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Does parental tree size determine acorn germination in *Quercus ilex* L. dehesas?

Hermine Houdas [a,*], Jaime Madrigal-González [b], Anna Pallàs Martín [c], Fernando Silla [c], Belén Fernández-Santos [c]

[a] *EiFAB-iuFOR, Universidad de Valladolid, campus Duques de Soria, Soria 42003, Spain*
[b] *ETSIIAA-iuFOR, Universidad de Valladolid, campus La Yutera, Palencia 34004, Spain*
[c] *Departamento de Biología animal, Ecología, Parasitología, Edafología y Química Agrícola, Universidad de Salamanca, campus Miguel de Unamuno, Salamanca 37007, Spain*

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ABSTRACT

Quercus ilex L. is an evergreen tree species widely spread throughout southwestern Europe. However, its poor natural regeneration poses major challenges since the 1980s, and so assisted regeneration is speculated to be critical for either maintaining existing populations or recovering degraded ones. This method, nonetheless, raises major operational challenges related to fruit harvesting and selection in the field. For instance, the link between parental tree traits, such as age and size, and acorn characteristics has seldom been addressed; yet it could be decisive for streamlining acorn selection. In this study, we employed Structural Equation Models (SEM) to examine the relationship between parental tree Diameter at Breast Height (DBH) and acorn traits determinant for seed germination in *Quercus* species worldwide. Specifically, we measured acorn dry mass (ADM), seed moisture (SM), and pericarp thickness (PT) in a *Q. ilex* population in central-western Spain. Our results indicate a significant positive influence of parental tree DBH on ADM, with larger acorns associated with higher germination percentages. Similarly, SM positively influenced germination, though it was influenced by acorn size through two contrasting pathways. PT, on the other hand, negatively impacted germination and was also negatively affected by ADM. These findings suggest that acorn selection should prioritize large/old trees to maximize germination via increased ADM. Further research, nonetheless, is needed to progress in the relationships between parental tree traits and acorn characteristics in this and other similar contexts in which large-scale plans for *Q. ilex* regeneration would be planned.

1. Introduction

Quercus ilex L. is the most abundant tree species in southwestern Europe (de Rigo and Caudullo, 2016). It is dominant in extensive natural and anthropogenic landscapes where, for centuries, it has had a significant contribution to the economy in rural areas (de Rigo and Caudullo, 2016). However, this tree species is currently experiencing widespread declines, especially in dehesas (Gallego et al., 1999; Lloret et al., 2004; Rodríguez-Calcerrada et al., 2017). Dehesas are traditional agroforestry systems widely spread by the territories of western Spain and Portugal, where open woodlands, typically formed by oaks or cork trees, are combined with areas for grazing livestock and sometimes cultivation (Eichhorn et al., 2006). Alongside unprecedented mortality due to aging and diseases (Bran et al., 1990; Bacilieri et al., 1993; Villar-Salvador et al., 2004; Leiva and Fernández-Alés, 2005; Pulido and Díaz, 2005), declines in holm oak populations are attributed to its unexpectedly low regeneration rates, which are insufficient to sustain long-term population recovery and stability (Pulido and Díaz, 2005). Multiple non-exclusive hypotheses have been proposed to explain this situation. For instance, while some authors emphasize the high vulnerability of this species to rising frequency and intensity of drought in the last decades, particularly at the very early stages of seedling development (Villar-Salvador et al., 2004; Pulido and Díaz, 2005; Ogaya and Peñuelas, 2007; Rodríguez-Calcerrada et al., 2017), others have pointed to potential negative self-allelopathic effects during germination (Bran et al., 1990; Bacilieri et al., 1993). The potential negative effect of pre-dispersal predation of acorns by insects (Leiva and Fernández-Alés, 2005; Espelta et al., 2009; Muñoz et al., 2014) and post-dispersal

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* Corresponding author.
E-mail address: herminejosephine.houdas@uva.es (H. Houdas).

