

Communication

Physiological Activity of *Quercus suber* with a High Presence of *Cerambyx welensii*

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Abstract: The wood borer *Cerambyx welensii* Küster is a key contributor to *Quercus* open woodland (dehesa) decline. Among other factors, olfactory and visual cues could influence host colonisation by this species. In this study, we investigated whether the physiological performance and morphological features of *Q. suber* trees under summer stress are affected by *C. welensii* infestation. Additionally, we analysed the relation between morpho-physiological variables and the emission of monoterpenes that potentially mediate host selection by *C. welensii*. Thirty-six *Q. suber* trees with known monoterpene emission profiles were selected: 18 trees highly visited by *C. welensii*, and 18 neighbouring trees not visited or at least not visibly damaged by this wood borer. For each tree, we assessed photosynthesis, stomatal conductance, and transpiration during the early evening, and also the perimeter and crown projection. Trees visited by *C. welensii* maintained higher photosynthetic activity than non-visited trees (1.5–2.15 times) from 19:35 to 20:45 h. Visited trees had larger perimeters and smaller crown projection area-to-perimeter ratios than non-visited trees. Results suggest that, under stress conditions, the physiological performance of trees infested by *C. welensii* could have favoured foliar emission of certain monoterpenes influencing intraspecific host selection by this species.

Keywords: Cerambycidae; dehesa; photosynthesis; stomatal conductance; transpiration; xylophagous; wood borer



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1. Introduction

The sclerophyllous Mediterranean open woodland (dehesa) is an agrosilvopastoral system that, when properly put into practice, can serve as a sustainable approach to natural resource management, in harmony with the maintenance of high levels of biodiversity. From a socioeconomic perspective, for centuries, dehesas have potentially allowed sustainable social development and economic activity in certain traditionally disadvantaged areas. For these reasons, dehesas are considered a model of High Nature Value (HNV) farming [1]. HNV systems constitute a key part of the European Union's biodiversity action plan and the Council of Europe's strategy on biological and landscape diversity. Both European and national policy guidelines on rural development have considered research on dehesas a priority, particularly in relation to integrated pest management in these agroforestry systems.

Stands of cork oak (*Quercus suber* L.) are continuously exposed to anthropogenic and natural stressors [2]. Among natural stressors, attack by wood-boring insects, such as *Cerambyx welensii* Küster (Coleoptera, Cerambycidae), is believed to play a major role in *Q. suber* decline in southwest Spain [3,4]. Several types of deciduous trees, especially in the genus *Quercus*, are infested by *C. welensii* [5]. Adults of this large cerambycid (≥ 60 mm long) have a flight period that spans from mid-May to late July, with early night activity (mainly from 21:00 to 23:00 h) [3]. Only its larval stage causes damage; larvae bore into

wood increasing the risk of branch and trunk breakage [3], as well as facilitating infection by wood-decaying fungi and plant pathogens [6]. Very high population densities of *C. welensii* in *Q. suber* stands are worrying since they have been shown to cause annual canopy cover loss of as much as 1.68% on average, potentially causing complete loss of the forest stand in a matter of decades (10–30 years) [7].

In addition to biotic stressors, trees in Mediterranean areas are exposed to severe summer stress, which causes physiological and biochemical changes, photosynthesis being one of the cellular functions most markedly affected by high temperatures and severe drought [8,9]. Notable decreases in both stomatal conductance (37%) and maximum carboxylation rate (43%) have been reported in *Q. suber* trees under severe drought [9]. Low photosynthetic and stomatal conductance rates, measured under extreme climatic conditions, have been considered an indicator of successful adaptation to severe stress in *Pinus halepensis* Mill. [10]. Leaves of *Q. suber* showed higher photosystem II efficiency under light stress than those of *Quercus ilex* L. [11].

