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RESEARCH PAPER

Variation of cork porosity along the stem in harvested cork oak (*Quercus suber* L.) trees

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Abstract

• ***Key message*** **Cork porosity, due to lenticular channels, varied along the stem of *Quercus suber* L. Lenticular channels' area, rather than their number, decreased upwards along the stem. Area decrease was observed regardless of tree size and of its intrinsic porosity.**

• ***Context*** The cork of *Quercus suber* L. is radially crossed by lenticular channels, defining cork's natural porosity. It has been suggested that porosity decreases from the stem base upwards, but studies on such variation have not yet been presented.

• ***Aims*** Three main research questions were addressed: (i) how large is the variation of cork porosity upwards along the stem; (ii) how does porosity variation relate with porosity traits, namely the size and number of lenticular channels and (iii) how much does porosity vary with stem height and between trees.

• ***Methods*** We set up a study at tree level to quantify the porosity of cork samples from fixed stem heights. Our statistical modelling approach was based on linear mixed-effects models, given the nested structure of the data. In the model fitting, porosity was described as a function of tree stem height, while the random effects explained the source of variability introduced by different tree size (as given by stem diameter at breast height, D_{bh}) and porosity (as given by intrinsic porosity, CP_{bh}).

• ***Results*** The lenticular channels' area rather than their number consistently decreased up the stem. The area proportion of the lenticular channels in the cork tissue (i.e. porosity coefficient) decreased by about 1.4% per metre upwards along the stem, regardless of tree size and of its porosity.

• ***Conclusion*** Our findings highlight that the lenticular channels' traits greatly vary among trees, much more than within-tree, which may be an important clue to predict variations in cork properties, for decision-making on cork oak management.

Keywords Lenticular channels · Lenticels · Image analysis · Porosity coefficient · Linear mixed-effects models

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Contribution of the co-authors
A.C. conceived the study and provided the data; A.C. and I.B. performed the analysis; C.M. and J.G. contributed to the discussion of the obtained results and the writing of the original draft. All the authors contributed to the final writing, review and editing.

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1 Introduction

The unique phellogen, or cork cambium, of cork oak (*Quercus suber* L.) intensively produces numerous suberized walled and hollow cork cells, arranged in continuous, regular and concentric layers and resulting in a thick outer bark tissue, covering stem and branches (Natividade 1950; Pereira 2007).

The cork tissue is radially crossed by lenticular channels produced by specialized zones of the phellogen, the lenticular phellogen. Lenticular cells are loosely arranged, with large intercellular voids, and are chemically different from the surrounding suberized cork cells, with non-suberized lignified cell walls (Graça and Pereira 2004). Lenticular channels are believed to play the important physiological role of allowing air exchange for cells in the inner living tissues of the stem (Pereira 2007). They are therefore a natural feature, present in the cork of all cork oaks (Natividade 1934, 1950; Pereira 2007).

The lenticular channels (or lenticels) are considered discontinuities in the cork tissue, known as "pores" and their number and size characterize "cork porosity". Some cork defects, namely woody inclusions ("nail") or insect galleries, are sometimes incorrectly associated with cork porosity. In the present work, only the lenticular channels will be considered to assess (biological) porosity.

Cork porosity in raw cork planks is a decisive quality parameter for the industry of cork products (Costa and Pereira 2010) and particularly for the flowsheet of natural stoppers or discs, the highly valuable end-products (Costa and Pereira 2006; González-Hernández et al. 2014). The abundance and area of the lenticular channels affect several properties of cork (e.g. permeability to liquids and gases and elasticity) and the performance of natural cork products (e.g. sealers, such as stoppers or discs) (Oliveira et al. 2015; Pereira 2015). The classification of cork planks is generally made in three commercial quality classes: good, medium and poor. Only good and medium cork planks, with lower porosity, are adequate to produce natural cork stoppers, the highest valuable product (Costa and Pereira 2004; Fernandes 2005; Lopes and Pereira 2000; Pereira et al. 1994; Prades et al. 2017).

Cork porosity varies considerably among trees in a stand (Pereira et al. 1996) and, not the least, within trees (Natividade 1934,1950). This variability might be largely determined by hybridization and high outcrossing rates, which lead to high genetic diversity within populations (Eriksson et al. 2017; Gandour et al. 2007; Natividade 1950; Toumi and Lumaret 1998) and can be considered a major strategy of cork oak for adaptation to changing environments (Hamrick 2004). To some extent, this genetic diversity in cork quality-related traits may be affected by forest management (e.g. selection of good-quality cork producing trees). On the other hand, the species' adaptation to cope with environmental pressures might reveal a high phenotypic plasticity related to cork porosity (Mendes et al. 2019; Natividade 1934; Ramírez-Valiente et al. 2011).

Within a tree, cork's natural porosity has been reported to decrease upwards along the stem (Costa and Barbosa 2019; Natividade 1934,1950). Considering the high costs of cork harvesting, an accurate evaluation of how porosity varies along the raw cork plank (i.e. along the stem) may result in economic advantages. However, previous studies only presented general descriptions of the porosity trend, and none showed a relationship between porosity traits and height in the stem; and, to our knowledge, no modelling approach has yet been presented to predict it. This may be explained by the difficulty to obtain accurate and affordable measurements of cork porosity at levels above breast height.

In this study, we wanted to assess the variation of cork's natural porosity upwards along the stem. Our research questions were: (i) How large is that variation at tree level? (ii) How does it relate with the porosity traits, namely the size and/or abundance of the lenticular channels? (iii) How much does porosity vary with stem height and between different trees?

We hypothesize that there is a general decrease of cork's porosity upwards along the stem, together with a reduction of lenticular channels' size, rather than of their number, as a result of the structural arrangement of the lenticels in the cork tissue (Natividade 1950). We further hypothesize that stem height effects on the lenticular channels' size are consistent among different trees, despite the high variability of porosity among trees, which may be under a strong genetic control (Natividade 1934, 1950; Pereira et al. 1996).

