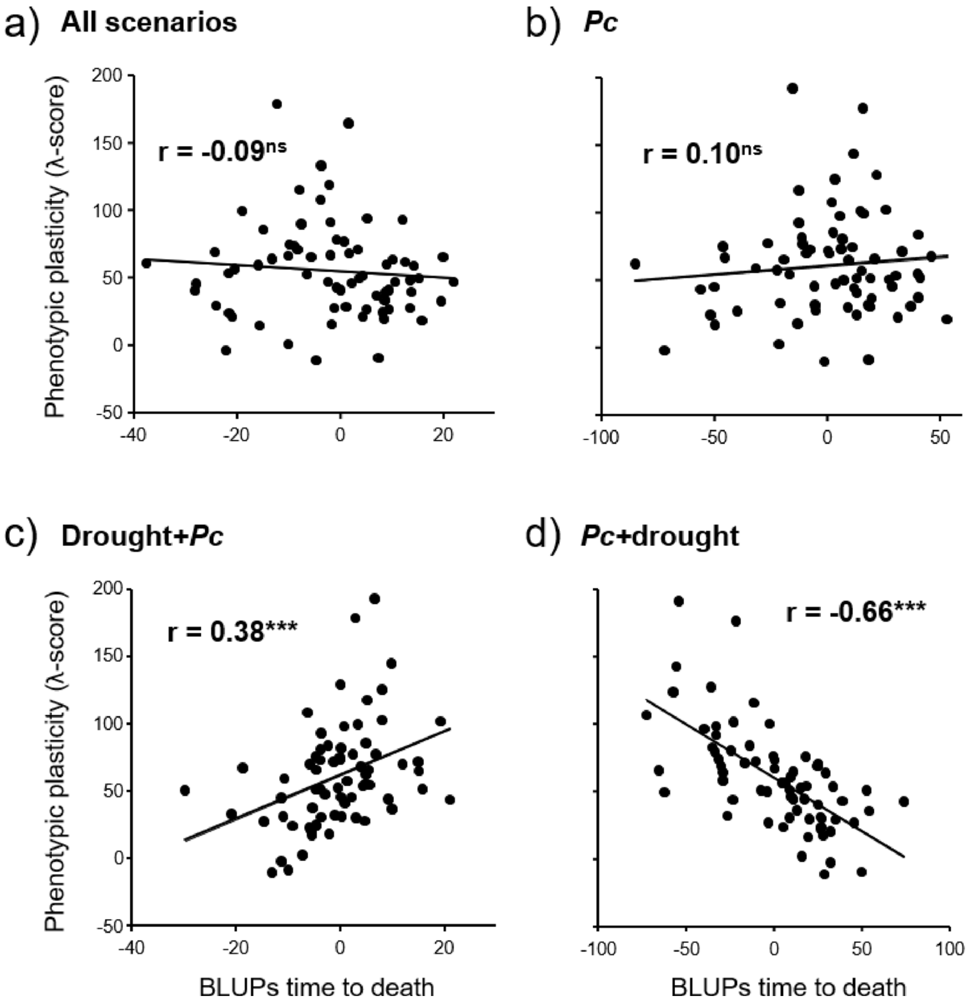


Fig. 6 Relation between phenotypic plasticity (λ-score; y-axis) and 'best linear unbiased predictors' (BLUPS) of time to death (x-axis) in all scenarios of drought and *Phytophthora cinnamomi* infection (**a**); and under the *Pc* (**b**); drought + *Pc* (**c**) and *Pc* + drought (d) scenarios for 70 *Quercus suber* families (dots). Regression lines and Pearson *r* coefficients are shown. Asterisks indicate significant *P-values* (ns: not significant; *** $p < 0.001$). Negative correlations indicate that families with longer life expectancy showed lower plasticity and thus higher stability

contrasts with studies that documented population differentiation in responses to drought (Peguero-Pina et al. 2014; Alderotti et al. 2023) and *Pc* infection (Rodríguez-Romero et al. 2022; Hernández-Lao et al. 2024). The absence of geographic variation in drought responses may be explained by inherent drought tolerance in holm oak and its ability to maintain photosynthetic activity while increasing water use efficiency under stress (Gimeno et al. 2009; San-Eufrasio et al. 2020). These species-wide adaptation strategies could override local adaptation processes, with phenotypic plasticity playing a more significant role than population-specific genetic adaptations (Gimeno et al. 2009). The discrepancy with former studies that found population-level variation in susceptibility for *Pc* tolerance could be explained by differences in experimental design, pathogen strains, or the specific populations sampled. Our findings suggest that holm oak may rely on species-wide defensive strategies rather than population-specific adaptations to combat this pathogen.