Terpenes and other volatile organic compounds (VOCs) have key functions in plant physiology and plant–environment interactions. They can protect plants against stressors and mediate plant communication [12,13]. Environmental factors such as temperature and photosynthetically active radiation are among the strongest determinants of short-term VOC emissions [14], as, for example, monoterpene precursors are derived from photosynthetic activity [15]. Under summer conditions, significant correlations were found between net photosynthetic rates and daily emission rates of terpenes (especially limonene, the least volatile monoterpene) by *Q. ilex* [16], though the correlations between monoterpene emissions and stomatal conductance were weaker [15]. Trees of the *Quercus* genus are considered among the highest VOC emitters [17], with *Q. suber* showing particularly strong monoterpene emission [11,18]. Further, *Q. suber* shows two marked foliar monoterpene emission patterns: a limonene chemotype (in which limonene is the most emitted compound) and a pinene chemotype (in which α - and β -pinene and sabinene dominate) [19]. Cerambycids seem to be attracted to VOCs such as monoterpenes, these compounds probably helping them identify weak and damaged host trees [20]. Higher rates of infestation by *C. welensii* have been observed in *Q. suber* with a limonene chemotype (limonene accounting for > 30% of total monoterpene emissions) [19,21].

The goal of this study was to explore cues potentially affecting host selection by *C. welensii*, particularly its relation with both physiological performance and morphological features of *Q. suber* trees under summer stress, as well as the effect of physiological activity on the emission of VOCs potentially mediating intraspecific host selection by *C. welensii*. Hence, the specific objectives of this study were: (i) to analyse short-term changes in photosynthesis (as reflected by net CO₂ assimilation, *A*), stomatal conductance (*g_s*) and transpiration (*E*) in *Q. suber* trees classified according to sightings of and damage attributable to *C. welensii*; and (ii) to investigate the link between morpho-physiological features of *Q. suber* trees and their foliar monoterpene emission profiles.

2. Materials and Methods

2.1. Site and Trees Studied

The study area was a *Q. suber* open woodland (dehesa, with 75 trees ha⁻¹) in southwest Spain (37°15'43.73" N, 6°28'34.65" O, 80 m a.s.l.) that is known to be majorly affected by *C. welensii*. The mean annual temperature and precipitation were 17.6 °C ± 0.2 and 588 mm, respectively. In 2008, we selected 36 trees classified into two groups (18 trees each) based on the history of sightings of *C. welensii* adults [3]. Specifically, the first group (here on called visited trees) included the trees visited most by different *C. welensii* adults (cumulative mean sightings of 54 ± 23 individuals per tree between 2002 and 2007, and evidence of substantial damage by large wood borers). The second group (here on called non-visited trees) comprised neighbouring *Q. suber* trees on which we had not observed either *C. welensii* adults or damage attributable to this wood borer (Figure 1). All the trees were estimated to be around 150 years old [7]. *Cerambyx welensii* identification was based on

visual examination of all adults captured between 2002 and 2007, using a dichotomous key for adult longhorn beetles [22].

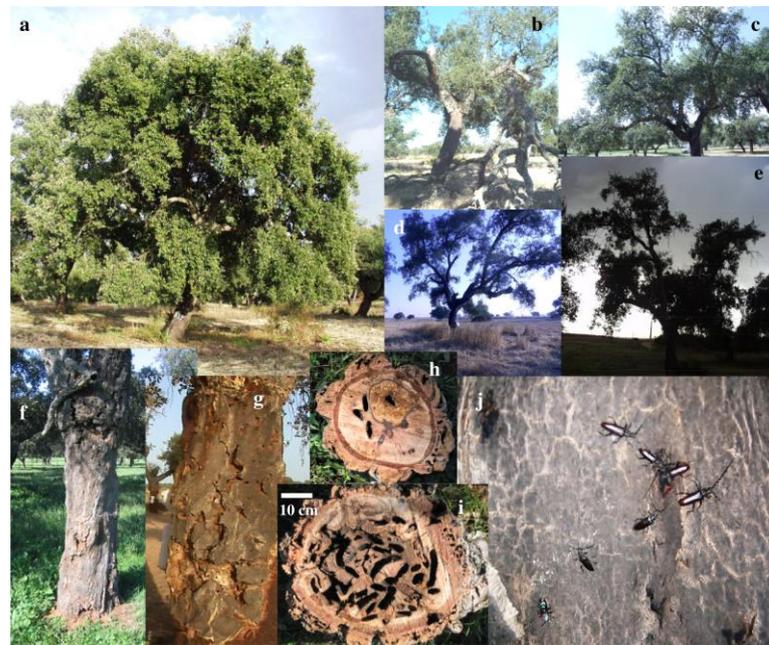


Figure 1. (a) *Quercus suber* not infested by *Cerambyx welensii*; (b–e) Several degrees of crown architecture alteration in *Q. suber*, due to *C. welensii* damage; (f–i) damage caused by *C. welensii*; note the rotting process around a larval gallery in (h); (j) a cluster of *C. welensii* adults near a *Q. suber* bark exudate.