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predation by vertebrates (Gómez, 2004; González-Rodríguez and Villar, 2012; Pemán et al., 2017) has also been proposed as contributing factors. More recently, the lack of nurse shrubs in grassland landscapes, which are usually removed during silviculture activities, has been identified as another detrimental factor for regeneration (Moreno and Pulido, 2009), since facilitation of seedlings during early developmental stages is decisive for seedling survival in dehesa-like systems (Pulido and Díaz, 2005; Pulido et al., 2010; Moreno and Rolo, 2014; Costa et al., 2017; Díaz-Hernández et al., 2021). The poor regeneration of *Q. ilex* in these Mediterranean environments is likely a consequence of a complex combination of the above-mentioned factors. Accordingly, ensuring the long-term viability of the species will require assistance in vast territories to maintain the multiple functions and services it provides to local settlements.

Regeneration of holm oaks in dehesas can take place through sexual reproduction, which is contingent upon processes such as dispersal and germination of acorns, and/or vegetative reproduction, which relies on the ability of trees to resprout after disturbance (Sánchez-Humanes and Espelta, 2011; Pemán et al., 2017). Although usually faster and more effective, resprouting has the disadvantage of not adding genetic variability to the offspring (Sánchez-Humanes and Espelta, 2011; Pemán et al., 2017; Rodríguez-Calcerrada et al., 2017), which can seriously compromise the species' ability to adapt to new climatic scenarios (Gratani et al., 2003; Lefèvre et al., 2014; Rodríguez-Calcerrada et al., 2017). For this reason, sexual regeneration is crucial in the face of ongoing climate change. Nonetheless, because of the interplay of different factors, regeneration is becoming increasingly compromised (Pulido and Díaz, 2005; Pulido et al., 2010), and so assistance from landowners is, and will continue to be, necessary. To this end, a good selection of acorns constitutes the first critical stage to make the process plausible and efficient in extensive territories. Many studies have attempted to evaluate the importance of characteristics such as acorn size, pericarp size, and moisture content on acorn germination (Gómez, 2004; Bonito et al., 2011; González-Rodríguez et al., 2011a; González-Rodríguez et al., 2011b). For this reason, acorn selection based on such characteristics seems reasonable and critical to save time and resources, as non-directed processes of acorn searching in the field can extend throughout the entire acorn yielding season. It would therefore be necessary to establish well-defined protocols starting with the selection of parental trees prior to proceeding with the acorn yielding. Nevertheless, a direct link between characteristics from parental trees and key traits in acorns remains poorly evaluated. Additionally, the influence of parental tree size or age on germination probability through these acorn characteristics is still underexplored (Fernández-Santos et al., 2013; Alonso-Crespo et al., 2020). In these types of anthropogenic ecosystems, the variability in the size and age of holm oaks is not usually conserved, since the establishment of new seedlings is scarcely encouraged (Plieninger, 2006).

In this study we aimed at unveiling the significance of size/age of parental trees driving acorn traits such as acorn dry mass (ADM), seed moisture (SM), and pericarp thickness (PT) using Structural Equation Models (SEM) applied to experimental data. Specifically, we aimed at addressing the following questions: 1) Does parental tree DBH influence key acorn traits such as acorn mass in *Q. ilex*?, and 2) Do these acorn traits mediate any relationship between parental tree DBH and germination? We hypothesize that parental trees will have a role in driving ADM, which in turn will be reflected in acorn germination directly, or via SM and/or PT indirectly. So far, only one study has briefly explored the potential mechanisms underpinning such a relationship between parental tree age and germination, finding that acorns from younger parental trees exhibit shorter germination and emergence times and higher germination percentages compared to those from older trees (Alonso-Crespo et al., 2020).

2. Material and methods

2.1. Study Area

The study area is located in Torresmenudas, a small village 20 km north of the city of Salamanca (central-western Spain). All the field measurements and acorns were collected in a recently abandoned dehesa system, which has been dedicated to the extensive grazing of Iberian pigs for decades. The dominant tree species are the holm oak (*Q. ilex* subsp. ballota (Desf.) Samp.) and the gall oak (*Q. faginea* Lam.), and the understory is mostly composed of native shrubs of the genus *Cytisus* and *Cistus* (Alonso-Crespo et al., 2020). Elevation is 800 m above sea level, with slopes up to 18 % (Alonso-Crespo et al., 2020). Geologically, the substrate is dominated by sedimentary deposits (Eocene period), terrigenous in nature but with carbonate crusts (Pineda et al., 2011). The predominant soil type in the area is cambisol (FAO soil classification), neutral or slightly acidic, with high water retention capacity and moderate cation exchange capacity (Dorronsoro, 1992). The climate is typically Mediterranean, with hot and dry summers. According to the Spanish National Meteorological Agency (AEMET), the average annual temperature is 12.2°C, and average annual rainfall ranges between 350 and 400 mm.