The results will meet the urgent need of robust quantitative information on the variation of cork quality, specifically cork porosity, within and among trees for forest managers and cork industrial processors for so that they can best utilize cork resources.

2 Material and methods

2.1 Tree selection and cork sampling

In the state-owned farm "Companhia das Lezírias, S. A.", located in the Tagus Basin (38.83°N–8.81°W), southwestern Portugal, we randomly selected 76 adult and mature cork oaks, in a cork oak woodland area of 270 ha (Costa et al. 2020). The selected trees were harvested for their cork in 2012, corresponding to their 3rd or 4th consecutive cork harvest onward.

The sampling procedures at tree level included the collection of cork samples during the cork harvesting season. Cork rectangular samples (10 × 10 cm) were taken from the shady (generally north-exposed) side of the stem, at fixed stem heights (h) above the ground: at h = 0.30 m (stem base) and at every 1 m upwards, to the nearest stem harvesting height, H, defined as the maximum stem harvested height above ground (Fig. 1).

Harvesting height at tree level (Table 1) is limited by a legal index, the cork harvesting coefficient, defined as the ratio between H and stem perimeter over cork (at the standard height of 1.30 m above ground), which must not exceed the value of 3.0, according to Portuguese forest legislation. Consequently, trees with smaller stem diameter at breast height (D_{bh}) present smaller H than larger trees. This fact constrained cork sampling, and measurements along a large section of the stem could only be assessed in large trees. In this study, the maximum harvested stem height (H = 4.5 m) was observed in only two trees, from which the highest number of stem sections (five) could be sampled at the considered stem heights (h) of 0.30 m, 1.30 m, 2.30 m, 3.30 m and 4.30 m (Fig. 1). Even with the unbalanced sampling design (e.g. a few trees with the highest H), the minimum requirements were met to perform statistical analyses on the main effects of the explanatory variables.

2.2 Characterization of cork porosity

Cork samples were prepared for image acquisition according to the methodology described by Ghalem et al. (2016). One cross-section of each cork sample was scanned at a minimum resolution of 300 dpi, and the image was stored in TIF graphic format. Cork porosity was determined using the image analysis software ImageProPlus®—modules threshold manipulation and area measurements (Media Cybernetics, Silver Spring, MD, USA)—operated on snapshot images of the cork samples' cross-sections. For all the selected trees and sampling heights, cork porosity was assessed with an accuracy of 0.01 mm^2 and using a rectangular frame (area of interest, AOI) on the cross-section of the cork sample, according to the methodology described in Ghalem et al. (2016).

The natural porosity of cork was automatically detected by its specific grey level of pixel intensity, i.e. by threshold manipulation, and only the lenticular channels were accounted for. Defects (e.g. ant galleries or lignified woody cells, nail) in the cork tissue were post-extracted and eliminated from the accounted porosity. In a few cases, it was difficult to preserve or isolate the lenticular channels, and these could not be accurately measured, so the final number of cork samples used to develop stem-based models for cork porosity was reduced from 216 (Fig. 1) to 212. Moreover, in the image processing, lenticular channels' data describing size and abundance were automatically detected and then post-filtered to exclude the small porosity (lenticular channels with an area < 0.5 mm^2). Only lenticular channels with an area ≥ 0.5 mm^2 were

