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Effects of Shrub Encroachment on Carbon Assimilation and Growth of Mediterranean Cork Oak Trees Depend on Shrub Cover Density

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Abstract: Mediterranean ecosystems are threatened by climate change and shrub encroachment. An increase in shrub cover can intensify the competition for water, aggravating the impacts of drought on ecosystem functioning. The effects of shrubs can be positive or negative, depending on the shrub species and density. We used a Mediterranean cork oak (*Quercus suber*) woodland to investigate the effects of increasing gum rockrose (*Cistus ladanifer*) cover on leaf carbon assimilation (A_{max}) and tree growth. The experiment consisted of a gradient of shrub cover, with four treatments: control, LD, MD, and HD, with 0%, 25%, 45%, and maximum shrub cover (>90%), respectively. Increasing shrub cover significantly decreased A_{max} in trees from HD (−15%) compared to control treatment, with intermediate effects on trees from LD (−5%) and MD (−12%). There was a large variability in tree growth, resulting in no significant effects of shrub cover, despite higher trunk diameter relative increments in LD (+40%), and lower in MD (−17%) and HD (−32%) compared to the control. The results indicate that a dense shrub cover (>90%) affected cork oak carbon assimilation and growth, while a low-to-medium shrub cover (≤45%) only induced mild intermediate effects. This information is important for the effective management of shrub density to improve the health and productivity of cork oak woodlands.

Keywords: *Quercus suber*; *Cistus ladanifer*; climate change; drought; forest management; shrub management; gas exchange; photosynthesis; growth

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Citation: Lobo-do-Vale, R.; Haberstroh, S.; Werner, C.; Nogueira, C.; Bugalho, M.N.; Caldeira, M.C. Effects of Shrub Encroachment on Carbon Assimilation and Growth of Mediterranean Cork Oak Trees Depend on Shrub Cover Density. *Forests* **2023**, *14*, 960. https://doi.org/10.3390/f14050960

Academic Editor: José Javier Peguero-Pina

Received: 8 March 2023
Revised: 3 May 2023
Accepted: 4 May 2023
Published: 6 May 2023

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1. Introduction

Mediterranean ecosystems are among the most threatened ecosystems on Earth due to climate change. According to the IPCC [1], the warming trends associated with more frequent and severe droughts will significantly increase aridity in the Mediterranean region, as well as in other arid and semi-arid regions. Additionally, these ecosystems are under threat from shrub encroachment caused by factors such as land abandonment or degradation, overgrazing, and wildfires [2,3]. In regions where water is the determining resource driving the functioning of ecosystems [4], such as the Mediterranean, shrub encroachment may greatly modify ecosystem dominant plant traits and affect major drivers of water fluxes (evapotranspiration and soil infiltration), strongly affecting tree functioning and growth. Indeed, the increase in shrub cover in water-limited ecosystems can exacerbate competition for water resources between shrubs and trees, leading to more deleterious effects of drought on ecosystem functioning [3,5–8] and services delivery [9–11]. However, shrubs can also have positive effects on ecosystem functioning, for example, by facilitating tree recruitment [12–14] or increasing water infiltration, soil fertility, and carbon

sequestration [10,15–18]. The magnitude and the sign of the net effects of species interactions (e.g., facilitation or competition) are often shrub density-dependent [18], species-specific [10,11,19,20], and can change with the intensity of drought [5,21,22].

The shrub gum rockrose (*Cistus ladanifer*), a pioneer native species to the Mediterranean region, for example, can have positive effects on ecosystems due to its ability to grow in poor and degraded soils, improving soil fertility and reducing erosion [23]. However, simultaneously, the gum rockrose has invasive characteristics due to its high growth rates [24], drought stress tolerance [25], and allelopathic characteristics [26,27]. Often it outcompetes other native plant species, namely herbs, forming dense stands. Gum rockrose can also increase the risk of wildfires as the shrub is highly flammable, and emits and stores a diverse blend of volatile organic compounds [28,29] which can increase the intensity and spread of fires [15]. In fact, due to the increased occurrence of droughts and wildfires, gum rockrose is spreading, and encroaching on Mediterranean cork oak (*Quercus suber*) woodlands [30–32].

Mediterranean cork oak woodlands are unique ecosystems, geographically limited to the western Mediterranean Basin, that depend on human management to persist [32]. Despite harboring high biodiversity and having high socio-economic value [32,33], mostly due to cork production, these ecosystems are losing vitality, driven especially by increased drought occurrence and poor management practices [34–37]. Shrub encroachment by gum rockrose has been identified as one of the causes of increased competition with oak trees [5,6], which may weaken trees and ultimately cause tree mortality and a lack of oak natural regeneration [27,31,37,38], but other negative effects such as a decrease in plant species richness [27] or in soil N content [10] were also reported.