2.2. Field data recording

We collected acorns in adult trees belonging to three different size classes (different Diameter at Breast Height, DBH), i.e., small trees (DBH < 20 cm), medium-sized trees ($20 \leq$ DBH < 40 cm), and large trees (DBH ≥ 40 cm) (see Table 1 for descriptive information). First, we randomly distributed 14 points across the study area and we selected the three nearest trees to each point, ensuring that one tree from each DBH-age category was represented in each point (corresponding to a total of 42 trees selected). When some of the trees were not considered due to the apparent scarcity of acorns, that is, when acorns could be counted individually with the naked eye (Gordon and Faulkner, 1992a), the next nearest tree from the same DBH-age category was selected instead. Each selected tree was numbered, double-marked, and geo-located using a GPS device.

Acorns were collected in November, as this is usually the ideal time for acorn maturity in the Mediterranean area (Leiva and Fernández-Alés, 1998; Branco et al., 2002; Bonito et al., 2011; Pasquini et al., 2011). We assumed acorns to be in a good state of maturity when the pericarp had already turned brown, the cupule could be easily removed, and the color of the top after the cupule's removal was white (Bonner and Vozzo, 1987; Pasquini et al., 2011). The fruits were collected manually by shaking the branches with a stick over a blanket spread out beneath the trees.

Although a total of 42 trees were initially selected, 14 from each category, some of them were posteriorly discarded from the analyses due to extensive damage of their acorns caused by insects or other affections such as visual cracks and chips, as it may have an impact on acorns viability. At the end, 37 trees were used in the study: 12 from the "Small" category, 14 from the "Medium" category, and 11 from the "Large" category (Table 1).

Table 1
Main features of the selected trees for each size category and all trees: (tree size category), number of trees, DBH in cm, tree age in years, total number of collected acorns, and healthy acorns among the collected acorns in %. DBH, tree age, and % of healthy acorns values are presented as mean ± standard error.

Tree category	N° trees	DBH	Tree age	Total acorns	% healthy
Small	12	14.5 ± 0.7	34 ± 2	1732	54.8 ± 6.6
Medium	14	29.9 ± 0.9	105 ± 9	2103	59.1 ± 5.1
Large	11	57.6 ± 4.0	279 ± 25	1922	61.2 ± 6.6
All	37	33.1 ± 3.1	139 ± 26	5757	58.3 ± 3.4

2.3. Experimental design and laboratory work

Following field recollection, acorns were visually inspected and subjected to a flotation test, and the damaged fruits were discarded (Bonner and Vozzo, 1987; Bonfil, 1998; Connor, 2004; Bonito et al., 2011). The remaining acorns were air-dried for two days to ensure that they lost all the moisture acquired in contact with water, since storing them with excessive moisture can lead to the proliferation of fungi (Pemán et al., 2017). After that, the acorns were stored in a refrigerator at a temperature between −2ºC and 3ºC to maintain the ideal conservation temperature (Pemán et al., 2017) until used to carry out the experiment. They were stored by tree in 100 µm thick polyethylene bags, since thicknesses between 75 and 100 µm allow for the exchange of gases such as CO_2 and O_2 but not water vapor, which is ideal for adequate conservation (Bonner and Vozzo, 1987; Gordon and Faulkner, 1992b; Lombardo and McCarthy, 2009; Pemán et al., 2017). In each bag, acorns were individually stored in highly thin bags with a small portion of silica gel to avoid any undesirable negative effect of excessive moisture.

To carry out the germination experiment, 20 acorns were randomly selected from each parental tree, constituting a total of 740 acorns. A template for alternate placement of fruits was designed: the 20 acorns per tree were individually sown in each one of the 20 germination trays (replicates with cells of 4 cm deep x 4 cm wide). The acorns were positioned vertically on the substrate (peat and vermiculite), with the tip containing the embryo slightly stuck in the substrate (Bonfil, 1998). The germination trays were placed in an unlit room at a constant average temperature of 23°C, ideal conditions for germination (Broncano et al., 1998; Branco et al., 2002; Pasquini et al., 2011; Pemán et al., 2017). We both watered with distilled water and checked out the germination of each acorn twice a week throughout the experiment, which lasted for two months.