2.2. Physiological and Morphological Measurements

Measurements were made during the seasonal flight peak of *C. welensii* (last week of June; [3]), in the hours before the start of the nightly flight activity of *C. welensii*. Specifically, measurements were carried out in five rounds between 19:00 and 21:20, at 35 min intervals. Three or four trees in each group were randomly assigned to each round, and in each round, we collected one sprig from each of the selected trees (a total of 6–8 sprigs per round). We harvested 30 cm long sprigs from areas that were exposed to the sun and at ≈ 2 m from the ground. These sprigs had between 53 and 187 leaves, and after drying at 60 °C for ≥ 48 h, a mean dry weight of 14.48 ± 0.7 g. Immediately after the sprig harvest, we identified leaves that had grown the previous spring and measured photosynthesis (net CO₂ assimilation, *A*), stomatal conductance (*gs*), and transpiration (*E*) in the field. Measurements of *A*, *gs*, and *E* were made using an infrared gas analyser with a wide leaf chamber (6.25 cm²; LCi system, ADC BioScientific, Hoddesdon, UK). Photosynthetic photon flux density, relative humidity, and temperature were measured during the aforementioned assessment of physiological parameters. Subsequently, we also assessed morphological variables that might be related to physiological performance, as well as host selection by *C. welensii*. Specifically, the perimeter of each tree was measured at breast height, and the crown projection area (*CPA*) was estimated from the vertical projection of the crown corresponding to each tree based on high-resolution satellite images [23] and using ArcGis 10.0.

The same evenings as the physiological measurements, foliar monoterpenes were sampled (see [21] for further details; data not included in this document). Briefly, monoterpene samples were obtained using an aeration system [24], comprising a measurement chamber (polyester oven bag; Albal, Cofresco, Madrid, Spain), connected to a Teflon sampling line leading to a pump (SP 200 EC–LC diaphragm pump; Schwarzer Precision, Essen, Germany). Charcoal-filtered air entering the chamber was drawn through a sorbent tube (403 Orbo Tenax TA glass tube, 150 mg, 60/80 mesh; Sigma-Aldrich, Madrid, Spain), for 5 min at a flow rate of 120 mL min^{−1}. All Orbo tubes were sealed immediately after collection

and stored at 4 °C in the field, and later, at −28 °C in the laboratory, until analysis which was always performed within 24 h. Blank controls (empty measurement chambers, not enclosing sprigs) were collected simultaneously using the same sampling system.

Monoterpene samples were analysed by gas chromatography-mass spectrometry (GC type 6890N, MSD 5973; Agilent, Santa Clara, CA, USA), using an HP-5ms column (0.25 mm × 30 m × 0.25 µm) and helium as the carrier gas (1 mL min^{−1}), with the following oven program: the starting temperature (46 °C) was increased to 70 °C (rate of 30 °C min^{−1}), held steady (4 min), and then increased to 80 °C (rate of 5 °C min^{−1}), to 90 °C (rate of 4.5 °C min^{−1}), and to 300 °C (rate of 50 °C min^{−1}). Peak identification was achieved by comparison with pure standards (Sigma-Aldrich; Madrid, Spain; purity ≥ 94%) and with mass spectra in the NIST 02 library (MSD Chemstation Build 75 software, G2070BA version). For quantitative analysis, calibration curves were obtained for α-pinene, β-pinene, sabinene, limonene, and myrcene.