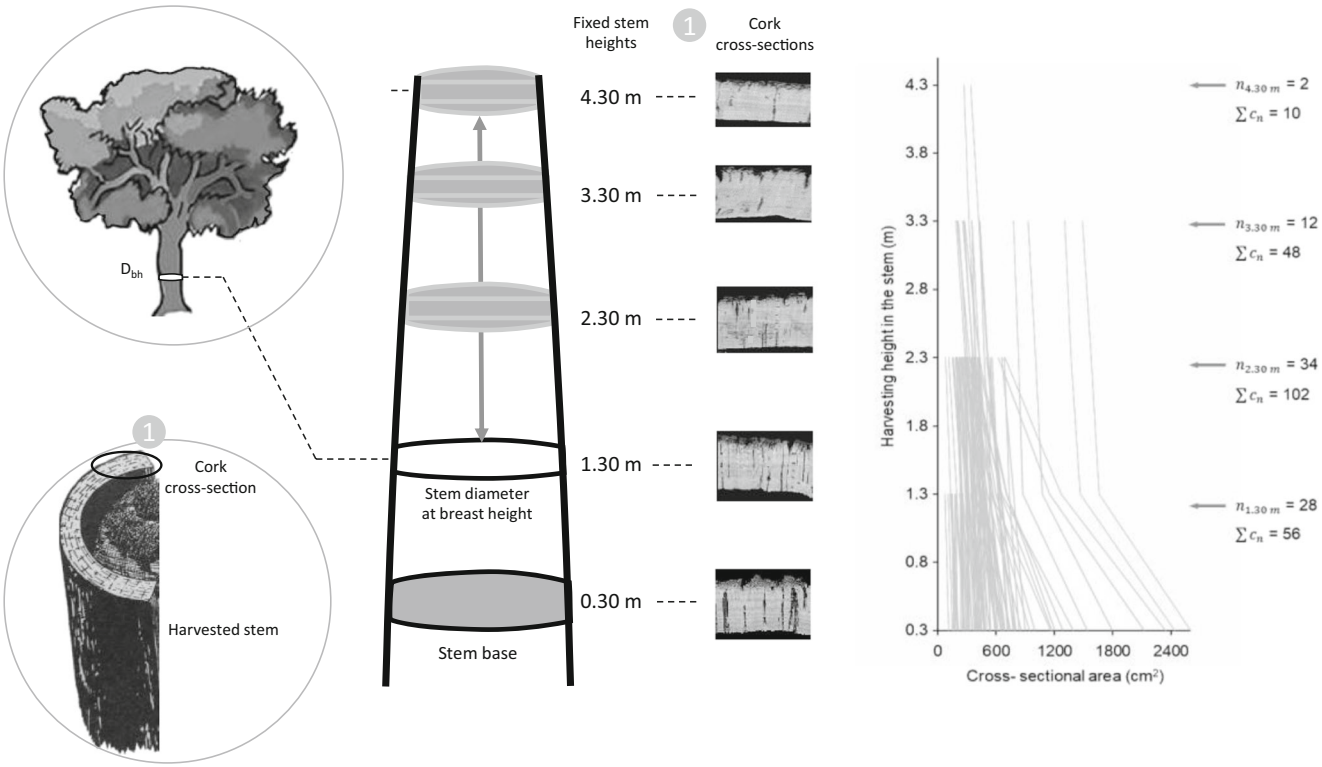

Fig. 1 Profile of stem cross-sectional area over cork (cm^2) assuming a circular outline and corresponding to stem diameters measured on the 76 sampled trees. Cork samples were collected from each tree at various fixed stem heights h (starting from 0.30 m above ground), and the lenticular channels were analysed in the cross-section of each sample. The number of trees (n) and corresponding number of cork samples (c_n) are also presented for each h, ranging from 28 trees and 56 cork samples (28 cork samples at each fixed stem height, h = 0.30 m and 1.30 m) to 2 trees with 10 cork samples (2 cork samples at each fixed stem height, h = 0.30 m, 1.30 m, 2.30 m, 3.30 m and 4.30 m)

Table 1 Tree and porosity variables used in the analysis, measured at fixed stem heights (h), from the base (h = 0.30 m) and at each 1-m interval upwards

Variables	Abbreviation (units)	Description
Tree data		
Diameter at breast height	D_{bh} (cm)	Mean stem diameter over cork, at 1.30-m height
Harvesting height	H (m)	Maximum stem harvested height above ground
Fixed stem heights	h (m)	Fixed heights above ground along the harvested stem
Diameter over cork	D_h (cm)	Mean stem diameter over cork at fixed height, h
Relative distance height	h_H	Ratio between fixed stem height h and the breast height (1.30 m)
Cork sample cross-section data at height		
Maximum area	A_{max} (mm^2)	Maximum value of the area of the lenticular channels
Maximum width	W_{max} (mm)	Maximum value of the width of the lenticular channels
Maximum length	L_{max} (mm)	Maximum value of the length of the lenticular channels
Porosity coefficient	CP (%)	Lenticular channels area relative to the total cross-section area
Number of pores	NP (n/100 cm^2)	Number of lenticular channels per 100 cm^2

Only the lenticular channels with an area ≥ 0.5 mm^2 were considered

considered in the analysis as porosity data. Small porosity is not detected in a visual human inspection and is considered functionally irrelevant (Pereira 2007).

Data required to develop individual tree stem profiles of cork porosity consisted of repeated measurements along the stem, at different stem heights, h, of five porosity (dependent) variables, specifically characterizing the size and abundance of the lenticular channels in the AOI of the cork samples cross-section (Table 1). Cork porosity was assessed through the porosity coefficient (CP, ratio of lenticular channels' area to total cork cross-section area), the abundance of lenticular channels (NP, number of lenticular channels per 100 cm^2) and variables describing the size of the lenticular channels: maximum area (A_{max}), the maximum length (L_{max}) and maximum width (W_{max}) (Table 1).

2.3 Data analysis

Our statistical modelling approach was based on linear mixed-effects models, given the nested structure and high correlation of data, from repeated measurements made in cork samples collected from the same tree (Trincado and Burkhart 2006). In the model fitting, individual tree porosity, selected as the response variable, was described as a function of tree stem height (fixed effect), while random effects explained the source of stochastic variability introduced by different tree sizes (i.e. stem diameter at breast height) and by tree-intrinsic characteristics of porosity. In fact, at the stand level, preliminary analyses showed large phenotypic variability among cork oaks, which may affect the size and/or abundance of lenticular channels of trees. For the adjustment of the linear mixed-effects models, the maximum likelihood algorithm (ML) of the *lmer* function, available in the *lme4* library of the R software (version 4.0.3), was used. The best model produced the lowest values of Akaike's information criterion (AIC).

The first step of modelling was to place emphasis on the fixed part of the model. For each tree, we calculated means and standard deviations of the porosity at tree level; we then assessed the linear correlation matrix between height in the stem and cork porosity to select only one porosity trait as response variable. To improve the variation explained by the model, other variables were added to the height in the stem, the main fixed effect.

Model fitting was initiated by adding random effects of tree, D_{bh}, and of intrinsic porosity (CP_{bh}), firstly through random intercept alone and then by random intercept and slope. The generalized linear mixed-effect models were formulated according to the following equation:

$$y_{ij} = \alpha_0 + (\alpha_1 + \beta_{Treej}) \times X_{ij} + \mu_{Treej} + \varepsilon_{ij},$$

where y_{ij} denotes the response variable, related with one selected cork porosity trait, of the cork sample i^{th}, in the tree j^{th}; X_{ij} is the height in the stem of the cork sample i^{th}, in the tree j^{th}; α_0 and α_1 are the parameters of the fixed part of the model; μ_{Treej} and β_{Treej} are the random parameters associated with the between-tree variations (in tree size or in intrinsic porosity); and ε_{ij} is the residual error term, with mean zero and variance σ_ε and independent on random effects.

3 Results

3.1 Relationship between porosity and height in the stem

The results showed a decreasing trend in the size of the lenticular channels along the stem upwards. The maximum area of lenticular channels (A_{max}) was the variable that most consistently decreased, when compared to the other size parameters, L_{max} and W_{max}. A_{max} decreased by about 10–15 mm^2 per metre of stem height (Table 2).

Porosity coefficient decreased with increasing stem height, in all the trees (Table 2). CP ranged from 10.2–14.9% at the stem base (0.30 m stem height) to 6.2–11.1% (at stem height 3.30 m). In contrast, the number of lenticular channels (NP) remained constant, or just slightly decreased, from the stem base upwards. On average, NP ranged between 20 and 28 lenticular channels per 100 cm^2 at the stem base (h = 0.30 m) and 25 lenticular channels per 100 cm^2 at h = 3.30 m.

