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EDITED BY
Ram P. Sharma,
Tribhuvan University, Nepal

REVIEWED BY
Nuray Çiçek,
Cankiri Karatekin University, Türkiye
Ali Suhardiman,
Mulawarman University, Indonesia

*CORRESPONDENCE
Ana Poeiras
apcp@uevora.pt

†PRESENT ADDRESS
José Nunes,
CERNA, Vila Real, Portugal

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Irrigation in the final years of a cork production cycle increased cork cell wall thickness, but had no effect on overall cork caliper

Ana Poeiras[1]*, Constança Camilo-Alves[1], Björn Gunther[2], Cordula Vogel[2], João Mota Barroso[1], João Ribeiro[1], José Nunes[1†], Margarida Vaz[1], Maria Emília Silva[3] and Nuno de Almeida Ribeiro[1]

[1]University of Evora, Évora, Portugal, [2]Technische Universitat Dresden, Dresden, Germany, [3]Universidade de Tras-os-Montes e Alto Douro, Vila Real, Portugal

This article presents an image-based analysis of cork cells from two cork rings within the same cork profile using a scanning electron microscope. The study also examines cork characteristics in relation to cork ring width and ring density. During the cork growth cycle, forest management practices were altered due to the additional irrigation applied to the plot. The objective of this study is to assess changes in cork cell walls and lumens' response to the additional irrigation by following their previously documented growth pattern or by deviations as a consequence of the altered forest management approach. Cellular analyses showed that both the year of the growth ring and the treatment influenced the measurements. In particular, thicker cell walls were observed in the 2022 ring under irrigation conditions. However, the results showed no statistically significant differences in overall cork growth between treatments.

KEYWORDS
cell walls, cork harvesting, cork rings, forest management, scanning electron microscope

1 Introduction

Cork, or phellem, is composed of dead parenchymatous cells characterized by a hollow, air-filled lumen, while the structural support of the tissue is provided by the solid material concentrated in the cell walls (Pereira, 2015). Phellem has meristematic capacity (Silva et al., 2005) and continues to grow throughout the lifespan of the tree, making this tissue both important and distinctive. Cork cells originate from the phellogen, a cambial tissue that produces cork cells externally and phelloderm cells internally in cork oaks (Pereira, 2007). The development of cork progresses centrifugally, from the pith toward the bark. As a result, the newest rings are located in the inner layer of the cork, where they are increasingly subjected to tangential tensions generated by the older cork rings (Natividade, 1934; Costa et al., 2002). Consequently, these tensions lead to a reduction in ring dimensions and the formation of narrower and denser rings (Pereira et al., 1992). Both variation in the number of cells produced per year and in cell dimensions results in different rings width (Pereira et al., 1992).

In addition to this radial pattern, an intra-annual pattern of ring formation is also observed, similar to that found in wood tissues. The intra-annual pattern results from enhanced growth during the growing season (spring and early summer), which appears as lighter-colored and

thicker layers corresponding to a greater number of larger thin-walled cork cells. In contrast, reduced growth during autumn produces denser and darker layers of thick-walled cork cells (Costa et al., 2022). This growth pattern can be significantly influenced by environmental factors, particularly variations in annual and seasonal precipitation, which affect cork ring width and ring density (Caritat et al., 2000; Costa et al., 2016; Oliveira et al., 2016; Ghalem et al., 2017; Costa and Cherubini, 2021; Costa et al., 2022). Cork moisture, a parameter widely used in commercial cork transactions, also depends on environmental conditions, particularly soil moisture and precipitation.

In a previous exploratory study, there was an indication that water availability during summer drought may influence cork characteristics, such as cork growth and cork porosity (Poeiras et al., 2021). The exploratory study was conducted on old trees subjected to 15 years of summer irrigation and compared them with cork from a nearby rainfed plot. The study was part of the *GO-REGACORK* project. The *GO-REGACORK* project aimed to promote cork oak growth and vitality through summer irrigation as a response to observed tree decline and productivity loss caused by multiple interacting factors, including climatic constraints, soil limitations, the presence of the pathogen *Phytophthora cinnamomi* Rands (Camilo-Alves et al., 2013, 2020, 2022), and changes in system management (Ribeiro et al., 2004; de Ribeiro et al., 2010). The project aimed to evaluate the feasibility of advancing cork production in new cork oak plantations through irrigation in a cost-effective manner in areas with available water resources. Additionally, it aimed to evaluate the effects of irrigation on cork formation, yield, and quality using existing plantations containing adult cork oaks or trees approaching their first stripping, and to transfer knowledge for the establishment of new cork oak stands using additional water.[1]

In the present study, the goal was to analyze the effects of irrigation on cork development. Since irrigation was applied only during the second half of the cork growth cycle, this design allowed for the evaluation of the effects of irrigation on cork development within the same tree.

Knowing this natural pattern of cork growth, the present study focused on two key research questions: (i) how does irrigation in the final rings of a cork production cycle influence cell size and cell wall thickness; (ii) how does irrigation influence ring width and ring density in those rings of the cork cross-section. This study will improve knowledge about the causal relationships between these characteristics and cork quality in the industrial process.