For each acorn, we measured acorn fresh mass at the beginning of the germination experiment, while the seed was separated from the pericarp using a scalpel for seed and pericarp fresh mass, as soon as acorns germinated or once the experiment was finalized. Subsequently, seed and pericarp dry mass, and thus ADM (seed dry mass + pericarp dry mass) were determined after oven drying for 48 hours at 70ºC so acorns would lose all the moisture (Bonfil, 1998; Leiva and Fernández-Alés, 2005; Lombardo and McCarthy, 2009). Acorns and their fractions were weighed with an analytical balance (Sartorius CP-124S, precision of 0.1 mg), and their length and width were measured using an electronic digital caliper (Mitutoyo 500–196–30, precision of 0.01 mm) to determine their volume, assuming acorns have an ellipsoidal shape. From the variables measured for each acorn, we focused on ADM, SM as the percentage moisture content of the seed (SM = [(seed fresh mass – seed dry mass) / seed fresh mass] x 100), and the ratio (pericarp dry mass / acorn volume) as a surrogate of PT to evaluate the indirect influence of parental tree size/age on acorn germination.

2.4. Statistical analyses

All data analyses were conducted using the statistical software R (R Core Team, 2024). To evaluate the relationship between parental tree DBH and the probability of acorn germination, with the acorn traits as conditioning factors, a SEM was developed. We firstly defined ADM as a linear function of parental tree DBH, and PT as a linear function of ADM. Secondly, we defined SM as a linear function of PT and ADM. These regressions were carried out with a gamma distribution of error and log link functions. Thirdly, we defined acorn germination (yes/no) as a function of ADM, SM, and PT through a binomial mixed-effects model with a logit link function. All regressions in the SEM were conducted using the ‘glmer’ function from the *lme4* R package (Bates et al., 2015). Mixed-effects models were used to account for dependencies associated with the parental trees as sources of the acorns yielded in the field. Thus, the parental trees were included in the models as a random factor and derived as a variance component affecting the intercept parameter. Finally, we used the Fisher’s C and the Chi-squared scores, respectively, as global goodness-of-fit tests to validate results within a local estimation framework. Both the SEM analysis and the calculation of Fisher’s C score were performed using the *piecewiseSEM* R package (Lefcheck, 2016).

3. Results

Mean DBH, considering all the parental trees, was 33.1 ± 3.1 cm (Table 1). Mean acorn fresh mass and standard error was 3.75 ± 0.04 g, with 1.17 g and 8.32 g being the lowest and highest values, respectively. As for ADM, the mean was 2.31 ± 0.03 g, with 0.87 g and 5.55 g as extreme values. ADM and acorn fresh mass were highly correlated (Spearman correlation test; $\rho = 0.962$; $p < 0.001$), so the choice of ADM as a variable associated to acorn mass was interpreted as equally valid. Seventy-five percent of acorns collected in small parental trees weighed less than 2 g, 75 % of acorns from medium-sized parental trees weighed between 2 and 3.75 g, and about 86 % of acorns weighing more than 3.75 g came from large parental tree (Fig. 1). Accordingly, ADM was notably correlated to the size of the parental tree ($r = 0.578$, $p < 0.0001$, Fig. 2).

ADM negatively influenced SM (p-value$_{ADM\_SM}$ = 0.0036; Fig. 3A). Moreover, we observed marked differences in SM (mean of 39.6 ± 0.2 %) between acorns that successfully germinated and those that did not, with germinated acorns exhibiting a moisture content up to 10 percentage points higher (41.9 ± 0.1 % vs. 31.7 ± 0.5 %). No additional acorns germinated for SM values below 33.5 %. Interestingly, moisture content varied between the pericarp and the seed, with averages of 31.3 ± 0.2 % and 39.6 ± 0.2 %, respectively. PT was negatively affected by ADM (p-value$_{ADM\_PT}$ < 0.0001; Fig. 3B). The mean PT was also lower in germinated acorns (0.116 ± 0.001) compared to non-germinated acorns (0.126 ± 0.002). However, no clear distinction was observed between PT values for germinated and non-germinated acorns, as PT ranged from 0.070 to 0.197 in non-germinated acorns and from 0.072 to 0.186 in germinated acorns.