Lenticular channels' size—as given by A_{max}, L_{max} and W_{max}—decreased with increasing height in the stem (Fig. 2a), but this correlation was not significant for W_{max} ($r = -0.144$, $p = 0.067$).

The porosity coefficient was significantly correlated with the height in the stem (Fig. 2b). CP decreased along the stem upwards ($r = -0.215^{**}$, $p < 0.01$). In contrast, no correlation was found between height in the stem and the number of lenticular channels.

A_{max} and L_{max} showed significant positive correlations with stem diameter (D_h) ($r = 0.158^{*}$ and $r = 0.171^{*}$, respectively, $p < 0.05$) (*data not shown*), which is not surprising given that longer lenticular channels may be expected in the thicker cork found at larger stem diameters. Also as expected, A_{max} was highly correlated with CP ($r = 0.583^{**}$, $p < 0.01$); based on these correlations, CP was selected as a response variable to represent porosity in our models to test the effects of height in the stem.

3.2 Effect of the height in the stem on the porosity coefficient

The values of CP in each mixed-effects linear model were plotted against the height in the stem (h_H), and the random effects were the tree size (given by the stem diameter at breast height, D_{bh}), in models M0, M1 and M2 and the tree's intrinsic porosity (given by porosity coefficient and breast height, CP_{bh}), in models M3, M4 and M5 (Table 3).

According to the main results of all models, the porosity coefficient (CP) decreased along the stem—the estimate of the parameter for the fixed part of the models related to the height in the stem (α_1) was negative (Table 3). The reduction in CP with the increasing height up the stem was about 1.4% (1.40–1.50%) per metre in stem height.

In the models, the height in the stem explained only about 5% of the total variation of CP along the stem (Table 4). Random-effects variations indicated by the variability of parameters according to tree's size (M0) and to tree's intrinsic porosity (M3) represented the same percentage of total variation, 47–48%. Moreover, total random variations due to differences between trees' sizes or to intrinsic porosities, were mainly linked with the variation in the intercept, in M1 and M4, respectively. Thus, all the groups of trees presented a common slope in their regression lines and, therefore, non-convergent

Table 2 Values (means ± standard deviations) of size and abundance variables of cork porosity in the cross-sections of cork samples: area (A), width (W) and length (L) grouped according to the highest sampling height

Porosity variables	Fixed stem height, h (m)				
	0.30	1.30	2.30	3.30	4.30
Cork sampling maximum height (1.30 m) (n=28)					
A_{max} (mm^2)	39.0±21.59	30.3±16.86			
W_{max} (mm)	7.4±3.24	6.0±2.80			
L_{max} (mm)	16.6±4.60	16.1±5.59			
CP (%)	13.3±5.53	10.3±3.32			
NP (n/100 cm^2)	28±11	27±9			
Cork sampling maximum height (2.30 m) (n= 34)					
A_{max} (mm^2)	49.2±22.31	35.4±19.99	26.9±16.80		
W_{max} (mm)	8.2±4.70	8.1±4.86	5.9±1.31		
L_{max} (mm)	19.5±7.06	17.9±6.11	14.3±5.67		
CP (%)	12.4±3.15	13.1±5.72	9.9±4.28		
NP (n/100 cm^2)	26±8	28±10	25±6		
Cork sampling maximum height (3.30 m) (n= 12)					
A_{max} (mm^2)	64.9±42.02	44.1±25.12	31.4±24.13	34.9±20.72	
W_{max} (mm)	7.0±4.53	7.9±4.51	5.5±3.54	7.7±3.11	
L_{max} (mm)	17.9±6.65	18.0±3.97	15.9±5.84	18.8±4.22	
CP (%)	14.9±9.49	13.3±4.88	11.6±6.25	11.1±3.82	
NP (n/100 cm^2)	21±11	26±8	25±10	22±6	
Cork sampling maximum height (4.30 m) (n= 2)					
A_{max} (mm^2)	95.0	64.8	44.1	33.0	30.6
W_{max} (mm)	13.1	8.4	7.6	4.8	7.3
L_{max} (mm)	25.1	27.6	23.7	10.3	18.1
CP (%)	10.2	8.9	10.3	6.2	8.8
NP (n/100 cm^2)	20	18	21	25	19

For the maximum height of cork sampling (4.30 m), there were two cork samples, and only their mean values are presented