2 Materials and methods

2.1 Study area

Mitra RegaCork is a plot located in Herdade da Mitra, Valverde, Évora, Portugal (38°31′34.11”N, 8°01′15.50”W UTM coordinates), a property of the University of Évora and maintained by the EcoDendro Research Forest Team. Herdade da Mitra is a 275-ha estate related to the clerical history of Portugal, with origins in the 16th century, and was transferred to the Portuguese government in 1834. The property—certified by the Forest Stewardship Council® (FSC)—includes oak and pine forests and agro-silvopastoral systems, olive trees, and vineyards. All of these areas function as living laboratories, closely integrating scientific research, higher education, and productive practices. The *Quercus suber* L. plot named Mitra RegaCork (Figure 1) was established in 1996 in a pure cork oak stand and has been systematically monitored for tree growth and cork production since then. The stand has been debarked every 10 years, with the most recent debarking occurring in 2023. It is a circular 1-hectare plot where an irrigation system was installed in 2020 under the GO-REGACORK Project (Ecodendro, 2018) to test the effect of water availability during summer drought on tree and cork growth and development. The plot characteristics prior to harvesting are presented in Table 1.

The plot is located in a typical Mediterranean climate, characterized by hot, dry summers and mild winters, as shown in the following climate diagram for the corresponding cork growth periods (Figure 2).

A surface drip system was installed in the plot across six randomly selected groups of five trees. Each tree was irrigated via a dedicated dead-end tube arranged in a spiral around the trunk at a maximum distance of 2 m, with five 2 L h^{-1} emitters per tree. The system includes a reservoir and an irrigation controller, delivering, on average, 13 m^3 of water every 15 days. After the installation of the water supply system in 2020, the irrigation campaign was conducted between the spring and autumn rainfall periods, mostly from June to October (Table 2). Since the cork debarking in the stand took place at the end of May, only the amount of water indicated in Table 2 was supplied during this cork production cycle.

To test the influence of intraspecific competition on the growth and density of cork rings, the spatially dependent size-ratio competition index proposed by Hegyi (1974) was applied. This index is based on the basal–area method: $\sum_{j=1}^{n} \frac{d_j}{d_i} * \frac{1}{dist_{ij}}$. In the mathematical formula: d_j - trunk diameter at 130 cm height of the competitor, d_i - trunk diameter at 130 cm height of the target tree, $dist_{ij}$ - distance between competitor and target tree. Hegyi determined the competitive relationship between trees within the physical growing space based on the sum of all competitors located within a fixed radius of the target tree, weighted according to their diameters (Fabrika and Pretzsch, 2013).

2.2 Analyses of cork samples

Cork samples were analyzed for cork ring width, ring density, cork moisture content, and cellular characteristics, including cell wall thickness and lumen area.

2.2.1 Cell wall thickness and cell lumen

During the 2023 cork harvesting, a cork sample with a 20 × 20 cm area was removed at a height of 130 cm from 12 irrigated trees and 12 rainfed trees, randomly chosen from the plot. Samples were prepared as described by Poeiras et al. (2022b). In short, samples were sliced in the transverse direction, from pith to bark, and in each cork profile, two distinct regions (rings) were analyzed (Figure 3): one corresponding to the irrigated period (the 2022 spring ring) and another corresponding to the rainfed regime (the 2017 spring ring, prior to the installation of the irrigation system). The selected rings were then cut and mounted onto aluminum specimen holders using conductive double-sided adhesive carbon tabs and coated with approximately 40 mm carbon using an EMITECH K905 Carbon Coater (Emitech Ltd., Ashford, Kent, United Kingdom).