The contrasting patterns of geographic differentiation between cork oak and holm oak highlight potential differences in evolutionary strategies even among two closely related species.

Substantial additive genetic variation in the tolerance of *Q. suber* and *Q. ilex* supports genetic improvement efforts, but *G* × *E* interaction should be addressed

Our findings reveal significant additive genetic variation in *Q. suber* and *Q. ilex* under *Pc* infection and *Pc* + drought (Table 3). The genetic control of tolerance observed supports the hypothesis of substantial intrapopulation variation in susceptibility in both cork oak and holm oak, indicating the potential for improving tolerance through selective breeding. Moreover, heritability estimates highlight the specific stress scenarios of *Pc* inoculation alone and drought following inoculation as optimal for selecting tolerant genotypes to maximize breeding efficiency. However, additive genetic variation was not detected for either species when drought preceded inoculation. Under this scenario, the absence of within population variation aligns with the lack

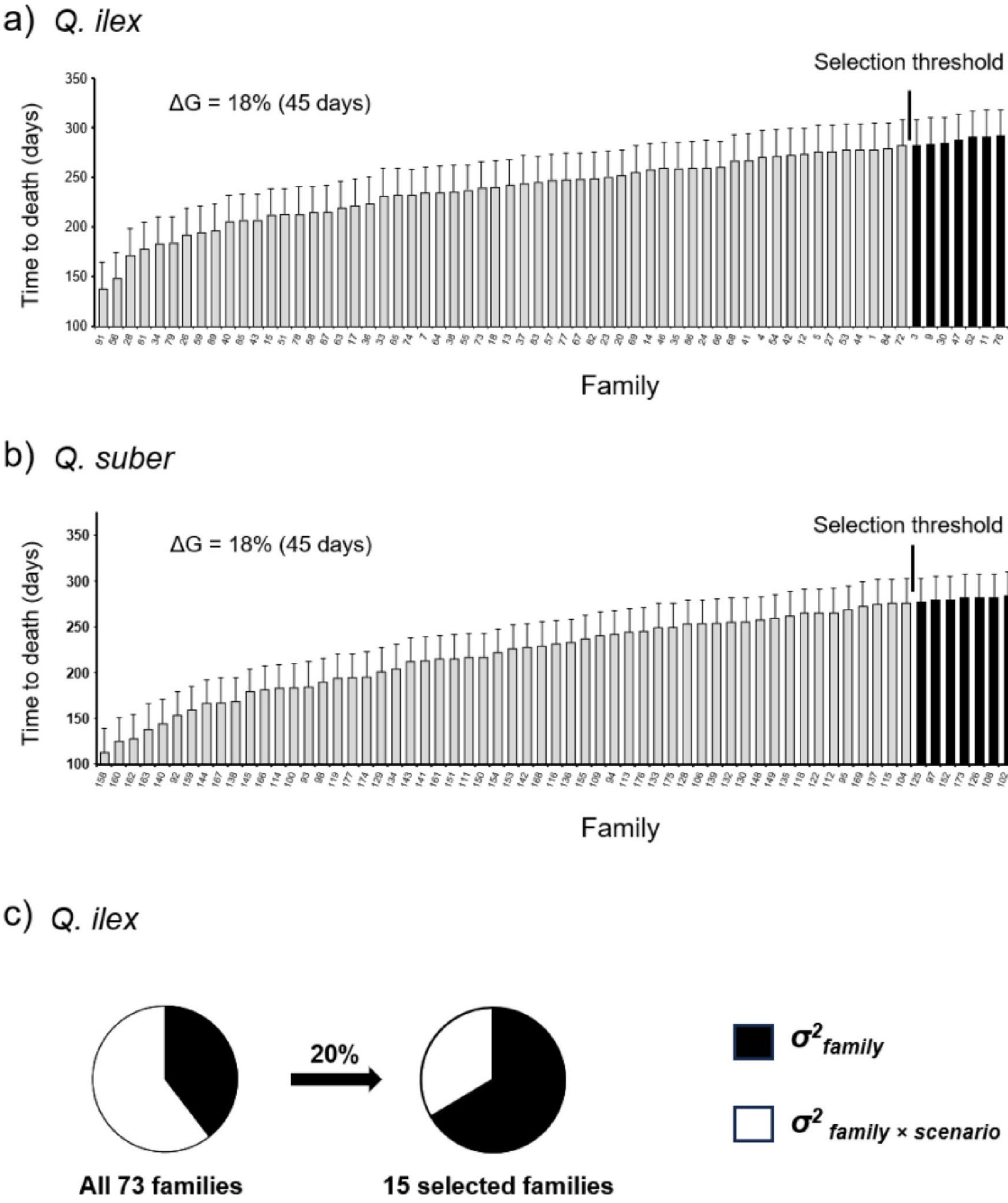


Fig. 7 Adjusted breeding values (grand mean + population estimation (BLUE) + family breeding value (2 × BLUP)) for time to death of 73 *Quercus ilex* (**a**) and 70 *Q. suber* (**b**) half-sib families tested under the *Phytophthora cinnamomi* (*Pc*) + drought scenario. A selection intensity of the 20% most tolerant parents would include the least susceptible 15 *Q. ilex* and 14 *Q. suber* mother trees (black bars) for an expected genetic gain (ΔG) of 18 and 14%, respectively, after one cycle of backward selection. Relative family × scenario (*G* × *E*) variance in relation to family (*genotypic*) variance for *Q. ilex* in all scenarios of drought and *Pc* infection (**c**, left chart) and after selection of the 20% most tolerant families to *Pc* + drought (**c**, right chart)

of geographic variation, suggesting that this combination of stresses obscured intraspecific differences.

Our study provides the first heritability estimates for *Pc* tolerance in *Q. suber*. These findings are in agreement with previous research demonstrating significant family-level genetic variation in cork oak for traits associated with survival (Sampaio et al. 2021) and drought tolerance (Ramírez-Valiente et al. 2015). In *Q. ilex*, a recent study by de la Mata et al. (2025) also identified significant heritabilities for *Pc* tolerance under drought and non-drought conditions, although heritability estimates here were generally lower.

Our results highlight the dynamic nature of genetic control in oak susceptibility under varying stress conditions, evidenced by a significant family × scenario (*G* × *E*) interaction (Table 2). Previous studies similarly reported population × site interactions for survival in both species (Ramírez-Valiente et al. 2021), highlighting relevant genetic variation in phenotypic plasticity at the population level. The complex interplay between genetic and environmental factors in tree-pathogen interactions can significantly influence host