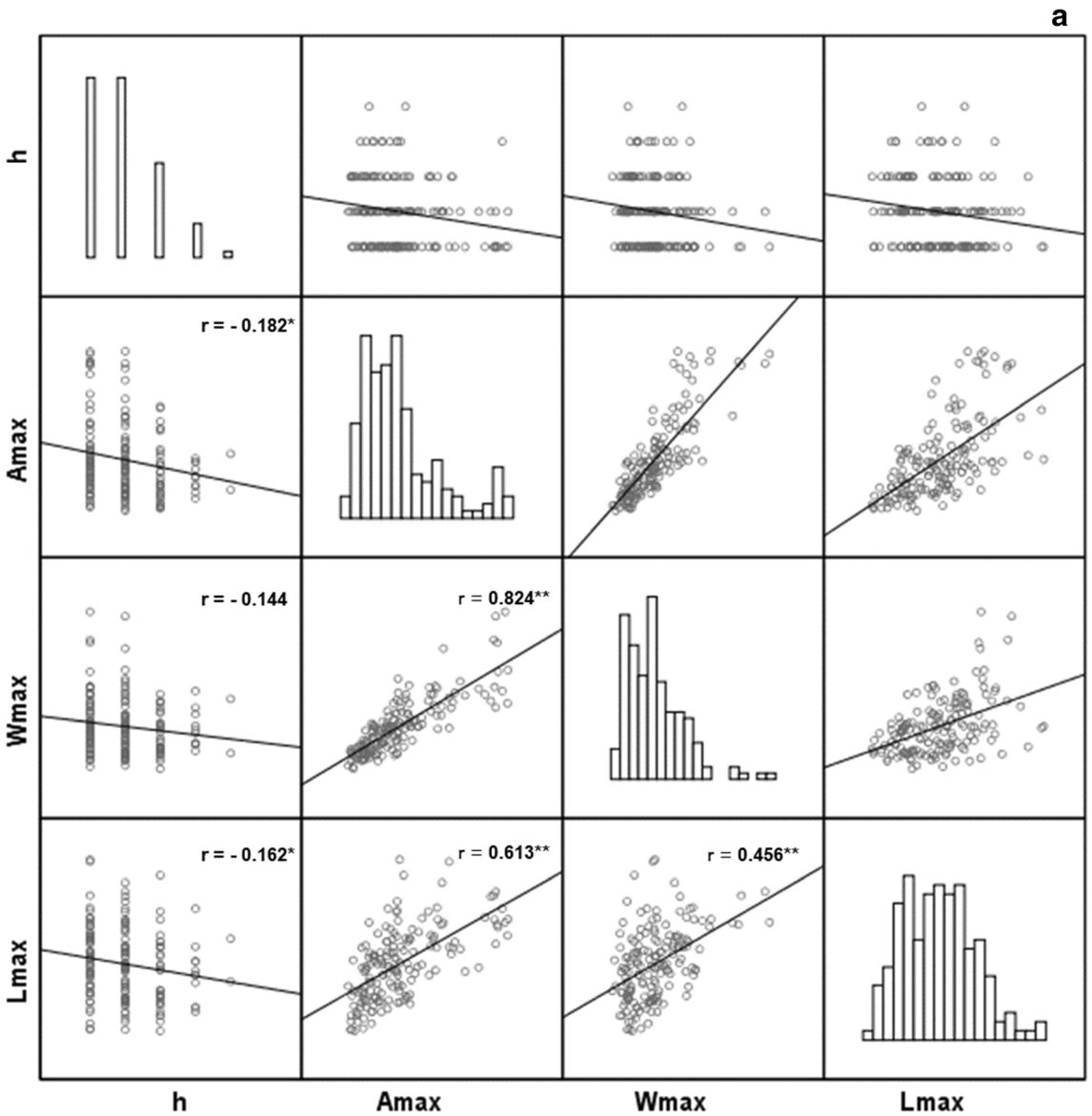

Fig. 2 **a** Correlation matrix: height in the stem (h) and size variables of cork porosity (maximum area, A_{max}; maximum width, W_{max}; maximum length, L_{max}). **b** Correlation matrix: height in the stem (h), porosity coefficient (CP), number of lenticular channels (NP) and stem diameter over cork (D_h)

but parallel trajectories of CP from the stem base (minimum h_H) to the maximum stem harvested height (maximum h_H).

Overall, our models gave poor estimations of the porosity coefficient, explaining about 53% of its variation within-trees, with random among-tree variance a major part of the variation and comparable to the residual variance (Table 4). In the Model M2, when the maximum area of the lenticular channels (A_{max}) was added to the height in the stem, the fitting of CP increased, and R^2 (Model) was about 0.58. However, even in this best model, Model M2, with the lowest AIC, little is explained by the fixed effects (6.02% of total variation) and by the variance between trees of different sizes (32.90% of total variation).

The distribution of the residuals in selected presented models, M0, M2 and M3, the three models with the lower AIC, was similar and satisfactory (Fig. 3).

4 Discussion

In this study, size and number of lenticular channels in transversal cross-sections of cork samples, at fixed stem heights, were used to determine base-to-crown porosity trends in cork oak trees. Results showed that the maximum area of the lenticular channels, as well as area proportion in the cork tissue (i.e. porosity coefficient), varied greatly among trees. However, at the tree level, these characteristics always