The relationship between ADM and size of parental trees was confirmed in the SEM ($\beta_{DBH\text{-}ADM} = 0.188$, p-value < 0.0001; $R^2 = 0.56$; Fig. 4). ADM, in turn, was significantly and negatively related to both SM and PT ($\beta_{ADM\text{-}SM} = -0.060$, p-value < 0.0001; $\beta_{ADM\text{-}PT} = -0.092$, p-value < 0.0001, respectively). Furthermore, there was also a significant and negative effect of PT on SM ($\beta_{PT\text{-}SM} = -4.719$, p-value < 0.0001). On the contrary, there was no significant direct relationship between the parental tree DBH and SM or PT in the model. Both ADM and SM positively affected germination ($\beta_{ADM\text{-}Germination} = 0.574$, p-value < 0.0001, and $\beta_{SM\text{-}Germination} = 0.933$, p-value < 0.0001, respectively), whereas PT exerted a negative effect on germination ($\beta_{PT\text{-}Germination} = -10.890$, p-value < 0.0001). We found a slight significant missing path in the SEM between the parental tree DBH and PT (p-value = 0.0135), yet this influence did not affect the model fit as shown by the Fisher’s C (C = 12.265, p-value = 0.056) and the Chi-squared ($X^2 = 6.787$, p-value = 0.079), respectively.

4. Discussion

Our results support the role of parental tree size in germination through its influence on acorn traits. Specifically, large/old parental trees produced larger acorns, which were associated with higher germination percentages. Similarly, SM contributed to higher germination percentages but was negatively affected through two distinct and opposing pathways. First, acorn size had a direct negative effect on SM. Second, larger acorns led to a reduction in PT, and this reduction, in turn, had positive effects on SM. Interestingly, PT had a significant negative influence on acorn germination.

Large-sized parental trees produced larger acorns in terms of ADM as shown by the significant linear relationship (Fig. 1; Fig. 2). While

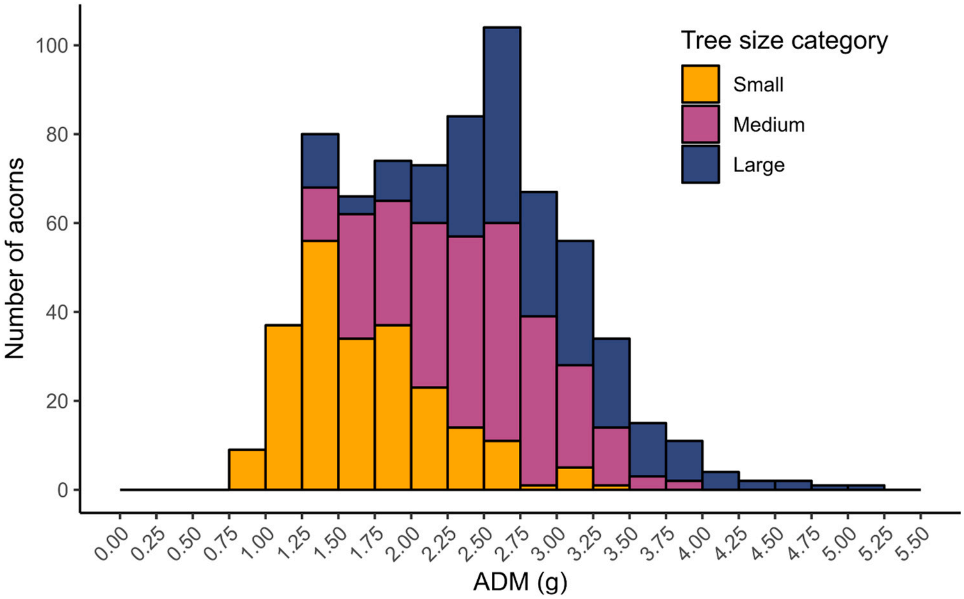

Fig. 1. Graphical representation of acorn dry mass (ADM) distributed by parental tree size categories. n = 37.