Recent studies have reported the strong impacts of shrub encroachment by gum rockrose on the water balance of Mediterranean cork oak and holm oak (*Quercus ilex*) woodlands [3,5,6,39], namely by significantly reducing tree transpiration and resilience to drought. Significant growth reductions were also observed as a consequence of shrub encroachment, drought, or both [6,19,40–42]. However, the impact of shrub encroachment on tree carbon balance received much less attention. Indeed, only a few studies reported tree carbon assimilation, which was shown to be negatively affected by gum rockrose shrub encroachment [7,11,43]. While the maximization of multiple ecosystem services, associated with plant diversity and soil properties, was observed under moderate levels (41%–60%) of shrub cover [18,44], the above-mentioned studies, despite the important and valuable information gathered, were performed in densely encroached areas (>60% of shrub cover), urging further investigation on the impact of increasing shrub cover on tree physiological responses. Additionally, there is a need to better understand the highly dynamic and non-linear transition from facilitation to competition for water between different species [6]. Similarly, understanding how different levels of shrub cover affect tree functioning and growth will be a critical contribution to the sustainable management of Mediterranean oak woodlands and other arid and semi-arid ecosystems [45,46], especially in a context of increasing aridity [1]. Periodic shrub removal is a common management practice in cork oak woodlands, aimed at improving the water status and growth of trees while decreasing the risk of fire [41]. However, this practice is costly and may have counterproductive effects, such as increased soil erosion, decreased carbon stocks, or damage to cork oak roots.

The objectives of this study were to investigate the effects of increasing shrub cover on cork oak water status, carbon assimilation and growth, and to identify the critical shrub cover density that may negatively affect tree functioning and growth. To achieve our goal, a field experiment was set up in a cork oak woodland by establishing a gradient with four levels of shrub cover. Tree water status, carbon assimilation, and growth were monitored over a 2-year study period. Specifically, we aimed to address the following questions: (1) Does cork oak carbon assimilation decrease with increasing shrub cover? (2) Is there a shrub cover threshold for which carbon assimilation decreases significantly? (3) Do these effects translate into lower cork oak growth? By answering these questions, we will also be

providing significant guidelines for land managers to improve management practices and conduct timely and cost-effective shrub removal operations.

2. Materials and Methods

2.1. Experimental Site and Set Up

The experiment was established in a Mediterranean cork oak (*Quercus suber*) woodland, located in a 900 ha estate in Vila Viçosa, Portugal (38°47′30″ N, 7°25′19″ W, 400 m a.s.l.). The climate is Mediterranean-type, characterized by warm-dry and cool-wet seasons [47], with an annual precipitation of 585 mm and a mean air temperature of 16.5 °C [48]. The soil is clay loam (44% sand, 29% silt, and 28% clay), acid (pH 5), poorly developed, and shallow, with a schist bedrock below and classified as haplic Leptosol (FAO, 2007). Cork oak trees were approximately 60 years old, with a density of 160 ± 19 trees ha^{-1}. The average tree's height was 6.3 ± 0.1 m.

To investigate the effects of shrub encroachment on cork oak water status, carbon assimilation, and growth, a gradient of shrub cover was set up using a randomized block design with three replicates of four levels of shrub cover (treatments): control (no shrub cover), LD (low density, 25% of maximum shrub cover at the site), MD (medium density, 45% of maximum shrub cover at the site), and HD (high density, maximum shrub cover at the site), resulting in 12 plots (3 blocks × 4 treatments) of ca. 12 m × 15 m. The cork oak woodland was encroached by the native shrub gum rockrose (*Cistus ladanifer*) prior to 2011, when the shrubs were cut above ground on control plots. Since then, shrubs that occasionally germinated (gum rockrose is an obligate seeder) in control plots were manually removed. The maximum shrub density at the site was 11,000 shrubs ha^{-1}, which corresponded to a cover higher than 90%. The gradient was established in May 2019 as a fraction of maximum shrub cover by adjusting shrub density.

2.2. Environmental Monitoring

A weather station was running in each block, as described in Haberstroh et al. (2021) [6]. Precipitation, air temperature, and relative humidity were measured continuously, and half-hourly data were stored on data loggers. Vapor pressure deficit (VPD) was computed from the half-hourly averaged air temperature and relative humidity. Meteorological data are presented as hydrological years, i.e., from October to September, as they better represent the water availability for tree functioning and growth across the growing season. For clarity, the meteorological years of 2018/2019, 2019/2020, and 2020/2021 will be henceforth named 2019, 2020, and 2021, respectively.

2.3. Ecophysiological Measurements

Within the three blocks, three trees per plot were randomly chosen for monitoring (36 trees in total). Four intensive field campaigns were performed to include periods with high water availability, i.e., during spring (11 June 2019 and 17 June 2020), and when water stress occurred, i.e., during summer (23 July 2019 and 03 August 2020). In these intensive field campaigns, leaf water potential and leaf gas exchange measurements were carried out.

Leaf water potential was measured at predawn (Ψ_{Pd}) to evaluate tree water status with a Scholander-type pressure chamber (PMS 1000, PMS Instruments, Corvalis, OR, USA) in two to three fully expanded and sun-exposed leaves per tree, similar to those used for gas exchange. The measurement times were 03:00–06:00.

Daily courses of leaf gas exchange (at 10:00, 13:00 and 16:00) were performed with two cross-calibrated portable photosynthesis systems (LI-6400XT, LI-COR Inc., Lincoln, NE, USA) with a light source and a CO_2 injector system, for controlled saturating light (1200 µmol photons m^{-2} s^{-1}) and CO_2 concentration (400 ppm), respectively. The air temperature and relative humidity in the chamber were set to match the environmental conditions. The measurements took place on clear sky days. Mid to top canopy, south exposed branches were detached and one to two mature leaves per tree were measured within two minutes after branch cutting. From daily courses, the maximal photosynthetic

rate (A_{max}) and the corresponding stomatal conductance ($g_{s@Amax}$) were obtained. Intrinsic water use efficiency (*iWUE*) was calculated as $A_{max}/g_{s@Amax}$.