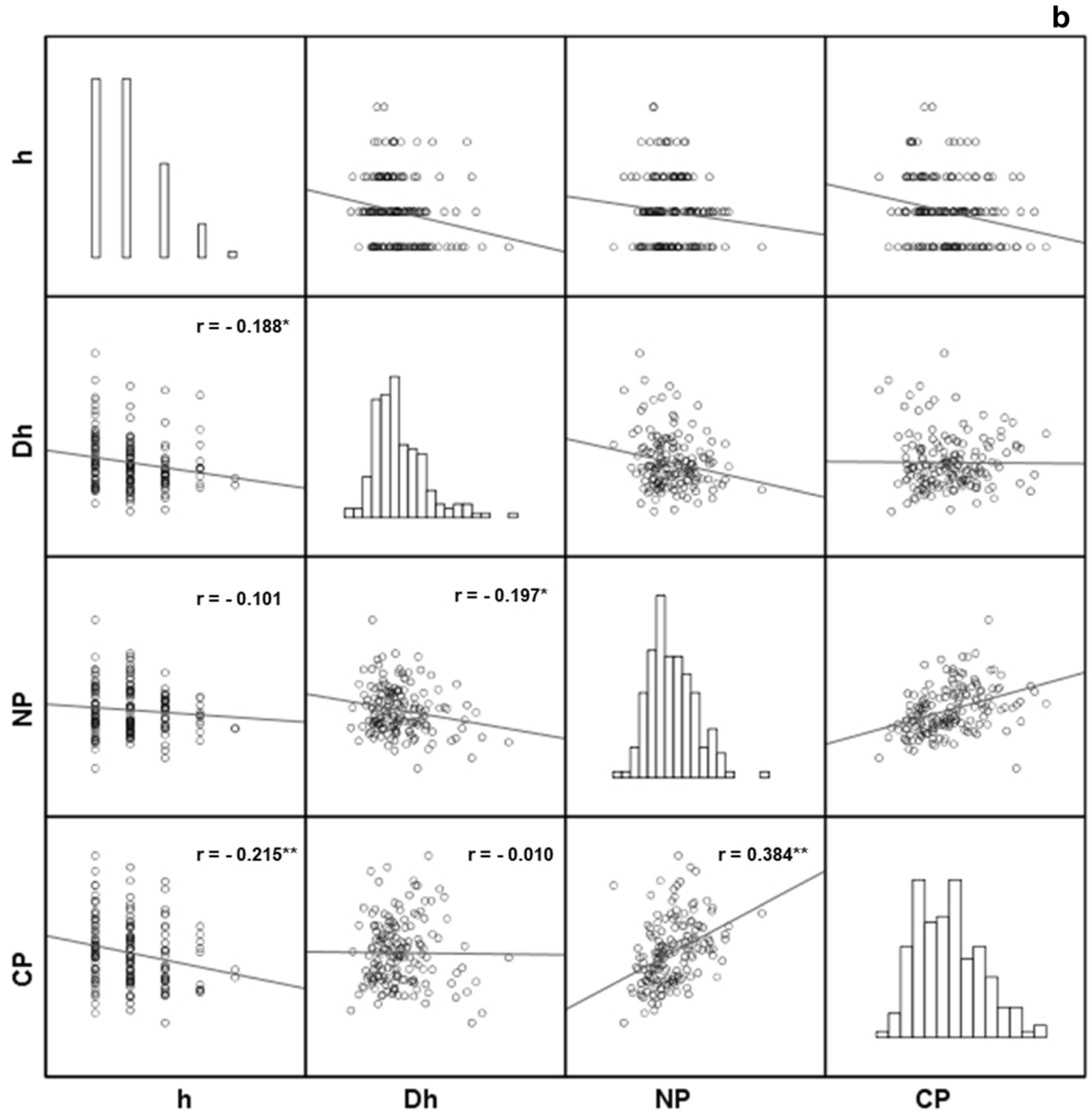

Fig. 2 (continued)

Table 3 Statistics of the mixed-effects linear models

Model	Model equation	α_0	α_1	α_2	$\sigma_{Treej}(\mu_j)$	$\sigma_{Treej}(\mu'_j)$	$\sigma\beta_{Treej}$	$\sigma\beta'_{Treej}$	$\sigma_{\varepsilon ij}$	AIC	BIC	LogLik
M0	$CP_{ij}=\alpha_0+\alpha_1 h_{Hij}+\mu_{Treej}+\varepsilon_{ij}$	12.99	−1.44**		3.06				3.05	904.8	917.1	−448.4
M1	$CP_{ij}=\alpha_0+\alpha_1 h_{Hij}+\mu_{Treej}+\beta_{Treej}\cdot h_{Hij}+\varepsilon_{ij}$	12.98	−1.42**		3.36		0.29		3.04	908.2	926.7	−448.1
M2	$CP_{ij}=\alpha_0+\alpha_1 h_{Hij}+\alpha_2 A_{maxij}+\mu_{Treej}+\varepsilon_{ij}$	9.01	−0.62*	0.09**	2.30				2.74	857.9	873.3	−423.9
M3	$CP_{ij}=\alpha_0+\alpha_1 h_{Hij}+\mu'_{Treej}+\varepsilon_{ij}$	12.98	−1.42**			3.03			3.04	904.6	917.0	−448.3
M4	$CP_{ij}=\alpha_0+\alpha_1 h_{Hij}+\mu'_{Treej}+\beta'_{Treej}\cdot h_{Hij}+\varepsilon_{ij}$	12.97	−1.40**			3.32		0.29	3.02	908.0	926.5	−448.0
M5	$CP_{ij}=\alpha_0+\alpha_1 h_{Hij}+\alpha_2 D_{hij}+\mu'_{Treej}+\varepsilon_{ij}$	13.60	−1.50**	−0.01*		3.03			3.04	906.5	921.9	−448.2

**Significant at the 1% level

*Significant at the 5% level

The response variable was the porosity coefficient (CP). Models M0, M1 and M2 considered the random effects of tree size (i.e. stem diameter at breast height, D_{bh}). In M2, the fixed part of the model included the height in the stem and the size of lenticular channels (i.e. A_{max}). Models M3, M4 and M5 considered the random effects of trees' intrinsic porosity (i.e. the porosity coefficient at breast height, CP_{bh}). In M5, the fixed part of the model included the height in the stem and the stem diameter over cork, D_h

Table 4 Contribution of the fixed effects and random tree effects to total variation in porosity coefficient for the five models, each one with the correspondent coefficient of determination (R^2Model)

Model	R^2 (Model)	Fixed effects				Tree random effects		
		Height ($\delta^2_h/\delta^2_{Tot}$)	Area ($\delta^2_{Amax}/\delta^2_{Tot}$)	Diameter ($\delta^2_{Dh}/\delta^2_{Tot}$)	$size_{intercept}$ ($\delta^2 Tree_{Dbh})/\delta^2_{Tot}$)	$size_{slope}$ ($\delta^2 Tree_{Dbh}\cdot h_{Hij})/\delta^2_{Tot}$)	$porosity_{intercept}$ ($\delta^2 Tree_{CPbh}/\delta^2_{Tot}$)	$porosity_{slope}$ ($\delta^2 Tree_{CPbh}\cdot h_{Hij}/\delta^2_{Tot}$)
M0	0.53	5.75			47.58			
M1	0.56	4.63			51.26	1.40		
M2	0.58	6.02	18.65		32.90			
M3	0.53	5.92					46.88	
M4	0.57	4.64					51.99	0.39
M5	0.53	5.11		0.08			47.64	

decreased with stem height (Table 2) and in a similar way (Table 3).

The porosity coefficient at the breast height (CP_{bh}) greatly varied between trees. Values of CP_{bh} ranged between 8.9 and 13.3%, which are within the range of previously reported values: 2.1 to 16.4%, concerning lenticular channels > 0.8 mm^2 (Pereira et al. 1996), 6.9–15.3% (Gonzalez-Adrados et al. 2000), 1.4–16.8% (Lauw et al. 2017) or even in the wider range 1.5–26.3%, reported by Gómez-Sánchez et al. (2013).