1 https://www.goregacork.uevora.pt/

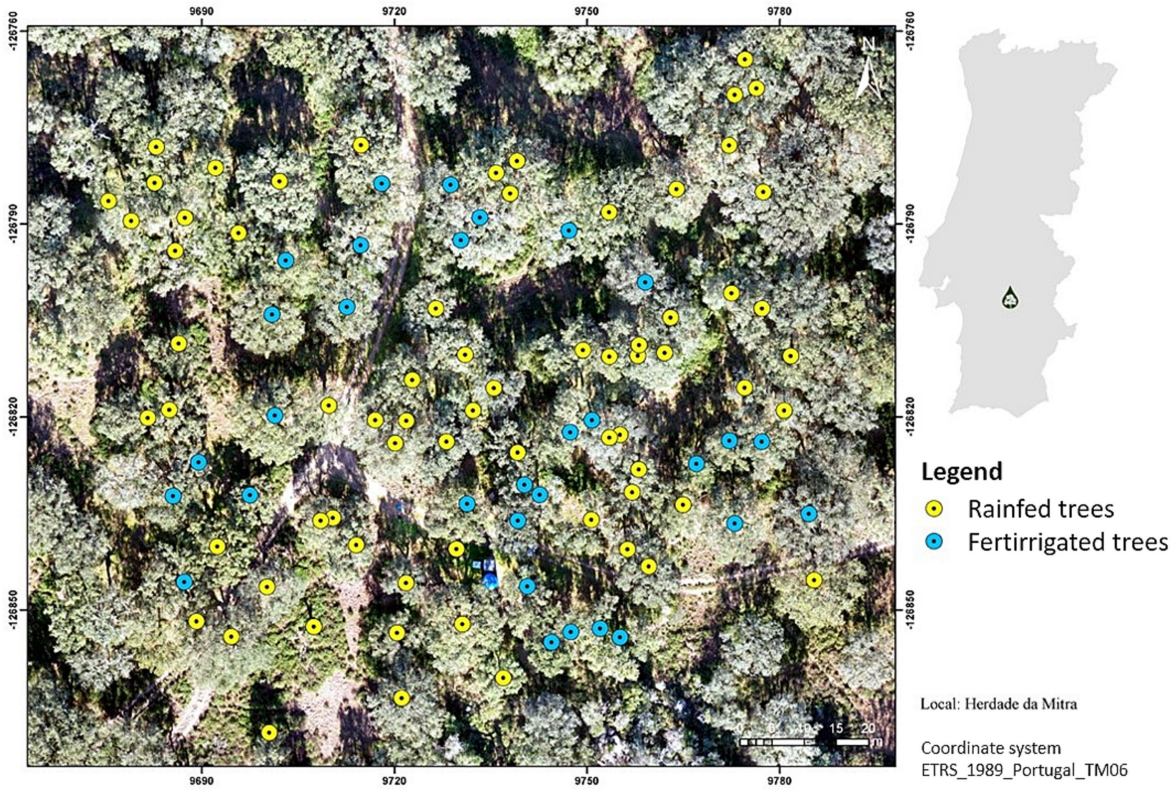

FIGURE 1
Research site: Mitra RegaCork plot. Coordinate system: ETRS_1989_Portugal_TM06. Image acquired with a DJI Mavic 2 Pro drone.

TABLE 1 Plot tree characteristics: basal area, stem circumference at breast height, height, and stem height of cork-harvesting.

Plot characteristics	Mean ± Std. deviation (except for the basal area)
Basal area (m^2ha^{-1})	15.00
Stem circumference at breast height (cm)	132.6 ± 40.6
Height (m)	8.70 ± 1.39
Stem height of cork harvesting (m)	2.36 ± 0.79

$N = 99$.

For each region, three images were obtained using MAPS software (MAPS version 2.1.38.1199, Thermo Fisher Scientific, Waltham, Massachusetts, United States) at 10 kV beam energy and 2.5 spot size under high vacuum conditions with a scanning electron microscope (Quanta FEG 650, Thermo Fisher Scientific, Waltham, Massachusetts, United States) and 50 measurements were performed for cell wall thickness analysis (150 measurements per region). In addition, 20 cell lumens were measured in the same three images per ring (60 measurements per region). The analysis was performed using ImageJ software, version 1.54 g, Java 1.8.0_345 (developed by Wayne Rasband and contributors at the National Institutes of Health, United States).

2.2.2 Cork growth and ring density

The cork ring width and ring density were analyzed using an X-ray microdensitometer in all trees present in the plot, using one sample per tree collected at a height of 130 cm, as described in Poeiras et al. (2021) and Poeiras et al. (2022a). For the analysis, complete cork rings were included, specifically rings 2 through 10, inclusive.

2.2.3 Cork moisture content percentage

An additional 5 × 5 cm cork sample was taken from each tree for moisture content analysis. The samples were stored in two sealed plastic bags to preserve their moisture content until weighing. They were then placed in an oven at 103 °C for 72 h, after which they were weighed again. Moisture content was determined using the following formula, as described in Duarte Vieira et al. (2009).

$$MC\,(\%) = \frac{(mw - md)}{mw}\, x\, 100,$$

where *mw* represents the initial mass of the sample (wet weight, g) and *md* the oven-dry mass of the sample (g).

2.3 Statistical analyses

Linear mixed models were used to compare cell wall thickness and cell lumen over time—2017 and 2022—and in relation to treatment (irrigation vs. control). Measurements were nested within images, and images were nested within trees, which were included as random effects to account for the hierarchical data structure. Time was included as a repeated measure and, together with treatment, was specified as a fixed effect. To account for correlations between repeated

10.3389/ffgc.2026.1755168

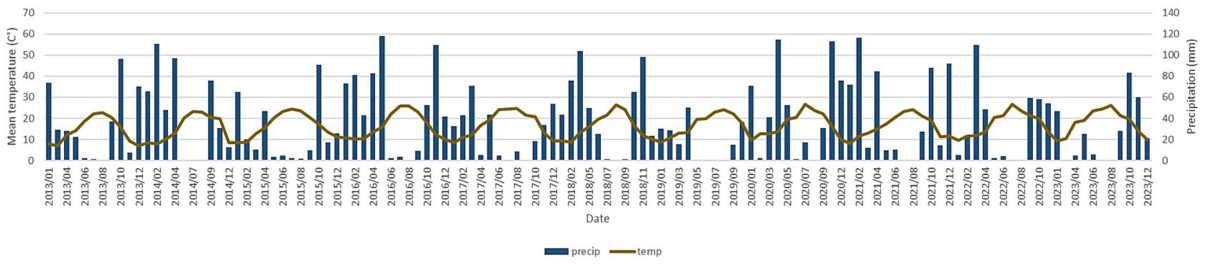

FIGURE 2
Ombrotermic chart for the period of cork growth (2013–2023). Climatic data from the University of Évora meteorological station (https://meteo.create.uevora.pt/estacoes/mitra/).

TABLE 2 Quantification of water inputs in the Mitra RegaCork plot by groups of watered trees.

Year	Irrigation volume (m^3)
2020	50
2021	102
2022	138

measurements on the same tree, the covariance structure was selected based on the Akaike Information Criterion (AIC).