2.4. Growth Measurements

Tree trunk diameter at breast height (*dbh*) increment was measured periodically in installed tree dendrometers (I-802-DI, UMS GmbH, Munich, Germany and DB20, EMS, Brno, Czech Republic) in the same 36 trees that were monitored for the ecophysiological measurements, from 12 December 2019 to 15 June 2021. Growth was expressed as the percentage of increment relative to *dbh* (*dbh* increment). Total *dbh* relative increment was calculated as a percentage of increment relative to initial *dbh*, and spring *dbh* relative increments were calculated as a percentage of increment relative to the initial *dbh* (January) of each year until spring.

2.5. Statistical Analysis

To evaluate the effects of increasing shrub cover on cork oak water status, gas exchange, and growth (Ψ_{Pd}, A_{max}, $g_{s@Amax}$, *iWUE* and *dbh* increment), a general linear mixed model (GLMM) was used. Block was considered a random factor and shrub cover (treatment) and measurement date (henceforth date) as fixed factors. When a significant factor effect was found for shrub cover and/or date, the post hoc Tukey test was performed for multiple comparisons of means. The GLMM was repeated for each date to identify significant differences between treatments within each date. Data were log- or square root-transformed, when needed, to meet the assumptions of GLMM (i.e., normal distribution of residuals and variance homogeneity). Statistical analyses were carried out with IBM SPSS Statistics 26 (IBM Corp., Armonk, NY, USA). All statistical relationships were considered significant at $p < 0.05$. Data are presented as mean ± SE (standard error of the mean).

3. Results

3.1. Environmental Conditions

The hydrological year of 2019 was very dry, with an annual precipitation of 387 mm, representing a −34% deviation from the long-term mean of 585 mm (Figure 1a, [48]) due to a long summer drought that started in early May. In the hydrological year of 2020, the precipitation was 12% above the long-term mean, indicating a regular year with normal levels of precipitation (657 mm). However, the year was marked by rainy periods interspersed with relatively long dry spells, including a long summer drought. The hydrological year of 2021 was wet (770 mm; +32% of long-term mean), with a shorter summer drought, starting later than in the previous years.

Regarding mean air temperature, there were no significant deviations from the long-term data nor between years (Figure 1b). However, in 2020, there was a heat wave in July (according to [49] definition), which lasted from the 10th to 20th of July.

The fluctuations in precipitation and air temperature between different years led to corresponding changes in VPD, especially during the spring and summer (Figure 1c).

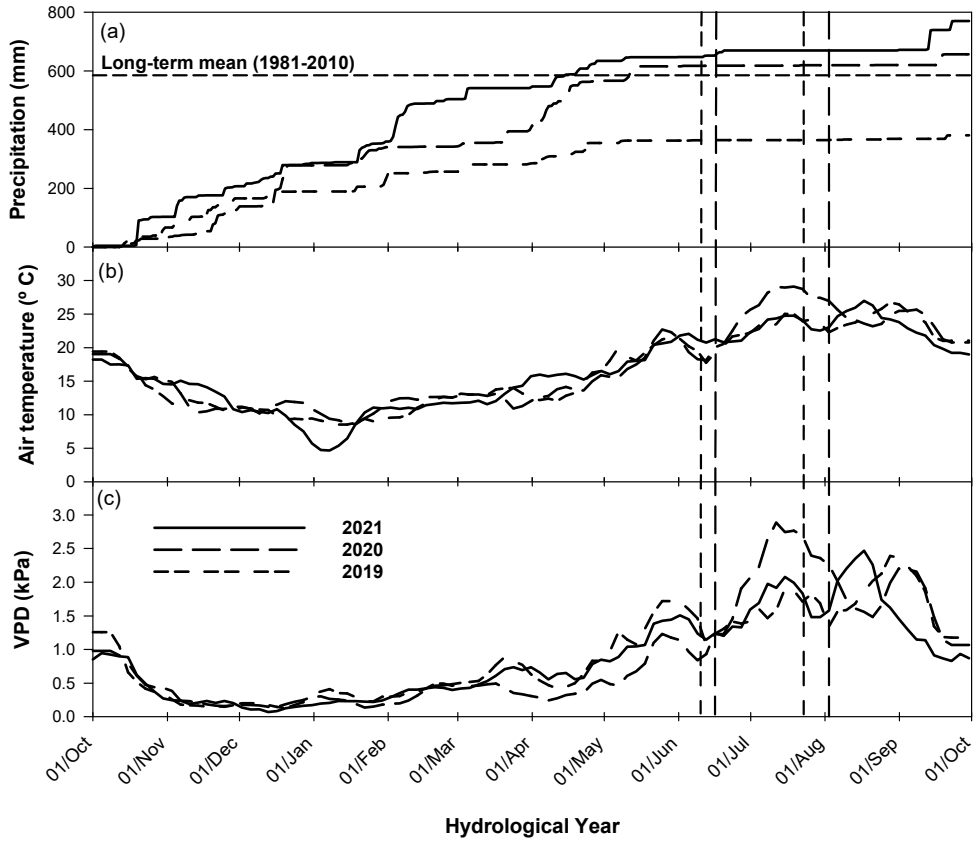

Figure 1. Meteorological conditions in the hydrological years of 2019, 2020, and 2021. Accumulated annual precipitation (**a**), daily mean air temperature (**b**), and daily mean vapor pressure deficit (VPD) (**c**). The dashed horizontal line indicates the precipitation long-term mean (1981–2010, IPMA [48]). The vertical lines indicate the intensive field campaigns. The temperature and VPD data were smoothed using the 7-day running average.