tolerance responses (Stenlid and Oliva 2016). The impact of the pathogen is shaped by how stressful conditions are for the host or how favorable they are for the pathogen, underscoring the critical role of environmental factors in predicting genetic variation in tree tolerance (Martín et al. 2023). For example, host responses to abiotic stress dictate resource allocation between defense mechanisms and tissue repair (Oliva et al. 2014), responses that are probably genetically controlled (Sniezko and Koch 2017). Consequently, genetic control of tree tolerance to *Pc* is further complicated by genetic determination of drought tolerance, potentially leading to divergent tolerance responses among tree genotypes depending on the abiotic conditions in which the infection occurs (Atkinson and Urwin 2012). Genotypes exhibiting tolerance under one environment may therefore become susceptible under different circumstances (Martín et al. 2023).

Importantly, in our study, the *G* × *E* interaction was particularly intense, with variance values far exceeding family-level variance, especially in *Q. suber*. This substantial *G* × *E* interaction reduced heritability estimates across the three stress scenarios, underscoring its impact on genetic control of tolerance. Understanding the causes and implications of this interaction is crucial for developing effective breeding strategies and predicting tree responses to changing environmental conditions (Busby et al. 2014; Li et al. 2017).

Causes and implications of genotype by environment interaction of tolerance

The primary cause of the relevant *G* × *E* interaction observed for tolerance was significant rank changes across scenarios (crossover interaction) rather than scale effects (the magnitude of differences among families varying across scenarios) (Table 4). While non-crossover interactions, caused by heterogeneity of either genetic or residual variances, are irrelevant for selection, crossover interactions caused by rank changes may have considerable impact in selection processes, as the most tolerant genotypes can differ across variable environments of stress (Hammer and Cooper 1996).

Analysis of *G* × *E* interaction for tolerance also revealed non-significant or low genetic correlations among scenarios (Table S4), indicating low similarity among scenarios in the relative tolerance of families. While high positive correlations would support common selections across scenarios, our results suggest that the best genotypes in one scenario tend to perform worse in others, implying a significant handicap for selection (Matheson and Cotteril 1990). However, the two scenarios involving drought stress showed a significant positive genetic correlation in both species, suggesting that drought responses were, to some extent, homogenizing the relative tolerance of families regardless of the timing of drought application relative to *Pc* infection. A strategy is therefore needed to address the negative consequences of *G* × *E* when selecting genotypes with enhanced tolerance to combined stress, including detailed investigation of plastic responses at the family level.