Annual cork ring width and ring density measurements were normalized using min–max scaling to remove scale differences among trees. Normalized values (N) were calculated as $\frac{Xi - Xmin}{Xmax - Xmin}$, where X_i is the measured value, and X_{min} and X_{max} are the minimum and the maximum values of the series, respectively. This procedure scales all measurements between 0 and 1 before statistical analysis, allowing direct comparison of interannual variations among trees. Statistical analysis was carried out using IBM SPSS Statistics v.29 software package (IBM Corp., Armonk, NY, USA). Generalized linear mixed models were used to compare cork ring width and ring density in relation to treatment (irrigation vs. control). Ring, treatment, their interaction, and the covariate CBH were included as fixed effects. Trees were specified as random effects, and ring position was treated as a repeated factor.

Repeated-measures ANOVA was also performed to compare cork moisture content at harvest. Significance levels were defined as follows: $p > 0.05$, not significant; $p < 0.05$, significant; $p < 0.01$, very significant; and $p < 0.001$, highly significant.

An exploratory graphical analysis of all variables was performed to assess data distribution patterns and detect outliers prior to statistical analysis.

3 Results

3.1 Cell wall thickness and cell lumen

Cell walls were thicker, and cell lumen area was smaller in the 2022 growth ring compared with the 2017 ring (Figure 4; Tables 3–9). Trees assigned to the irrigation group already exhibited greater cell wall thickness and smaller cell lumens before the treatment began. During the irrigation period, the increase in cell wall thickness was significantly greater than in the rainfed group. In contrast, lumen size decreased proportionally in both groups, indicating that the treatment had no significant effect on this parameter (Table 7).

The relationship between cell wall thickness and cell lumen area was highly significant, according to the linear mixed model ($p < 0.001$, $t = -6.655$).

Regarding the influence of growth ring (year) and additional irrigation (treatment) on cell wall thickness, the linear mixed model showed highly significant effects ($p < 0.001$) for both (Tables 4–6).

With respect to the influence of *year* and *treatment* on cell lumen area, the same linear mixed model analysis found a highly significant effect of year, but no significant effect of treatment (Tables 7–9).

Regarding the estimation of covariance parameters for both cell wall thickness and cell lumen area—which represent the variance among and within subjects—the analysis revealed high variability both between and within trees ($p < 0.001$) (Tables 6, 9).

3.2 Cork growth and ring density

The cork growth followed the previously observed growth trend, as described by Costa et al. (2002) and Natividade (1934), showing a decreasing trend in growth as successive growth rings were formed (Figure 5), which is supported by the highly significant effect of the *Ring* source of variation.

There appeared to be a visual tendency for growth rings to become wider once the trees began receiving irrigation. However, no statistically significant differences were observed in either cork ring width or ring density with respect to the sources of variation, treatment, or circumference at breast height (CBH) (Tables 10–14). Intraspecific competition was also not significant.

The estimated covariance parameters indicated that variation among trees minimal and not significant, with most of the variation occurring within trees for both parameters, cork ring width and density.

3.3 Cork moisture content percentage

Cork moisture was higher in samples from fertirrigated cork oaks ($p = 0.034$) (Figure 6). The mean ± standard deviation (%) was 21.537 ± 2.992 for non-fertirrigated samples and 22.081 ± 3.167 for fertirrigated samples.

4 Discussion

Cell walls, which provide support and structure to cork tissue, originate from successive divisions of the phellogen. They