3.2. Cork Oak Ecophysiological Responses to Increasing Shrub Cover

The predawn leaf water potential (Ψ_{Pd}), an indicator of the tree water status, reflected mainly the variation in precipitation between years. A seasonal and inter-annual pattern was observed in Ψ_{Pd}, declining from spring to summer in both years (Figure 2a), with significant differences between all dates ($p < 0.001$, Tables S1 and S3). However, during spring 2019 (dry year), the trees were already experiencing water stress. This was evident from the overall low value of Ψ_{Pd} of -1.08 ± 0.03 MPa. The water stress was aggravated during the summer, with values dropping to -1.58 ± 0.04 MPa. In contrast, in 2020, which was a normal year, the high Ψ_{Pd} values recorded in spring (-0.41 ± 0.03 MPa) decreased to intermediate values compared to the values registered in 2019 (-1.22 ± 0.04 MPa).

The shrub cover had a significant effect on Ψ_{Pd} ($p = 0.002$, Table S1). Trees growing in control and LD treatments showed a better overall water status than trees in the HD treatment (Figure 2a, Table S2). However, while there was a decreasing gradient observed in the trees from encroached plots (LD, MD, and HD), differences between treatments were only significant in spring 2019 and summer 2020 (Figure 2a). In spring 2019, the Ψ_{Pd} of trees growing in control plots was significantly higher than trees in HD plots (-0.99 ± 0.06 MPa, and -1.19 ± 0.08 MPa, respectively), while in summer 2020, the significant differences were observed between LD and HD covers (-1.10 ± 0.07 MPa, and -1.38 ± 0.08 MPa, respectively).

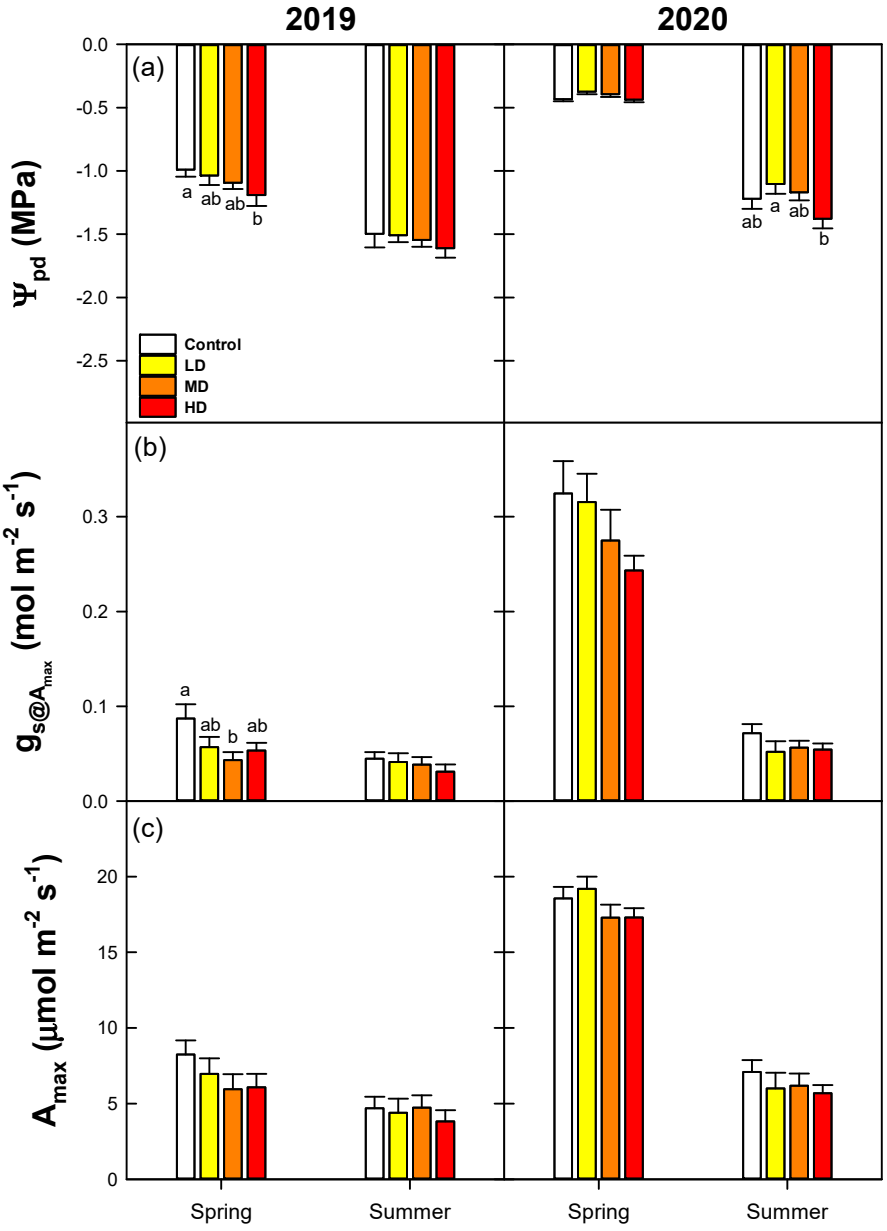

Figure 2. Predawn leaf water potential (Ψ_{Pd}) (**a**), stomatal conductance ($g_{s@Amax}$) (**b**), and maximal photosynthetic rate (A_{max}) (**c**) of cork oak by treatment, measured in spring and summer of the hydrological years of 2019 and 2020. Different letters indicate statistically significant differences between treatments within each date ($p < 0.05$).