Comparative analyses for each physiological variable were carried out using linear mixed models (LMM, lme4 package; [25]), with mean values of each variable as the dependent variables, sampling time and visits by *C. welensii* as fixed factors, and tree identity as a random factor (intercept). Likelihood ratios were used to assess the significance of the main factors. The Benjamini-Hochberg method was used to adjust *p* values for multiple comparisons [26] to control for the false discovery rate (expected proportion of tests that are classified as significant erroneously, Lsmmeans package; [27]).

To investigate the relation of both physiological performance and morphological features with monoterpene emissions, we carried out partial canonical correspondence analysis (pCCA, Vegan package; [28]), taking the perimeter as a covariate. Previously, data were scaled to a mean of zero and unit variance within each sampling round. Multicollinearity was tested using variance inflation factors. Finally, the explanatory variables included photosynthesis (*A*), transpiration (*E*), and the crown projection area-to-perimeter (*CPA/perimeter*) ratio. The response variables were relative emissions of α-pinene, β-pinene, sabinene, limonene, and myrcene, and *pinene-type* VOCs, a new variable created by summing the relative emissions of α-pinene, β-pinene, and sabinene. These emissions were assessed for individual trees and expressed as percentages of the sum of observed emissions for the five main compounds emitted by *Q. suber*, namely, α-, and β-pinene, sabinene, limonene, and myrcene. The significance of the canonical axes was assessed with permutation tests using the Vegan package.

The aforementioned statistical analysis was carried out using R software, version 3.1.0. Thresholds for significance and marginal significance were set at $\alpha = 0.05$ and $\alpha = 0.1$, respectively.

3. Results

Over the early evening, the photosynthetic photon flux density decreased sharply (from 1097.5 to 75 µmol m^{−2} s^{−1}). Nonetheless, the air temperature remained high (>28.1 °C), and relative humidity remained very low (<40% throughout the study period). Given the low light intensity at 21:20, we were not able to obtain accurate measurements for the three physiological variables (*A*, *gs*, and *E*) at this time, and hence, these data were not included in the analysis (Figure 2b–d).

A very significant (*p* < 0.01 overall) positive correlation was found between standardised values of *E* and *gs* in both non-visited (*R* = 0.61) and visited (*R* = 0.82) trees. Both *gs* and *E* increased until 20:10, after which the values dropped. Overall, these two variables had slightly higher values in non-visited than visited trees; however, there were neither significant effects of the main factors, time and visits, nor interaction effects on the rates of *gs* and *E*. In contrast, the main effect of time on *A* rates showed a trend towards significance (LMM: $\chi^2_3 = 3.58$, *p* = 0.06; Figure 2b) and was affected by visit status (significant time × visits interaction effect; LMM: $\chi^2_3 = 9.83$, *p* < 0.01). Specifically, the *A* rates of non-visited trees exceeded those of visited trees at 19:00 (*t* = 1.69, *p* = 0.08; Figure 2b), after which a sharp increase in *A* was observed in visited trees, reaching values significantly higher

(2.15 times) than those measured in non-visited trees at 19:35 ($t = -1.99$, $p = 0.04$) and 20:45 ($t = -2.35$, $p = 0.03$).