10.3389/ffgc.2026.1755168

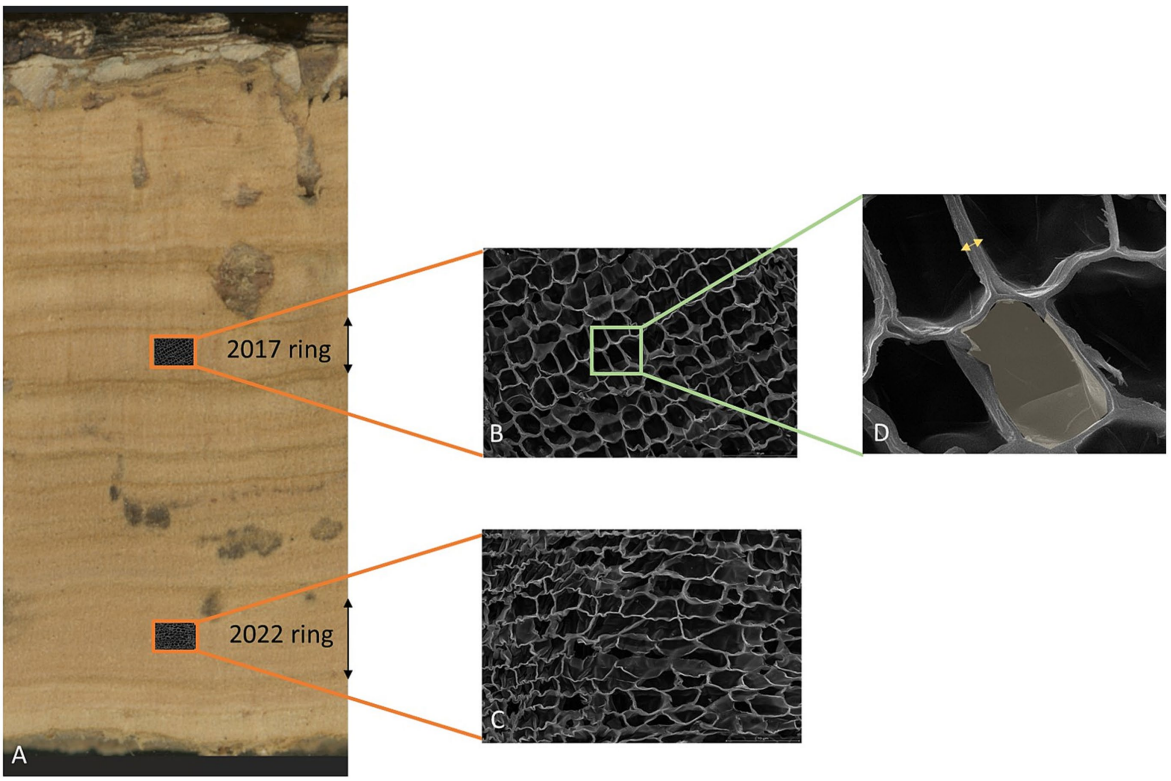

FIGURE 3
Cork features measured: **(A)** cork sample profile showing the locations where scanning electron microscope images were acquired; **(B)** Scanning electron microscope image from the 2017 ring; **(C)** SEM image of the 2022 ring; **(D)** example of measurements: cell wall thickness and lumen area.

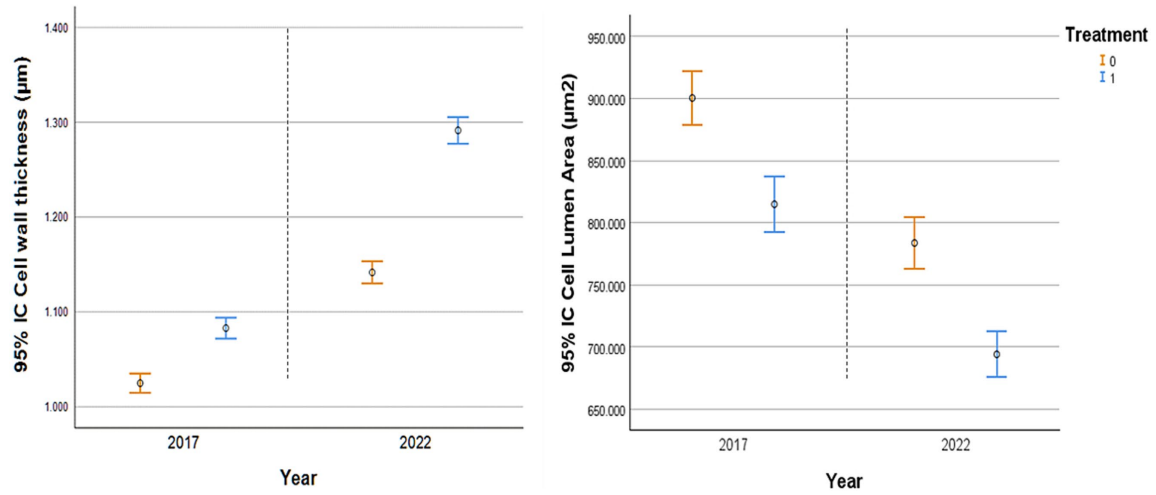

FIGURE 4
Graphs of cell wall thickness and cell lumen area by year, before and during treatment, and separated by treatment (0 = control, 1 = irrigation). * In 2017, all trees were rainfed with no additional water; however, for clarity regarding future treatments, they were already categorized into treatment groups, splited by colours in 2017.

TABLE 3 Cell wall thickness and cell lumen area for both regions (2017 and 2022) by treatment.

Feature	Region	Treatment 0	Treatment 1
Cell wall thickness (µm)	2017*	1.025 ± 0.221	1.083 ± 0.241
	2022	1.142 ± 0.253	1.290 ± 0.300
Cell lumen area (µm²)	2017*	900.371 ± 290.456	814.845 ± 301.761
	2022	783.677 ± 282.707	694.025 ± 251.633

*In 2017, all trees were rainfed with no additional water; however, for clarity regarding future treatments, they were already categorized into treatment groups.

are responsible for cork density, as chemical compounds are deposited within them. According to Costa et al. (2002) and our previous observations (Poeiras et al., 2022a), the density of the cork profile increases from the oldest to the newest rings. This pattern results from thicker cells located on the inner side of the cork profile, as demonstrated in this study. Although the *year* of cell formation had the greatest influence on cell wall thickness ($F = 229.723$), with greater values observed in 2022 than in 2017 (Table 3)—consistent with the typical cork profile

TABLE 4 Type III tests of fixed effects for cell wall thickness.

Source of variation	Numerator df	Denominator df	*F*	Significance
Year	1	7152.363	229.723	< 0.001
Treatment	1	6731.276	79.966	< 0.001

TABLE 5 Estimates of fixed effects for cell wall thickness.

Parameter	Estimate	Std. error	df	*t*	Significance	95% confidence interval (lower bound)	95% confidence interval (upper bound)
Intercept	1.264	0.015	97.486	82.929	<0.001	1.233	1.294
Treatment = 0	−0.095	0.011	6731.276	−8.942	<0.001	−0.116	−0.074
Treatment = 1	0	0	–	–	–	–	–
Year = 2017	−0.115	0.008	7152.363	−15.157	<0.001	−0.130	−0.100
Year = 2022	0	0	–	–	–	–	–
Treatment 0 × Year 2017	0	0	–	–	–	–	–
Treatment 0 × Year 2022	0	0	–	–	–	–	–

TABLE 6 Estimates of covariance parameters for cell wall thickness.