Stomatal conductance ($g_{s@Amax}$, Figure 2b) exhibited a pattern similar to Ψ_{Pd}, and significant differences in $g_{s@Amax}$ between dates ($p < 0.001$, Table S1) were observed, except between spring 2019 and summer 2020 (Table S2). Trees were enduring water stress in spring 2019, resulting in low values of $g_{s@Amax}$ (0.060 ± 0.006 mol m^{-2} s^{-1}). This stress was further intensified during summer 2019, leading to strong stomatal closure (0.039 ± 0.004 mol m^{-2} s^{-1}). In spring 2020, when the soil had ample water as evidenced by the highest Ψ_{Pd}, $g_{s@Amax}$ also reached its maximum value of 0.290 ± 0.015 mol m^{-2} s^{-1}. However, in summer 2020, $g_{s@Amax}$ declined sharply to values similar to those observed in spring 2019 (0.059 ± 0.004 mol m^{-2} s^{-1}).

The increasing shrub cover significantly reduced $g_{s@Amax}$ ($p = 0.006$, Table S1). While a gradient of $g_{s@Amax}$ can be identified, the large variability observed among treatments smoothed the differences, and only trees from the control treatment had significantly higher

$g_{s@Amax}$ (0.132 ± 0.021 mol m^{-2} s^{-1}) than trees from MD and HD covers (0.103 ± 0.019 and 0.096 ± 0.015 mol m^{-2} s^{-1}, respectively, Table S2). The overall mean of LD $g_{s@Amax}$ was 0.116 ± 0.021 mol m^{-2} s^{-1}. When the statistical analysis was performed by date, differences between treatments were only significant in spring 2019, where the $g_{s@Amax}$ of trees from control plots was significantly higher than of trees from MD plots (Figure 2b).

Similar to $g_{s@Amax}$, the leaf carbon assimilation, as indicated by maximal photosynthetic rate (A_{max}), also changed significantly over time ($p < 0.001$, Figure 2c, Table S1), with no differences between spring 2019 and summer 2020 (Table S3). During the spring 2019 dry year, A_{max} was already inhibited (6.81 ± 0.48 µmol m^{-2} s^{-1}) as compared to spring 2020 (18.08 ± 0.39 µmol m^{-2} s^{-1}). This inhibition was further intensified in summer 2019 to 4.41 ± 0.39 µmol m^{-2} s^{-1}. In 2020, a strong reduction in A_{max} occurred from spring to summer, resulting in an overall mean similar to spring 2019 (6.24 ± 0.40 µmol m^{-2} s^{-1}).

Leaf carbon assimilation decreased with increasing shrub cover ($p = 0.046$, Figure 2c, Table S1), with trees growing in control plots presenting higher A_{max} than trees growing in HD plots (9.65 ± 0.98 and 8.22 ± 0.96 µmol m^{-2} s^{-1}, respectively, Table S2). The overall mean A_{max} values of trees from LD and MD covers were 9.14 ± 1.09, and 8.54 ± 0.95 µmol m^{-2} s^{-1}, respectively. Although there was no significant treatment effect when the statistical analysis was performed by date, the shrub cover accounted for reductions in A_{max} of up to 28% (MD cover in spring 2019, relative to control, Figure 2c).

The statistical analysis revealed significant effects of both date and shrub cover, as well as their interaction, on intrinsic water use efficiency (*iWUE*, Table S1). *iWUE* was significantly lower in spring 2020 compared to the other dates ($p < 0.001$), while control treatment trees had significantly lower *iWUE* ($p = 0.001$) than the trees from the other treatments, irrespective of shrub cover level (Table S2). The interaction effect ($p = 0.042$) was driven by different patterns according to leaf water status. *iWUE* increased with increasing shrub cover, when Ψ_{Pd} was either high or low (spring 2020 and summer 2019, respectively), and for intermediate values of Ψ_{Pd}, higher *iWUE* was achieved with intermediate levels of shrub cover (LD and MD covers, Figure 3). When the analysis was performed by date, a significant treatment effect was found in spring 2019, with control treatment trees having significantly lower *iWUE* than trees from MD.

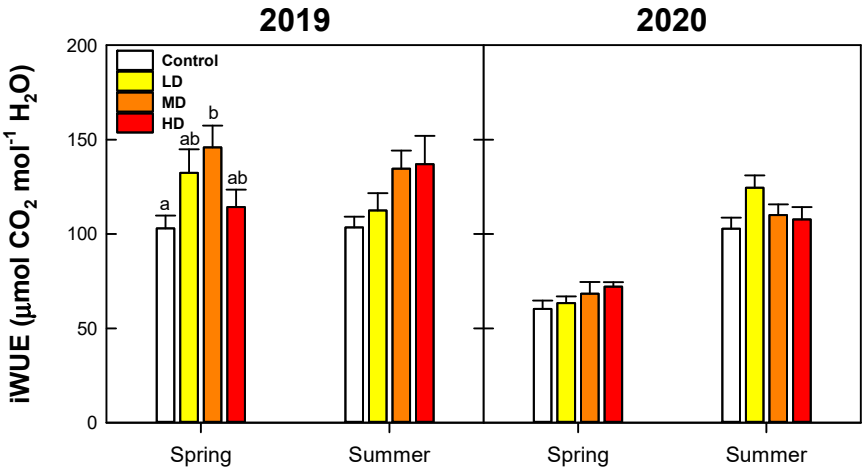

Figure 3. Intrinsic water use efficiency (*iWUE*) of cork oak by treatment, measured in spring and summer of the hydrological years 2019 and 2020. Different letters indicate statistically significant differences between treatments within each date ($p < 0.05$).