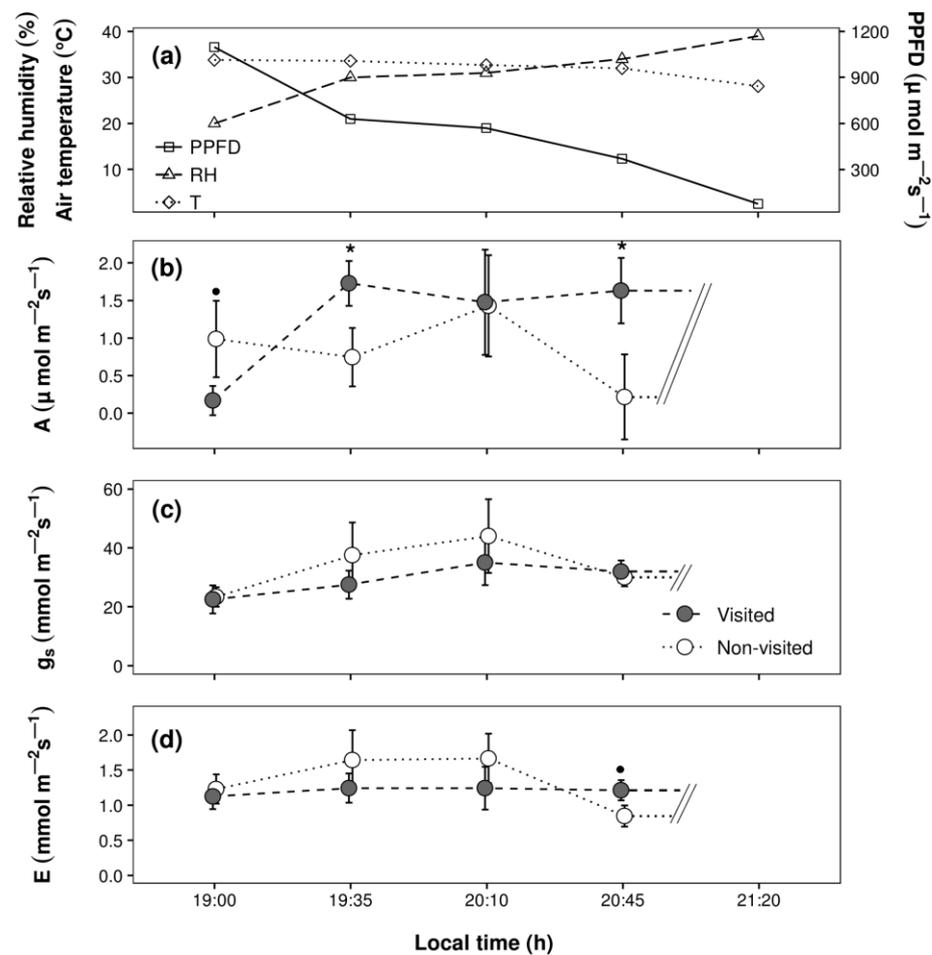


Figure 2. (a) Environmental conditions over the early evening: relative humidity (RH), air temperature (T), and photosynthetic photon flux density (PPFD); (b) photosynthesis (A), (c) stomatal conductance (g_s) and (d) transpiration (E) from *Quercus suber* trees classified as highly visited or not visited by *Cerambyx welensii*. Symbols over mean (\pm SE) values at some time points indicate significant differences by visit status (* $p < 0.05$; • $p < 0.1$ in LMM with Benjamini-Hochberg correction for multiple comparisons; $N = 3\text{--}4$ /sampling round for each visit status). Data for A, g_s , and E measured at 21:20 are not shown.

The visited trees had a significantly larger mean perimeter than non-visited trees (168.4 and 131.1 cm, respectively; $p = 0.01$), and the two groups of trees had similar CPA values (48.2 and 46.4 m^2 for visited and non-visited trees, respectively; $p = 0.41$). Accordingly, the CPA/perimeter ratio was slightly lower for visited than non-visited trees (31.5 and 36.3 m, respectively; $t = -1.10$, $p = 0.2$).

For non-visited trees, the pCCA model was not significant (Permutation test: $p = 0.38$). In contrast, for the two groups considered together, the two first pCCA axes explained a low amount of variance corresponding to the emissions of limonene, myrcene, and *pinene-type* VOCs (19%, Permutation test: $F_3 = 2.02$, $p = 0.07$) (Figure 3a). The results of the pCCA model improved when it was applied to visited trees only, explaining 62% of the variance corresponding to limonene, myrcene, and *pinene-type* emissions (Permutation test: $F_3 = 6.01$, $p = 0.001$) (Figure 3b).