In contrast with the porosity coefficient, the number of lenticular channels per unit area (NP) did not much vary between trees, nor, more importantly, in each tree (Table 2 and Fig. 2b). About 20–30 lenticular channels per 100 cm^2 could be found in all cork samples, at the breast height, corresponding to less lenticular channels than those referred in previous studies, 49–170 per 100 cm^2 (lenticular channels >0.8 mm^2) (Pereira et al. 1996). This discrepancy may be related to the fact that only lenticular channels (area >= 0.5 mm^2) were considered in our study and other type of discontinuities (e.g. nail, galleries or other) were discarded during image analysis processing (Ghalem et al. 2016).

Overall, the within-tree consistency of the variation of the porosity coefficient confirmed our hypothesis of a general decreasing trend of porosity upwards along the stem. Primarily the area (A_{max}) and, more precisely, the proportion of such area in the cork tissue (CP) vary with the height in the stem rather than with the number of lenticular channels. This agrees with previous studies (Natividade 1934, 1950) that suggested an overall reduction of cork porosity upwards along the stem related with lenticular channels' area reduction as the number of lenticular channels remained relatively constant. Furthermore, our results allow us to suggest that the between-tree variation in lenticular channels' maximum area and area proportion in the cork tissue, similarly to stomatal length and density, may depend on genetic factors and prevailing environmental conditions (Bertolino et al. 2019; Zhang et al. 2012).

Regarding the size variables, the maximum area of the lenticular channels (A_{max}) ranged between 30.3 and 64.8 mm^2, at 1.30-m stem height, and dropped to lower values up in the stem. These values, found in cross-sections from the standard stem breast height, agree with those reported in other studies (Ghalem et al. 2016; Ferreira et al. 2000). Overall, the trend of the maximum area of the lenticular channels along the stem can be related mainly with the trend of maximum length (L_{max}) and, only to some extent, to the trend of maximum width (W_{max}). In fact, lenticular channels presented a length-to-width ratio between 4 and 6, which is in accordance with previous studies (Ghalem et al. 2016; Pereira 2007).

While the length trend would be mostly growth related, the decreasing trend of width would be mostly mechanically driven. The lenticular channels radially cross the full thickness of the cork planks because the lenticular phellogen spots within the phellogen maintain their activity in consecutive years of cork growth, along with phellogen. Our results showed a range of maximum lengths (between 10.3 and 27.6 mm) which are lower than the general range of values of cork planks' thicknesses, around 30 mm (Costa et al. 2020; Oliveira and Costa 2012). This sometimes happens not because the lenticular channels are interrupted but, in most cases, because the cross-section plane for analysis did not fully coincide with the channel's longest axis (Natividade 1934). Despite this possible sampling bias, the lenticular channels varied at the individual tree level, and their maximum length consistently dropped in the upper parts of the stem, similarly to their area. The decrease of the lenticular channels' maximum length upwards along the stem (Fig. 2a) can be explained by the concurrent decrease of cork thickness (Costa et al. 2020; Natividade 1934,1950).

On the other hand, the width of the lenticular channels is related with the width of the lenticular phellogen spots within the phellogen (Pereira 2007). These spots or zones can be narrow, comprising only a few hundreds of cells and forming the narrowest lenticular channels, or wider, with a few thousand cells forming the widest ones. Our results showed that the widest lenticular channels kept a roughly constant size of

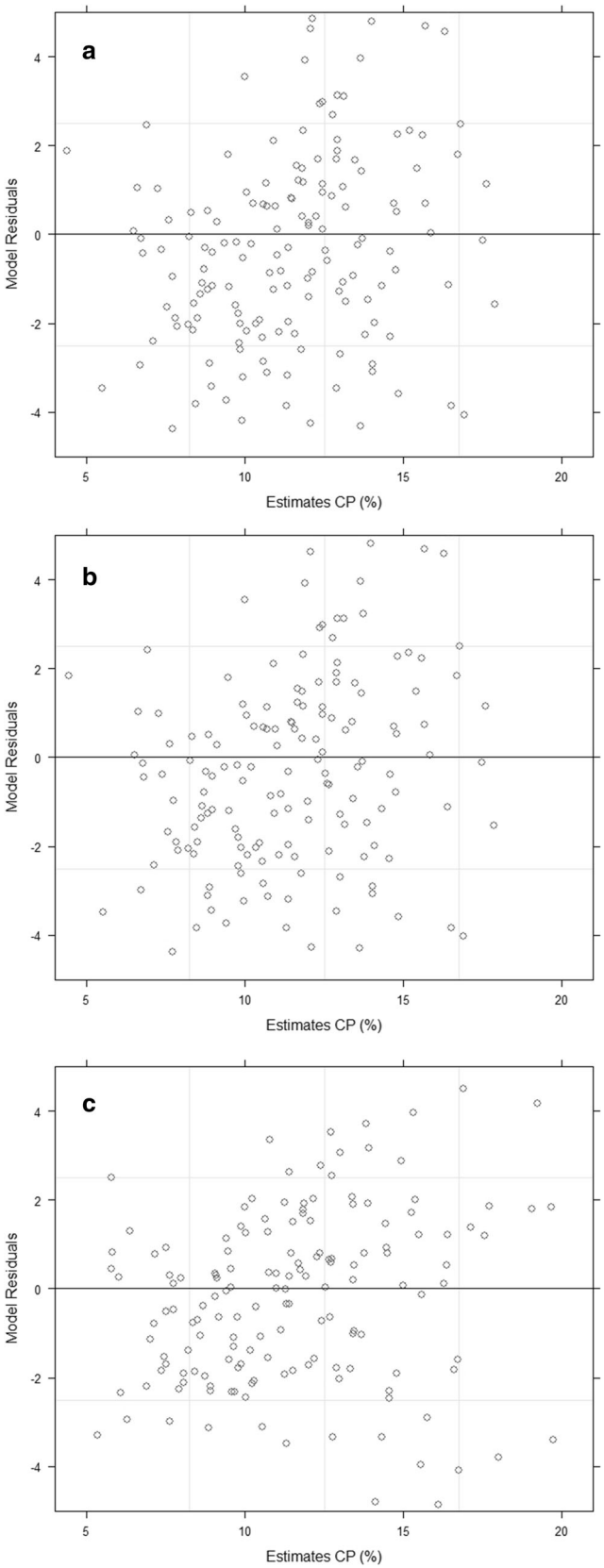

Fig. 3 Residuals against the estimates of porosity coefficient (CP) in models M0 (**a**), M3 (**b**) and M2 (**c**)