Parameter	Estimate	Std. error	Wald Z	Significance	95% confidence interval (lower bound)	95% confidence interval (upper bound)
Residual	0.053	0.001	59.686	<0.001	0.051	0.054
Intercept tree × image variance	0.014	0.002	5.725	<0.0001	0.010	0.019

TABLE 7 Type III tests of fixed effects for cell lumen areas.

Source of variation	Numerator df	Denominator df	*F*	Significance
Year	1	2839.821	67.896	<0.001
Treatment	1	2453.005	1.112	0.292

TABLE 8 Estimates of fixed effects for cell lumen areas.

Parameter	Estimate	Std. error	df	*t*	Significance	95% confidence interval (lower bound)	95% confidence interval (upper bound)
Intercept	729.210	18.505	137.849	39.405	<0.001	692.619	765.801
Treatment = 0	19.283	18.288	2453.005	1.054	0.292	−16.579	55.145
Treatment = 1	0	0	–	–	–	–	–
Year = 2017	109.116	13.242	2839.821	8.240	<0.001	83.150	135.082
Year = 2022	0	0	–	–	–	–	–
Treatment 0 × Year 2017	0	0	–	–	–	–	–
Treatment 0 × Year 2022	0	0	–	–	–	–	–

TABLE 9 Estimates of covariance parameters for cell lumen areas.

Parameter	Estimate	Std. error	Wald Z	Significance	95% confidence interval (lower bound)	95% confidence interval (upper bound)
Residual	66056.574	1763.858	37.450	<0.001	62688.382	69605.735
Intercept tree × image variance	15333.128	2874.392	5.334	<0.0001	10618.473	22141.113

TABLE 10 Generalized linear mixed model (GLMM) estimates of the independent fixed effects on the cork ring-width and ring-density.

Source of variation	df	Ring-density			Ring-width		
		Denominator df	*F*	*p*-value	Denominator df	*F*	*P*-value
Ring	8	441.364	5.346	<0.001	441.565	18.631	<0.001
Treatment	1	57.837	0.055	0.816	57.992	0.002	0.961
Ring × treatment	8	441.364	0.797	0.606	441.565	1.005	0.431
CBH	1	55.464	0.056	0.813	55.576	0.888	0.350

TABLE 11 Estimates of fixed effects for N ring-density.

Parameter	Estimate	Std. Error	df	*t*	Significance	95% CI (lower bound)	95% CI (upper bound)
Intercept	0.685	0.083	189.043	8.239	<0.001	0.521	0.849
Ring 2	−0.281	0.087	437.527	−3.220	0.001	−0.452	−0.109
Ring 3	−0.436	0.087	437.527	−5.004	<0.001	−0.608	−0.265
Ring 4	−0.433	0.087	437.527	−4.967	<0.001	−0.604	−0.262
Ring 5	−0.351	0.087	437.527	−4.023	<0.001	−0.522	−0.176
Ring 6	−0.296	0.087	437.527	−3.392	<0.001	−0.467	−0.124
Ring 7	−0.235	0.087	437.527	−2.694	0.007	−0.406	−0.063
Ring 8	−0.344	0.099	456.306	−3.487	<0.001	−0.538	−0.150
Ring 9	−0.299	0.097	453.444	−3.081	0.002	−0.490	−0.108
Ring 10	0	0	–	–	–	–	–
Treatment 0	−0.160	0.086	492.270	−1.871	0.062	−0.328	0.008
Treatment 1	0	0	–	–	–	–	–
Ring 2 × Treatment 0	0.166	0.120	437.527	1.378	0.169	−0.071	0.402
Ring 2 × Treatment 1	0	0	–	–	–	–	–
Ring 3 × Treatment 0	0.261	0.120	437.527	2.173	0.030	0.025	0.498
Ring 3 × Treatment 1	0	0	–	–	–	–	–
Ring 4 × Treatment 0	0.164	0.120	437.527	1.364	1.73	−0.072	0.400
Ring 4 × Treatment 1	0	0	–	–	–	–	–
Ring 5 × Treatment 0	0.210	0.120	437.527	1.744	0.082	−0.027	0.446
Ring 5 × Treatment 1	0	0	–	–	–	–	–
Ring 6 × Treatment 0	0.204	0.120	437.527	1.692	0.091	−0.033	0.440
Ring 6 × Treatment 1	0	0	–	–	–	–	–
Ring 7 × Treatment 0	0.087	0.120	437.527	0.720	0.472	−0.150	0.323
Ring 7 × Treatment 1	0	0	–	–	–	–	–
Ring 8 × Treatment 0	0.157	0.129	448.869	1.216	0.225	−0.067	0.410
Ring 8 × Treatment 1	0	0	–	–	–	–	–
Ring 9 × Treatment 0	0.128	0.128	446.965	1.004	0.316	−0.123	0.379
Ring 9 × Treatment 1	0	0	–	–	–	–	–
Ring 10 × Treatment 0	0	0	–	–	–	–	–
Ring 10 × Treatment 1	0	0					
DBH	0.000	0.000	55.464	0.237	0.813	−0.001	0.001

pattern—*treatment* also had a considerable effect on cell wall thickness ($F = 79.966$). The additional water supplied during the most recent years of cork growth has promoted an increase in cell wall thickness rather than in cell size. This finding may be relevant for the production of cork stoppers, since they are produced from the cork closest to the inner portion of the cork profile. It should be noted that cork in this study was analyzed in its raw state to maintain its original characteristics, before any industrial processing. When boiled, cork expands by approximately 15% transversely and 6% tangentially, resulting in an increase in thickness (Fortes et al., 2004).