Family variation in phenotypic plasticity enables selection of tolerant families stable across variable scenarios

When significant *G* × *E* interaction affects genotypic rankings, as observed in this study, a practical approach is to select families based on their average tolerance while also considering their stability across different scenarios (Johnson and Burdon 1990; de la Mata et al. 2012). This approach would involve selecting families that demonstrate consistently high tolerance across most scenarios (i.e., above average), even if they do not rank as top performers in any single scenario. Selection based on stability is also a safeguard decision regarding current climate change that is challenging the prediction of future stress scenarios (Ledig and Kitzmiller 1992).

Stability analyses revealed large genetic variation in phenotypic plasticity, with some families showing significantly more stable tolerance than others across scenarios (Table S6). Notably, in *Q. ilex* under drought + *Pc* and *Pc* + drought (Fig. 5) and *Q. suber* under *Pc* + drought (Fig. 6), highly significant negative relations were observed between average tolerance and its phenotypic plasticity at the family level. These correlations indicate that certain families can maintain stable tolerance across varying stress conditions, enabling selection of genotypes that exhibit both high tolerance and stability under environmental variation in stress factors. Certain scenarios therefore appear to be suitable for identifying and selecting tolerant genotypes with stable performance across variable stress.

Pc infection followed by drought was the best scenario to select tolerant families with stable behavior to oak decline

Heritability estimates for tolerance in both species were highest under *Pc* and *Pc* + drought. Moreover, positive relations between average tolerance and stability in both species were observed under the *Pc* + drought scenario only. The *Pc* + drought scenario therefore met the requirements of significant genetic control and adequate correlation between tolerance and stability, and is ideal for effective selection. Under this scenario, a backward selection strategy focusing on replicating the best-performing parents in a seed orchard, with a selection intensity of 20%, would allow genetic gains of 18% in delayed time to death in both *Q. suber* and *Q. ilex* (equivalent to 45 days) (Fig. 7).

Previous studies have recommended including genotypic stability across environments as a selection criterion to address relevant $G \times E$ interaction (e.g., Johnson and Burdon 1990; Martín et al. 2023). In our study, stability-based selection not only minimized the effects of $G \times E$ interaction, reducing their relative importance by 27%, but also entails a precautionary approach in the face of climate change. Forest reproductive materials derived from selected parents installed in seed orchards could be used to restore oak forests severely impacted by decline.

Conclusions

The results confirm our first hypothesis about differential response of *Q. suber* and *Q. ilex* to *Pc* infection under variable drought occurrence. Our second hypothesis was partially supported by the geographic variation observed in cork oak, but not in holm oak, for tolerance to combined stress.

Both species exhibited significant additive genetic variation in tolerance to combined stress, supporting our third hypothesis. This intrapopulation variability in susceptibility underscores the potential for improving tolerance through selective breeding. Stability analyses also revealed substantial genetic variation in phenotypic plasticity within populations (i.e., some families exhibited more stable tolerance than others across scenarios), confirming our fourth hypothesis. Notably, a positive relation was identified between tolerance and stability under the *Pc* + drought scenario, allowing for selection of genotypes that exhibit both high tolerance and stable performance across varying stress conditions. Consequently, the *Pc* + drought scenario provided the most informative conditions for selecting genotypes with high tolerance and stability.

This study reports the possibility of selecting tolerant families with stable performance across variable environments of stress, enabling genetic gains in tolerance. Our findings provide a solid foundation for developing genetic improvement programs to increase the tolerance of Mediterranean oaks to decline. To further confirm the durability and stability of tolerance, we will establish long-term field trials involving selected genotypes in areas affected by oak decline.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10342-025-01857-3.

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Author contributions R.M. and A.S. conceived the manuscript; R.M. refined the raw data, performed the statistical analyses and created the figures and tables; A.S., B.C., R.T., R.G. and F.A. performed the greenhouse experiments and provided data of the assessments; A.S. and F.P. secured funding and managed the project; R.M. wrote the first version of the manuscript and all authors contributed to it.

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Data availability The data that support the findings of this study is available in Zenodo Digital Repository at https://doi.org/10.5281/zenodo.17969915.

Declarations

Conflict of interest The authors declare that there is no conflict of interest.

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