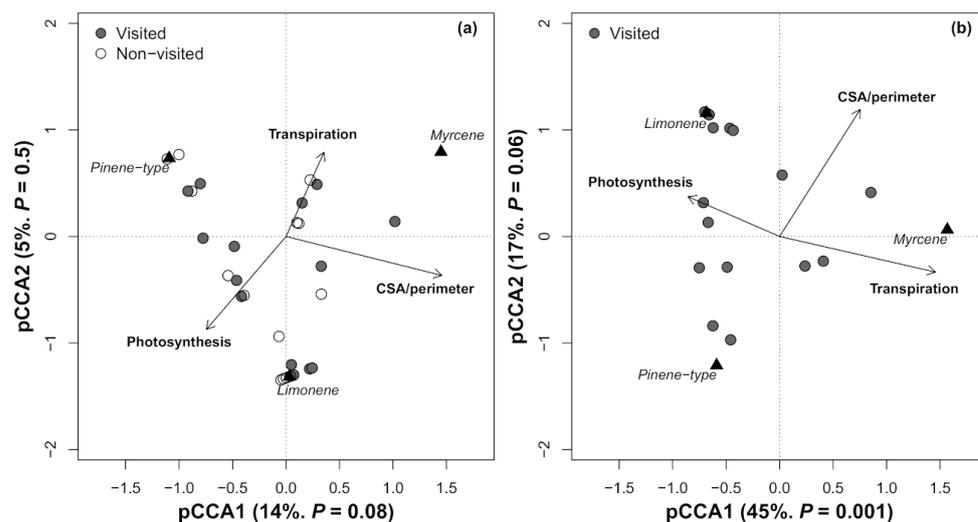


Figure 3. Partial canonical correspondence analysis triplot (Scaling 1) for (a) All *Quercus suber* trees together, i.e., both those highly visited and those not visited by *Cerambyx welensii*, and (b) *Q. suber* trees classified as highly visited by *C. welensii*. The analysis illustrates the effect of physiological variables (photosynthesis and transpiration) as well as the crown projection area-to-perimeter ratio ($CPA/perimeter$) on emission composition, specifically on the emissions of limonene, myrcene and pinene-type VOCs (sum of α - and β -pinene and sabinene) expressed as a percentage of the total emissions of these five main monoterpenes.

Analysing both groups together, the first pCCA axis (pCCA1) was marginally significant (Figure 3a); in contrast, for visited trees only, pCCA1 was significant ($p = 0.001$), while the second pCCA axis (pCCA2) was marginally significant ($p = 0.06$) (Figure 3b). For all the trees, pCCA1 was related mainly to the $CPA/perimeter$ ratio (biplot score: 0.17). For visited trees, pCCA1 was related primarily to A and secondarily to E (biplot scores: -0.46 and 0.42 , respectively), and pCCA2 was mainly related to the $CPA/perimeter$ ratio (biplot score: 0.41). In the model applied to visited trees, limonene emissions had moderate values (absolute value = 0.57) for both pCCA axes; in contrast, the pinene-type variable had a low value for pCCA1 (-0.16) but a moderate value for pCCA2 (0.63) (Figure 3b).

In brief, both pCCA models suggest that high limonene emissions were associated with low transpiration rates and high photosynthetic rates. High pinene-type emissions were found in trees with low $CPA/perimeter$ ratios (smaller canopies). Conversely, high limonene emission was found in visited trees with high $CPA/perimeter$ ratios (Figure 3). The least abundant monoterpene in *Q. suber* foliar emissions overall (myrcene) was strongly related to high transpiration rates; the association (positive) between the $CPA/perimeter$ ratio and myrcene emissions was weaker in visited trees.

4. Discussion

In the Mediterranean area, environmental constraints, stress due to drought, high temperatures, and high insolation can cause oxidative stress, and reductions in photosynthesis linked to a decrease in stomatal conductance, even in species suited to the local environment, such as *Q. suber* and *Q. ilex* [29,30] and studies cited therein. Showing resiliency under such stressful conditions is an adaptive behaviour [31]. There is evidence that the impact of some abiotic stresses is mitigated by non-stored constitutively released VOCs, as these compounds can stabilise membranes and/or serve as antioxidants, at least in the absence of photorespiration [12,13,32,33]. On the other hand, less is known about the role isoprenoids and monoterpenes, especially limonene may play in such defence mechanisms [13].

Across our study period, we found low values for the physiological variables A , gs , and E , as reported before for similar times of day in *Q. suber* and *Q. ilex* [34–36]. High air

temperatures (>25 °C) have been found to either reduce or inhibit photosynthesis in *Q. suber* and *Q. ilex* [37–39], and hence, the high temperatures during our samplings, presumably linked to low soil water availability, could also have negatively influenced *A* rates [14,36]. Nonetheless, even considering the moderate net CO₂ assimilation rates found, the *A* values measured differed significantly between trees that were and were not visited by *C. welensii*.