Silva et al. (2005) observed values of cell wall thickness between approximately 1 and 1.5 μm in early cork and approximately 2 μm in late cork. Regarding the effect of irrigation on cell wall thickness, Poeiras et al. (2021) and Poeiras et al. (2022a) reported thinner cell walls in cork oaks subjected to irrigation than in cork oaks growing in a traditional stand. However, that exploratory study did not use the same provenance trees for the control group. Therefore, the observed differences in the cell wall thickness may have been associated with other factors, such

TABLE 12 Estimates of covariance parameters for N ring-density.

Parameter	Estimate	Std. error
Residual	0.106	0.007
Intercept tree Variance	0.001	0.003

TABLE 13 Estimates of fixed effects for N ring-width.

Parameter	Estimate	Std. Error	df	*t*	Sig.	95% CI (lower bound)	95% CI (upper bound)
Intercept	0.236	0.074	192.966	3.210	0.002	0.091	0.381
Ring 2	0.462	0.078	437.669	5.955	<0.001	0.310	0.615
Ring 3	0.461	0.078	437.669	5.931	<0.001	0.308	0.613
Ring 4	0.429	0.078	437.669	5.521	<0.001	0.276	0.581
Ring 5	0.316	0.078	437.669	4.065	<0.001	0.163	0.468
Ring 6	0.153	0.078	437.669	1.976	0.049	0.001	0.306
Ring 7	0.310	0.078	437.669	3.993	<0.001	0.157	0.463
Ring 8	0.261	0.088	456.735	2.974	0.003	0.089	0.434
Ring 9	0.152	0.086	453.831	1.756	0.080	−0.018	0.322
Ring 10	0	0	–	–	–	–	–
Treatment 0	−0.052	0.076	492.558	−0.682	0.495	−0.201	0.098
Treatment 1	0	0	–	–	–	–	–
Ring 2 × Treatment 0	0.037	0.107	437.669	0.342	0.732	−0.174	0.247
Ring 2 × Treatment 1	0	0	–	–	–	–	–
Ring 3 × Treatment 0	0.046	0.107	437.669	0.430	0.667	−0.164	0.257
Ring 3 × Treatment 1	0	0	–	–	–	–	–
Ring 4 × Treatment 0	0.068	0.107	437.669	0.633	0.527	−0.143	0.278
Ring 4 × Treatment 1	0	0	–	–	–	–	–
Ring 5 × Treatment 0	0.105	0.107	437.669	0.984	0.326	−0.105	0.316
Ring 5 × Treatment 1	0	0	–	–	–	–	–
Ring 6 × Treatment 0	0.222	0.107	437.669	2.074	0.039	0.012	0.433
Ring 6 × Treatment 1	0	0	–	–	–	–	–
Ring 7 × Treatment 0	0.061	0.107	437.669	0.573	0.567	−0.149	0.272
Ring 7 × Treatment 1	0	0	–	–	–	–	–
Ring 8 × Treatment 0	−0.012	0.115	449.190	−0.101	0.920	−0.237	0.214
Ring 8 × Treatment 1	0	0	–	–	–	–	–
Ring 9 × Treatment 0	−0.049	0.114	447.256	−0.432	0.666	−0.273	0.174
Ring 9 × Treatment 1	0	0	–	–	–	–	–
Ring 10 × Treatment 0	0	0	–	–	–	–	–
Ring 10 × Treatment 1	0	0					
DBH	0	0	55.576	−0.942	0.350	−0.001	0

as genetics, soil conditions, or even sample size. For this reason, the present study was conducted to confirm the results from the exploratory study. Using a *pre-test–post-test* control group design helped control for the effect of genetics on the cell wall thickness. Thus, in this study, the increase in cell wall thickness was associated with cork development under tension forces and with water availability provided by summer irrigation. All the values found, both in previous studies and in the present study, fall within the ranges reported by Fortes et al. (2004) and Pereira (2007), regardless of the management type.

TABLE 14 Estimates of covariance parameters for N ring-width.

Parameter	Estimate	Std. error
Residual	0.084	0.006
Intercept tree variance	0.001	0.002

Regarding cork calliper and density, no statistical differences were observed between treatments, though irrigated rings showed a tendency to become larger. These trees presented thicker cell walls, whereas cell lumen size remained unchanged; therefore, the increase in ring size was not noticeable, at least toward the end of the cork production cycle (8th–10th year) (Figure 5).

These cork characteristics, such as thickness and density, play an important role in cork products, especially in the cork stopper industry. Natividade (1934) reported a wide range of raw cork density values (120–200 kg m $-^{3}$), reflecting the high variability of the cork. In the cork stopper industry, stoppers are usually produced from the inner portion of cork planks, meaning that the older cork rings are discarded during industrial processing. Cork density, according to the cork density trend (Natividade, 1934), is higher in these inner cork rings.

The local-scale factors studied in this work may contribute to multi-scale modeling, as suggested by Príncipe et al. (2022) in their study.