3.3. Cork Oak Growth Responses to Shrub Cover

A large variability was observed in *dbh* relative increments from December 2019 to June 2021 (Figure 4). The periods with higher growth increments were observed in spring and autumn, but the LD and MD trees were also able to grow during winter/early spring or late spring/summer (LD).

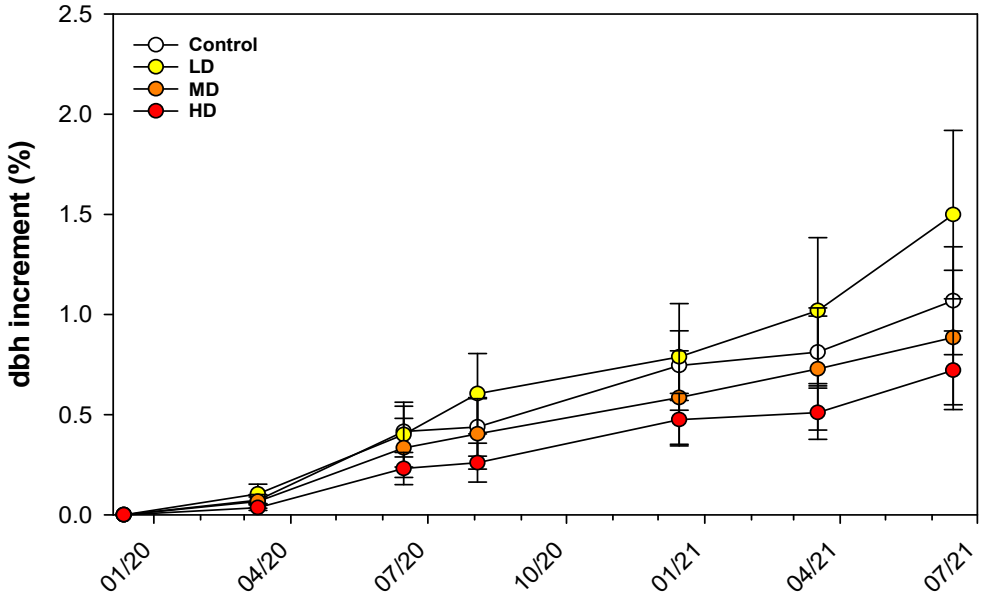

Figure 4. *dbh* relative increments of cork oak by treatment over the study period, calculated as a percentage of increment relative to initial *dbh*, when dendrometers were installed in all trees.

Despite an overall non-significant effect of shrub cover on total relative *dbh* increment (Figure 5a) when growth was analyzed separately by year, it resulted in a marginally significant higher *dbh* increment of trees from the LD treatment in comparison to trees from HD in 2021 (p = 0.068, Figure 5). Overall, the highest relative increments in *dbh* were observed in LD (1.5 ± 0.4%), followed by trees growing in the control treatment (1.1 ± 0.3%), MD (0.9 ± 0.3%), and finally HD (0.7 ± 0.2%) covers (Figure 5a). The relative *dbh* increment in LD trees was 40% higher than that of control trees, whereas MD and HD trees had deviations of −17% and −32%, respectively.

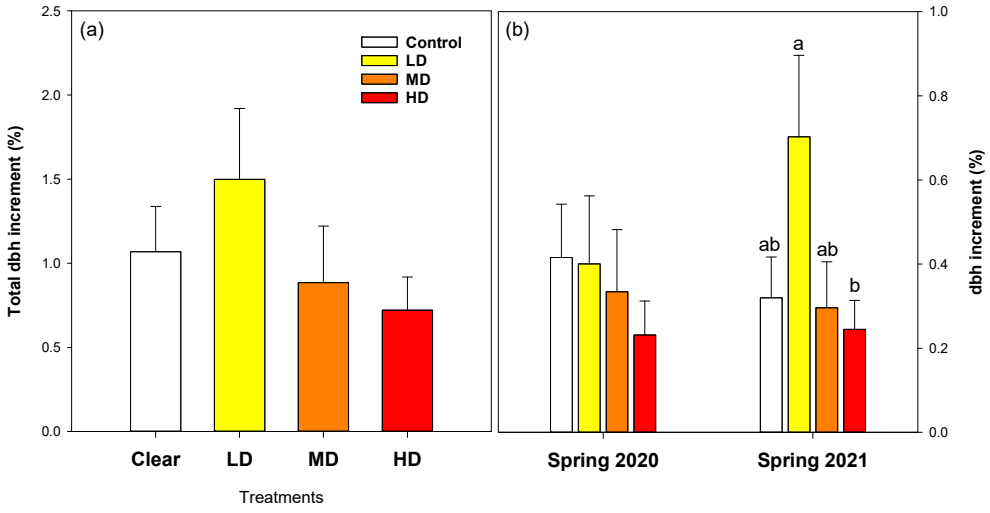

Figure 5. Total *dbh* relative increments of cork oak by treatment (**a**), and spring *dbh* relative increments of cork oak of each year (**b**). Note the different scales. Different letters indicate statistically significant differences between treatments within each date (p < 0.10).