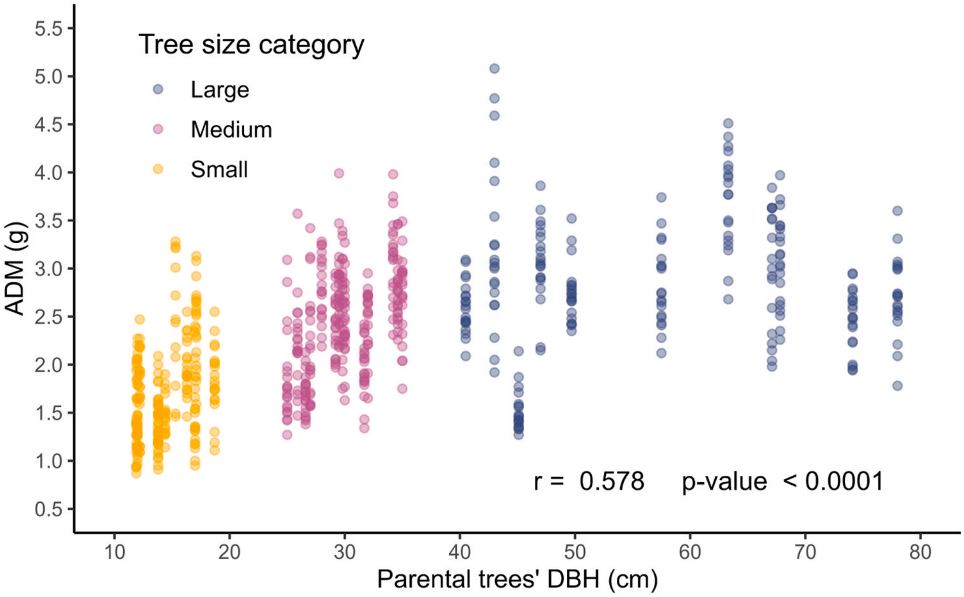

Fig. 2. Relationship between parental tree DBH and the acorn dry mass (ADM). Pearson correlation (r) and p-value of the linear model are also indicated. n = 37.

previous studies focusing on tree-level determinants of acorn size in *Quercus* species have stressed the importance of individual tree features for acorn size using categorical approaches (Alonso-Crespo et al., 2020; Dobrosavljevic et al., 2022), other support neglective relationships using continuous metrics of tree size (Alejano et al., 2011). Moreover, Martiník et al. (2014) demonstrated that the tree size-acorn size relationship can be contingent upon the year of study. However, it is noteworthy that beyond a certain tree size, ADM seemed to reach asymptotic values and may even begin to decrease. Gea-Izquierdo et al. (2006) pointed out that, although acorn production at very early stages of development is significantly low due to limited first flowering and reproductive immaturity, patterns of acorn production tied to tree size or age remain elusive. From carbon storage dynamics and losses in photosynthetic efficiency to source-sink carbon dynamics related to resource economy, a number of hypotheses on productivity decay with tree age have been formulated. However, most of the time, productivity and wood production are made exchangeable, while it is currently well known that acorn production or size and radial growth are not necessarily related, especially in masting species (Hoch et al., 2013; Patterson et al., 2023). More research is needed to fix patterns of acorn size with tree age in *Quercus* species and to unveil the underlying mechanisms of such relationships.

SM and PT were not influenced by DBH, but SM was linked to acorn size through two contrasting pathways (Fig. 3; Fig. 4). On one hand, acorn size had a direct negative effect on SM, likely due to the lower surface-to-volume ratio of larger acorns, which induces them to have lower permeability and reduced water uptake efficiency (Upretee et al., 2024). Additionally, acorns of our germination experiment were positioned vertically with the seed tip slightly embedded in the soil, which may have limited uniform water access across the cotyledon areas, especially in larger acorns (Finch-Savage and Clay, 1994). On the other hand, larger acorns tended to have thinner pericarps, which indirectly