6 mm along the stem (Table 2) and are formed by a few hundreds of cells of lenticular phellogen, at most. Changes of the lenticular channels' width along the stem were not highly significant (Fig. 2a). Additionally, we suggest that the existent within-trees variation in lenticular channels' width mostly results from a mechanical change of the structure of their cells, which enlarge tangentially due to the tension stresses associated with cork and wood growths, underneath a cork back that has a relatively lower elasticity. Intuitively, stem diameters being larger at the base, the higher tension of wood and cork growths in trees that are larger and have higher growth rates, the greater the widening of the lenticular channels will occur, through deformation of their boundaries (see Fig. 1); this would contrast with the upper parts of the stem, where the tree diameter is smaller and growth tensions are weaker (Natividade 1950).

In accordance with our results, models presented the coefficient of porosity as a function of the height in the stem, showing that the latter had a significant effect on cork porosity (Table 3). However, this fixed explanatory variable explained only about 5% of the total variation; most of the remaining variance was explained equally by the variance among tree sizes (i.e. stem diameter at breast height) and by residual variance (M0) (Table 4). Furthermore, model fitting did not improve by including height in the stem and stem diameter as fixed effects and with between-tree variations of intrinsic porosity (M5). In the latter model, the effect of the height in the stem was dominant over that of the stem diameter, and both contributed to account for the same 5% of total model variation. This relatively weaker influence of tree size (as given by stem diameter, D_h) on the porosity coefficient and, basically, on the lenticular channel area, sharply contrasts with several studies showing that wood properties (e.g. cell's area, in latewood) are influenced by cambial maturity and tree age (Lenz et al. 2010). A simple explanation for these discrepancies may be that the lenticular phellogen, renewed after each cork harvesting in cork oaks, follows similar trends. These trends keep the growth patterns of their lenticular channels close to an asymptotic value (Lenz et al. 2010) which in turn would be only slightly influenced by the distance between higher parts of the stem (near the live crown and the physiological signals produced in apical meristems) and the stem base (Barnett and Jeronimidis 2003), as well as by the changes in cells' arrangement, which should not be neglected.

By adding the maximum area of lenticular channels as a fixed effect in the models expressing coefficient of porosity, the proportion of the explained variation increased by 20% units (M2) (Table 4). In this model fitting, the between-tree's size variation was also evident, accounting for 33% of total variation. Our findings on cork oak agree with numerous studies in other forest trees indicating that some wood properties, such as density or fibre length, are highly diverse between trees, and generally under strong genetic control, in contrast

with wood growth, which is much more influenced by site conditions and tree physiology (Lamara et al. 2016; Lenz et al. 2010; Stackpole et al. 2010; Zeltinš et al. 2018). It seems that cork growth traits, e.g. cork thickness or cork-ring width, which were tree-size related and linked with biological changes with tree ageing (Costa et al. 2015, 2020; Mendes et al. 2019; Natividade 1950) contrast with cork porosity traits, e.g. area of the lenticular channels or porosity coefficient, which are not directly influenced by tree stem diameter (Fig. 2b) and thus by trees' growth.

All the presented models consider only the random intercept variation, as the random slope did not improve the model fitting (see statistical results for models M0 and M1) (Table 3). In addition, the models fitting showed a relatively high residual variance, and the best model (M2) yielded only a relatively high coefficient of determination ($R^2 = 0.58$) (Table 4). However, these models produced important clues about the fitting curve of cork porosity against height in the stem. Cross-sections of cork at breast height will underestimate the porosity coefficient given by lenticular channels at the stem base and overestimate it above 1.30 m. Furthermore, trees with highly porous cork reduce their porosity with stem height in a similar way of trees with less porous cork. In other words, the curves of cork's porosity vs. height in the stem showed similar variation patterns in trees with higher and lower porosity. This is in accordance with our hypothesis: the effect of the height in the stem on the lenticular channels area proportion in the cork tissue is consistent across different tree groups. These results are also in accordance with previous studies suggesting a strong intraspecific genetic variation and phenotypic variability in the porosity properties of cork, at tree level (Natividade 1934, 1950).

The presented models for the porosity of cork applied to trees in the Tagus Basin peneplain, in southwestern Portugal. Although these models may produce reliable results when used in neighbouring regions, one must be cautious in interpreting the results, and it must be stressed that an extrapolation to other climatic, edaphic or biophysical conditions may produce biassed stem profiles of cork porosity at tree level, mainly because our results suggested a high percentage of residual variation.

5 Conclusions

Our results indicate that the properties of cork's porosity are highly diverse and much less influenced by the environment than cork growth traits, e.g. cork thickness or cork growth rates, which are strongly influenced by environment and tree size (age). Surprisingly, the consistency of the lenticular channel's abundance (number of lenticular channels per area unit) among trees and along the stem, and of lenticular channels' width, which seem to vary mainly as a mechanical response to cork growth tension, reveals that a general decrease of cork's porosity upwards along the stem accompanies a reduction of lenticular channels' size, rather than of lenticular channels' number.

Models fitting cork porosity can be useful to predict the quality of a cork plank in the harvested stems of cork oak. These models could be used either to plan the harvesting season or simply to describe the variation of cork porosity properties. In either case, they have economic implications for cork trading in the field, by optimizing the harvesting costs and by improving cork piles with cork that will better suit specific industrial requirements of porosity, hence more valuable. Although these models produced important clues about the variation of porosity in cork cross-sections along the stem, they show high between-tree variation and residual variation. Future modelling studies should include distinct woodlands, under distinct site conditions, and a broader range of trees with (more) larger trees.

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Data availability Data will be shared upon reasonable request.

Declarations

Conflict of interest The authors declare no competing interests.

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