In 2020 (Figure 5b), a decreasing gradient from control to HD treatment trees was observed, with the *dbh* increment ranging from 0.232 ± 0.081% (HD) to 0.416 ± 0.127% (control). In 2021, the *dbh* increment also decreased from control (0.320 ± 0.097%) to

HD trees (0.245 ± 0.069%), but a notably high *dbh* increment was observed in LD trees (0.703 ± 0.194%).

4. Discussion

Our study demonstrates that A_{max} was significantly reduced in trees from densely encroached plots (HD treatment) compared to control, while marginally significant effects of shrub cover were observed in trunk diameter relative increments in spring 2021, in which trees from LD treatment exhibited higher growth than trees from HD treatment.

4.1. Shrub Cover Effects on Cork Oak Ecophysiology

Overall, the effects of shrub cover on cork oak ecophysiological responses (Ψ_{Pd}, A_{max}, $g_{s@Amax}$) resulted in a slight but significant decrease in these variables from trees when comparing control and HD treatments (Figure 2). The LD and MD covers corresponded to intermediate states, meaning that the effects on tree ecophysiological variables were in general not significantly different from control or HD. The considerable variability between trees may have masked some of the differences. Indeed, when data were analyzed by date, only a few differences between treatments were observed, particularly when drought stress was moderate (in spring 2019 and summer 2020). Nevertheless, the trees from the control treatment exhibited higher $g_{s@Amax}$ which enabled higher A_{max}. Conversely, the HD trees showed a poorer water status, lower $g_{s@Amax}$, and lower A_{max}, which caused an overall 15% decline in carbon assimilation. This is in agreement with Haberstroh et al., 2022 [39], who found a significant negative effect of dense shrub cover on the hydraulic strategy of cork oak, resulting in earlier stomatal closure under drought. In addition, in previous studies [11,43], with a dense gum rockrose cover (60%–95%), a significant negative impact on cork oak and *Quercus ilex* trees' carbon assimilation and stomatal conductance was reported. Although the decrease in A_{max} originating from the gum rockrose cover might seem minor, in the long term and with the forecasted increase in drought years, it can lead to significantly less carbon assimilation and growth, which might jeopardize the functioning and resilience of cork oak trees [5,39]. This will not only affect tree growth but can also impact the tree's carbohydrate reserves, which are crucial for withstanding prolonged periods of water scarcity [50]. Gum rockrose shrubs exhibit a water-spending behavior, being highly competitive regarding the use of available water resources [39,51]. This was evident in the weak leaf water status observed in the HD trees (Figure 2a). The varying and intermediate physiological responses of LD and MD trees may be partially linked to the shrubs' ability to improve soil moisture heterogeneity, creating different microenvironmental conditions [52]. These conditions may be transitory and not present when water is abundant, or when there is severe drought, but may translate into meaningful improvements in tree functioning. A longer study may be necessary to unveil these effects.

The trees encroached by shrubs showed a significant increase in *iWUE*, regardless of the extent of shrub cover. This increase was mainly due to a stronger stomatal control (lower $g_{s@Amax}$) rather than an increase in A_{max}, which highlights the water-saving strategy of cork oak [53,54].

4.2. Shrub Cover Effects on Cork Oak Growth

Despite the large variability observed in tree growth responses to shrub cover, as indicated by *dbh* relative increments which may have obscured treatment effects (Figures 4 and 5), significant differences in *dbh* increment between trees from control and HD treatments were shown between April 2018 and April 2020 for the exact same trees and treatments (see Figure 6 in [6]). Most probably, these significant effects resulted from a longer period of observation and drier conditions than in the present study. The higher *dbh* increments observed in our study in spring and autumn (Figure 4) were expected, as in spring soil moisture is usually available and temperatures are mild, and it is the most productive period for cork oak growth [40,55–59], while autumn growth is typically less intense. However, the increases observed in winter/early spring and late spring/summer in LD and MD trees suggest that

the trunk growing period was longer in these treatments. This effect could be mediated by enhanced water infiltration in the soil [60] or by the buffering of environmental conditions such as high temperatures [61]. When the shrub cover becomes dense (HD), competition occurs, resulting in a reduction in available water for tree carbon assimilation and growth (Figures 2–4). This is consistent with findings from other studies [3,6,39].

In terms of overall *dbh* increments (Figure 5a), the LD trees exhibited a 40% increase as compared to control trees, despite high variability and the non-significant effects of shrub cover. Conversely, the MD and HD trees showed negative deviations, with reductions of 17% and 32%, respectively, indicating that denser gum rockrose covers decreased tree growth. Previous studies have also shown a negative impact on tree growth in sites with high gum rockrose cover (>67%) [6,10,19,41] or in response to drought [40,62]. Excluding the exceptional growth of LD trees in spring 2021, a decreasing trend was observed from control to HD trees, with lower growth in spring 2021 compared to spring 2020 (Figure 5b). The lower growth in spring 2021 was most probably due to a dry spell which started in May (Figure 1a), restricting water availability, and inducing earlier growth cessation. In encroached plots, particularly in HD, this was likely to have occurred earlier due to the competition with gum rockrose. The overall higher growth observed in 2020 is in accordance with the observed carbon assimilation rates, which were very high (Figure 2c). As our growth data were only collected over 1.5 years, the modest increments and the marginal differences between treatments are likely to be translated into significant reductions due to increased shrub cover in the long term. More studies covering longer measurement periods are needed.