There is a paucity of knowledge about cues used by xylophagous longhorn beetles to select deciduous host trees. It is known, however, that visual cues may influence host location by *Cerambyx* species [4]. In relation to this, considerable numbers of *C. welensii* individuals were found to be transient in our study area [3], supporting the hypothesis that host selection mechanisms mediate adult movement across adjacent areas. In the study reported herein, the visited trees had a significantly larger mean perimeter than non-visited trees, though a non-significantly smaller *CPA/perimeter* ratio. This pattern is consistent with an observed preference of *C. welensii* for old and/or damaged trees [3].

Secondly, VOCs released by damaged or stressed plants can serve as olfactory cues for cerambycids, for finding host plants as well as conspecific mates [20,40]. In particular, traps baited with sources of fermentation odours have been shown to attract *C. welensii* [41]. Further, this species is known to have olfactory sensitivity to a wide spectrum of tree volatiles, especially the main monoterpenes emitted by its hosts, namely, α - and β -pinene, sabinene, limonene, and myrcene [42]. In particular, colonisation by *C. welensii* was found to be more likely in *Q. suber* trees with a limonene chemotype; while the emission of *pinenetype* compounds was more common in trees with no signs of activity of this species [21]. It has been suggested that *C. welensii* may use certain ratios of the aforementioned five monoterpenes in host emissions to help it distinguish between leaf chemotypes, and in particular, females may be involved in the detection of the limonene chemotype [21]. Nonetheless, traps baited with monoterpenes alone only weakly attracted *C. welensii*, compared to the efficacy of traps baited with synthetic fermentation odours [43].

Both the significant pCCA model we obtained for trees visited by *C. welensii* and the differences we observed in net CO₂ assimilation between trees that were and were not visited by this species, suggest, in accordance with [18], that the maintenance of photosynthetic activity during the early evening could favour the release of the less volatile monoterpene (limonene), precisely in a period when *C. welensii* starts its nightly flight activity. Further, infestation by *C. welensii* in old *Q. suber* trees increases the risk of modifying the crown architecture (e.g., changes in *CPA/perimeter* ratio) (Figure 1b–e), as a result of breakage of branches due to larval activity, and such crown alterations are expected to become increasingly common over the years in the study area [7]. We found the *CPA/perimeter* ratio was 14% lower in trees affected by *C. welensii* than in adjacent trees with no presence of this wood borer. This difference was not significant; however, this observation suggests an area for further research, because the pruning of large branches damaged by *C. welensii* is a common silvicultural practice in *Q. suber* stands, and it leads to a reduction in the *CPA/perimeter* ratio. These alterations in crown architecture could modify the tree silhouette, potentially influencing host selection through visual stimulation [4]. Such changes in crowns could also influence—due to changes in sunlight interception and/or hydraulic conductivity—trees' physiological performance and VOC emission behaviour [44], as well as wood density—which affects larval growth in xylophagous insects [45].

5. Conclusions

Based on this study, photosynthetic rates seem to remain higher during the early evening in *Q. suber* trees highly visited by the wood borer *C. welensii* than neighbouring trees not visited or at least not visibly damaged by this species. The physiological performance we observed in trees infested by *C. welensii* could have favoured the foliar emission of certain VOCs, especially those less volatile and less influenced by environmental factors (in particular, light and temperature) such as limonene. These results are of interest as they help deepen our understanding of plant-insect interactions, in particular, those that may

influence host selection by *C. welensii*, and in turn, may have applications in the integrated management of this pest.

Nonetheless, more studies are required to explore how the emission of given monoterpenes (especially, limonene and pinene-type compounds) affects the attraction of *C. welensii* in both laboratory and field conditions. Additionally, more research is needed to determine how changes in the physiological performance of *Q. suber* (associated with environmental stress and wood borer damage) influence, on the one hand, the foliar emission pattern of *Q. suber*, and on the other, the suitability of these trees for *C. welensii* larval growth and development.

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