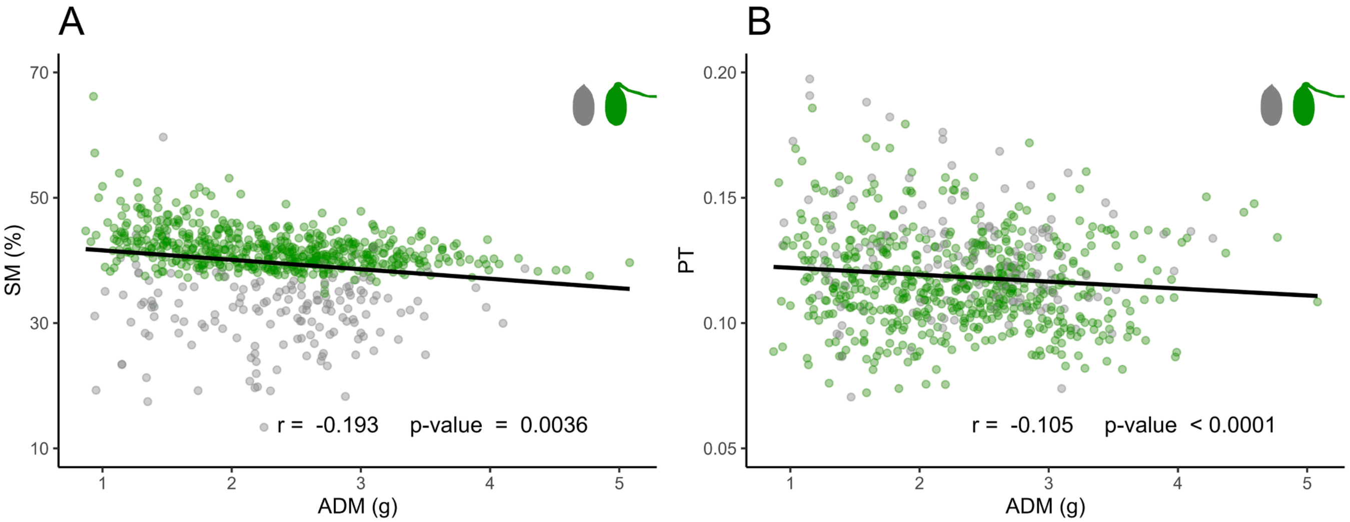

Fig. 3. A) Relationship between acorn dry mass (ADM) and seed moisture (SM), and B) between acorn dry mass (ADM) and pericarp thickness (PT). Germination status is indicated by schematic acorn illustrations and colors (germinated acorns in green and non-germinated in grey). Black solid lines represent fitted linear relationships. Pearson correlations (r) and p-value of the linear models are also indicated. n = 37.

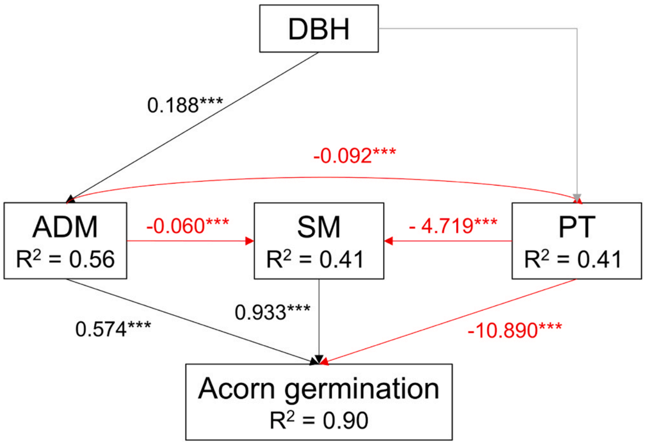

Fig. 4. Structural equation model (SEM) fitted to evaluate the hypothesis that parental tree DBH drives acorn germination indirectly through direct influence on acorn dry mass (ADM), seed moisture (SM), and pericarp thickness (PT). Red arrows represent negative relationships, whereas black arrows represent positive relationships. The grey arrow indicates a significant missing path from parental tree size to acorn germination. Significance is indicated as follows: p-value < 0.05 ('), p-value < 0.01 (*), p-value < 0.001 (**), and p-value < 0.0001 (***). All estimates included in the figure are standardized estimates. n = 37.

promoted higher SM, as PT was negatively correlated with SM. These results are consistent with the literature, as desiccation in *Quercus* fruits have primarily been associated with the thickness of the palisade parenchyma and the cuticular wax layer of the pericarp (Daws et al., 2006; Bonner., 1968; Sobrino-Vesperinas and Viviani, 2000). Given that our acorns were regularly watered instead of being allowed to dry during the germination experiment, the observed decrease in moisture values with PT thus reflects the role of pericarp as well as a mechanical barrier for water uptake. However, recent studies suggest that the dynamics of water entry and exit depend more on the surface area and anatomical features of the cupule scar than on pericarp thickness. This structure facilitates a higher rate of water flow through the scar compared to the rest of the pericarp (Xia et al., 2012; Kang et al., 2023). This may be particularly important in natural environments, where the vascular scar is in direct contact with the soil. In contrast, under our experimental conditions, acorn position prevented the vascular scar from contacting the soil, so the rest of the pericarp was the only available structure for water movement. If these assumptions were true, it would mean that our results are only applicable to similar germination experiments.