4.3. Implications for Management

Land mismanagement or abandonment can lead to shrub encroachment in cork oak woodlands [30,32]. Here, we show that high shrub cover may compromise tree carbon assimilation and eventually tree growth, which may ultimately affect cork production, the main service provided by these ecosystems. Our results underline the importance of the management of shrub understory to avoid negative effects on tree ecophysiological and growth responses. These effects add to the increased fire hazard of the encroached system [15] and phenomena such as arrested succession (Acácio et al., 2009 [30]). The results also suggest that a low to medium shrub cover does not negatively affect tree ecophysiology, indicating that the potential benefits of shrub cover (e.g., lower soil erosion, soil fertility, carbon storage) may still be obtained by maintaining a low to moderate shrub cover. This is a significant result for cork oak woodland managers who must balance the negative and positive effects of shrub clearing when making management decisions.

Effective management practices can also improve the resilience of forest ecosystems to drought [5,63]. In the case of cork oak woodlands, maintaining or removing the shrub layer requires careful planning due to the implications on ecosystem functioning, as shown in the present study and in other studies [11,41,64,65]. Different levels of shrub cover may have different implications, as is suggested in our study. For example, Soliveres et al. (2014) [44], investigating different systems including semi-arid ecosystems, found that a shrub cover of 41%–60% was able to maintain ecosystem multifunctionality (mainly assessed by soil properties) and plant diversity. The positive net effects of shrub cover on ecosystem functioning, however, are frequently species-specific [11] and vary with other factors such as soil type or climate (e.g., frequency of dry years). In particular, the gum rockrose, which is a shrub highly competitive for water [5] that can negatively affect cork oak recruitment [38], or seed germination, and the growth of understory species [27], may need to be managed for the maintenance of a lower shrub cover. López-Díaz et al. [66], for example, suggested that a very low shrub cover (<10%) of gum rockrose in a silvipastoral system with *Quercus ilex* may combine the positive effects of shrubs on ecosystem functioning, simultaneously maintaining overall ecosystem productivity. Other authors [67,68] suggested that the maintenance of small shrubby patches would be enough to improve other benefits such as biodiversity conservation. The present study clearly shows that management of the

gum rockrose shrub cover is needed to improve the overall functioning of the cork oak ecosystem, including its productivity. In particular, shrub removal should be performed before the shrub cover becomes too dense (45%–90%). Nevertheless, additional validation studies are recommended on different sites and for longer periods. Conversely, assessing which levels of shrub cover may promote a net positive effect on the functioning of cork oak ecosystems remains a challenge that will further contribute to the adaptative management of the system.

5. Conclusions

Our study findings indicate that gum rockrose shrub cover affects the carbon assimilation and growth of cork oak in different ways, with a high dense cover (HD, >90%) causing significant negative effects on cork oak performance. Cork oak trees under HD treatment showed reductions in leaf carbon assimilation and tree growth by 15% and 32%, respectively, compared to the control treatment without any shrub cover. On the other hand, low to medium shrub cover (LD and MD, 25%–45%) did not result in any significant physiological responses compared to the control treatment.

Our study confirms the hypothesis that high shrub cover negatively affects the cork oak tree physiological responses, leading to a high variability in growth. However, overall non-significant differences were observed between treatments. These findings provide important guidelines for improving the management strategies of Mediterranean oak woodlands, especially for planning shrub removal operations to avoid a dense shrub cover that negatively affects cork oak functioning.

Further studies are necessary to confirm the observed tree growth trends and to identify the critical level of shrub cover that is favorable for cork oak functioning. In conclusion, the findings of this study highlight the importance of considering the density of shrub cover when planning forest management strategies to maintain the health and productivity of cork oak woodlands.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f14050960/s1, Table S1: Summary of General Linear Mixed Model results for ecophysiological variables; Table S2: Results of post-hoc Tukey test for multiple comparison of overall treatment means; Table S3: Results of post-hoc Tukey test for multiple comparison of overall date means.

Author Contributions: Conceptualization and methodology, M.C.C., R.L.-d.-V. and M.N.B.; data analysis, R.L.-d.-V.; investigation, R.L.-d.-V., M.C.C., S.H. and C.N.; writing, R.L.-d.-V. with inputs from M.C.C. and M.N.B.; review and editing, R.L.-d.-V., M.C.C., M.N.B., C.W., S.H. and C.N. All authors have read and agreed to the published version of the manuscript.

Funding: This work was supported by the Portuguese Fundação para a Ciência e Tecnologia (FCT) (2022.09115.PTDC and EXPL/ASP-SIL/1259/2021). R.L.-d.-V was funded by an FCT researcher contract (CEECIND/02735/2018). M.N.B was funded by a contract DL 57/2016/CP1382/CT0030 and also acknowledges financial support from FCT through the project CertFor (PTDC/ASP-SIL/31253/2017). Centro de Estudos Florestais (CEF) is a research unit funded by FCT (UIDB/00239/2020). CEABN-InBIO is a research unit funded by FEDER funds (Operational Programme for Competitiveness Factors—COMPETE; POCI-01-0145-FEDER-006821) and by FCT (UID/BIA/50027/2020).

Data Availability Statement: The data presented in this study are available on request to the corresponding author.

Acknowledgments: We sincerely thank Joaquim Mendes, Joana Martins, James Ryder, and Vera Prazeres for help and support during the field work. We also thank Fundação da Casa de Bragança for permission to undertake research in Tapada Real de Vila Viçosa.

Conflicts of Interest: The authors declare no conflict of interest.

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