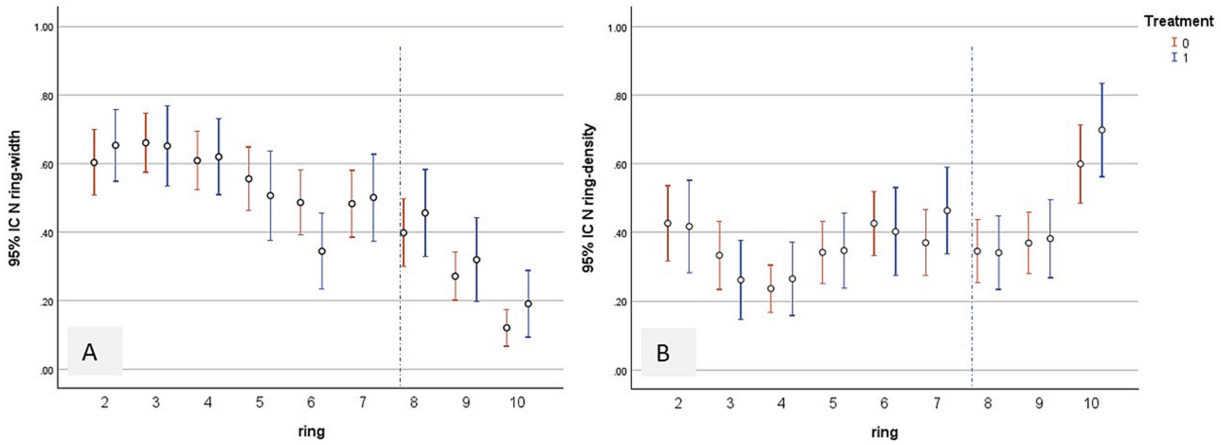

FIGURE 5
Cork ring-width **(A)** and ring-density **(B)** by treatment. The blue vertical line represents the moment when irrigation started.

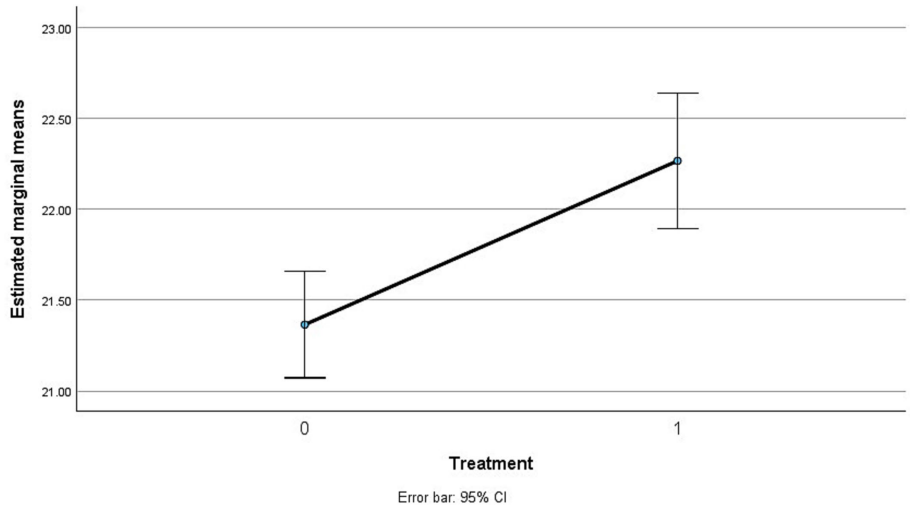

FIGURE 6
Estimated marginal means of cork moisture content for samples from irrigated (1) and rainfed (0) trees.

Finally, regarding cork moisture content, under ideal conditions it is usually approximately 20% after cork removal, but decreases rapidly once the inner surface is exposed to air (Gil, 1998; Costa and Pereira, 2013). Cork moisture depends on edaphoclimatic conditions, particularly in case of recent precipitation events or adequate soil moisture. On the contrary, during long periods of drought, cork moisture tends to decrease, which may impair cork debarking. The presence of plasmodesmata in cork tissue (Teixeira and Pereira, 2009) and the wood anatomical feature may contribute to the moisture content allocation, facilitating the movement of moisture from the xylem into the cork. The additional water provided by summer irrigation contributed to the higher moisture observed in irrigated trees (22.081 ± 3.167%). This indicates that, under summer drought conditions, irrigation may facilitate the debarking process, allowing easier cork extraction. With water available, the phellogen cells are more active, which helps avoid damage during stripping, allowing the removal of larger, intact planks. This result is particularly relevant for forest management, since the window of opportunity for cork removal is relatively short during late spring/early summer, and this window is expected to shorten with climate change. Extending spring-like conditions through irrigation may help maintain cork debarking as a sustainable process.

We therefore cannot draw definitive conclusions regarding the effects of this level of irrigation during the final years of cork growth on ring width and ring density under the specific site conditions. However, cork density does not appear to decrease as a result of irrigation; on the contrary, there may be a tendency toward an increase, likely due to cell wall thickening. Moreover, the addition of irrigation increases the moisture content of the cork, which facilitates its extraction and may influence its cell structure.

Data availability statement

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

AP: Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. CC-A: Data curation, Formal analysis, Investigation, Methodology, Writing – review & editing. BG: Data curation, Software, Writing – review & editing. CV: Data curation, Software, Writing – review & editing. JM: Conceptualization, Supervision, Writing – review & editing. JR: Data curation, Methodology, Writing – review & editing. JN: Data curation, Methodology, Writing – review & editing. MV: Conceptualization, Supervision, Writing – review & editing. MS: Writing – review & editing. NA: Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Validation, Visualization, Writing – review & editing.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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