Our results supported multiple causal pathways from acorn traits to acorn germination (Fig. 4). Firstly, larger acorns showed a significantly higher probability of germination than smaller ones directly, which is coherent with outcomes obtained in other oak species (Sánchez-Montes de Oca et al., 2018; Woziwoda et al., 2024). However, some studies dealing with the acorn size-germination rate relationship are seemingly inconclusive. For instance, a study with *Q. faginea* in a nearby field site supported somewhat contradictory findings using a field survey approach (Alonso-Crespo et al., 2020). Authors observed that acorn size did not directly determine germination, but young parental trees, which mainly produced small acorns, were associated to higher percentages of germination than old parental trees, in which acorns were larger. These results, nonetheless, were achieved using only two size/age categories of parental tree size with very young (29 years old) and very old individuals (> 200 years old). Further efforts should be directed towards the standardization of tree size/age gradients among populations and species to make studies more suitable for comparison. Secondly, our results confirm that SM content positively impacts acorn germination. It is well-established that recalcitrant seeds, such as those of most *Quercus* species, are highly sensitive to moisture levels during the pre-germination phase (Gosling, 1989; Gordon and Faulkner, 1992b; Pasquini et al., 2011; Joët et al., 2013). Germinated acorns had seed moisture contents of around 42 %, while those that failed to germinate averaged only 32 % moisture at the time of germination, aligning with values reported in the literature (Gosling, 1989; Pasquini et al., 2011; Pemán et al., 2017; León-Lobos and Ellis, 2018). Finally, we found a direct effect of PT on acorn germination (Fig. 4). It agrees with Amimi et al. (2020), who found that PT in Mediterranean oaks significantly constrained acorn germination rates, supporting the hypothesis that the pericarp acts as a mechanical barrier for germination, potentially limiting germination success. Interestingly, other factors, such as shedding date, may play a more decisive role in germination than seed size and moisture content (Finch-Savage and Clay, 1994), suggesting the need for deeper research on the effects of acorn traits in relation to their maturation and shedding timing on germination.

5. Conclusion

Seed selection should be the first step in conservation programs to promote the successful regeneration of *Q. ilex*. Based on the results of the present work, it could be assumed that an older *Q. ilex* population is indirectly associated with a higher probability of acorn germination. Although this assertion may be true in the short term, it has been suggested in other studies that maintaining size variability, whether of trees or fruits, is a good strategy to provide the species with greater versatility and adaptability to changes that may occur eventually (Kikuzawa and Koyama, 1999; Alonso-Crespo et al., 2020). For example, large acorns have been found to have an advantage over small acorns in germination, whereas the scenario may change completely in natural conditions during an especially dry winter, as small acorns, with thicker pericarp, are more resistant to desiccation during the pre-germination phase (Daws et al., 2006). In addition, other studies have pinpointed a higher speed of germination of small acorns (Norden et al., 2009; Alonso-Crespo et al., 2020). Even if large acorns generally lead to large seedlings with a higher survival rate (Shi et al., 2019; Woziwoda et al., 2024), they also tend to be preferentially selected by their predators (Gómez, 2004; Pons and Pausas, 2007). In contrast, small acorns probably have the advantage of being more numerously produced and more easily dispersed (Kikuzawa and Koyama, 1999). The importance of the results obtained here, therefore, relies on the need to know exactly which scenarios are advantageous and disadvantageous for each type of acorn and tree in order to have more information to face the serious problem that exists in the natural regeneration of Iberian *Quercus* species, particularly in dehesa-like ecosystems.

CRediT authorship contribution statement

Silla Fernando: Writing – review & editing, Validation, Project administration, Conceptualization. **Fernández-Santos Belén:** Writing – review & editing, Writing – original draft, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization. **Houdas Hermine:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation. **Madrigal-González Jaime:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Pallàs Martín Anna:** Writing – original draft, Investigation, Formal analysis, Data curation.

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.

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Data availability

Data will be made available on request.

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