Hydraulic and photosynthetic limitations prevail over root non-structural carbohydrate reserves as drivers of resprouting in two Mediterranean oaks

Running head: Hydraulics and photosynthesis limit resprouting

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Funding: the present study has been supported by the National Natural Science Foundation of China (No. 31850410483), the talent funds of Southwest University of Science and Technology (No.18ZX7131), the MICINN (AGL2015-69151-R), INIA (RTA2015-00054-C02-01) and Generalitat de Catalunya (SGR2017-1518), Spain.

Abstract

Resprouting is an ancestral trait in angiosperms that confers resilience after perturbations. As climate change increases stress, resprouting vigor is declining in many forest regions, but the underlying mechanism is poorly understood. Resprouting in woody plants is thought to be primarily limited by the availability of non-structural carbohydrate reserves (NSC), but hydraulic limitations could also be important. We conducted a multifactorial experiment with two levels of light (ambient, 2-3% of ambient) and three levels of water stress (0, 50 and 80 percent losses of hydraulic conductivity, PLC) on two Mediterranean oaks (*Quercus ilex* and *Q. faginea*) under a rain-out shelter (n = 360). The proportion of resprouting individuals after canopy clipping declined markedly as PLC increased for both species. NSC concentrations affected the response of *Q. ilex*, the species with higher leaf construction costs, and its effect depended on the PLC. The growth of resprouting individuals was largely dependent on photosynthetic rates for both species, while stored NSC availability and hydraulic limitations played minor and non-significant roles, respectively. Contrary to conventional wisdom, our results indicate that resprouting in oaks may be primarily driven by complex interactions between hydraulics and carbon sources, whereas stored NSC play a significant but secondary role.

Keywords: construction costs, growth, fire, hydraulics, nonstructural carbohydrate concentrations, perturbation, resilience, resprouting vigor, survival, photosynthesis

Acknowledgements We acknowledge technical support from MJ Pau, MP Sopeña, A Cunill, J Hedo, B Lavaquiol and C Maier. This manuscript benefited from the insightful comments provided by two reviewers and the Associate Editor and from statistical advice by JG Alday.

Introduction

Understanding the effects of climatic changes in land cover during this 21st century is becoming a major research effort globally (IPCC, 2019). Associated with rapid climate change, a drying atmosphere and more variable precipitation patterns are enhancing water scarcity in many areas of the world. Moreover, as forested ecosystems become drier, the prevalence of mega-fires has accelerated, burning unprecedented fractions of forested ecosystems (Boer *et al.*, 2020, Nolan *et al.*, 2020). In combination with other biotic and abiotic stresses, large scale replacements of forests by shrublands or grasslands may become more common (Karavani *et al.*, 2018).

The capacity for resprouting, particularly widespread across angiosperm trees, is a major mechanism providing post-fire and post-drought resilience in Mediterranean ecosystems and other parts of the world (Sánchez-Pinillos *et al.*, 2016). However, the capacity for resprouting appears to have limits and is diminishing (Karavani *et al.*, 2018, Resco de Dios 2020), notably with increased drought severity or fire recurrence (Batllori *et al.*, 2018, Collins, 2019, Fairman *et al.*, 2019, Pratt *et al.*, 2014).

The mechanisms underlying reductions in the capacity to resprout are still relatively unknown. The classic paradigm is that the availability of stored carbohydrate reserves is the major driver of resprouting (Bowen & Pate, 1993, Pate *et al.*, 1990) and that re-sprouting exhaustion would be more likely if carbohydrate reserves are reduced, particularly in plants growing under deep shade or that experience protracted drought. There is some debate regarding the impact of protracted drought on carbohydrate reserves because declines in sink activity under drought may preclude the decline of source photo-assimilates (Korner, 2003, Palacio *et al.*, 2014).

The role of carbohydrate reserves and plant function has been the topic of considerable research (Dietze *et al.*, 2014). Non-structural carbohydrates (NSC) account for, on average, 10% of dry plant biomass (Martínez-Vilalta *et al.*, 2016). Despite the significant investment into NSC, plant growth is seldom limited by carbon, even under extreme droughts, and NSC depletion is a rare phenomenon in angiosperm trees (Adams *et al.*, 2017, Duan *et al.*, 2013, Martínez-Vilalta *et al.*, 2016, Mitchell *et al.*, 2013). Some authors have proposed that the major function of carbohydrate storage is to serve as a bet-hedging strategy that promotes survival after a perturbation that removes a large part of the aboveground biomass (Wiley & Helliker, 2012).

However, other authors consider that hydraulic limitations developed during drought, either in stems or roots, depending on resprouting type, may impose a higher limitation to post-fire resprouting (Cruz *et al.*, 2003, Karavani *et al.*, 2018). Post-fire resprouting requires new growth, which cannot occur if the capacity for transporting water to meristems is impaired. Additional factors, such as nutrients or bud scarcity, may also limit resprouting (Clarke *et al.*, 2013, Karavani *et al.*, 2018), but the interaction between hydraulics and C starvation (i.e. lack of carbohydrates to support plant function) as drivers of post-fire resprouting is particularly important to resolve under climate change. The frequency of drought-induced defoliation and mortality events are increasing globally (Allen *et al.*, 2015, Carnicer *et al.*, 2011). Subsequently, fire following a protracted drought could catalyze the conversion of forests to shrublands or grasslands through interactive, but largely unknown, effects on plant hydraulics and carbon balance (Karavani *et al.*, 2018, Parra & Moreno, 2018).

Numerous studies have examined the interactive effects of hydraulics and carbohydrate reserve depletion on drought-induced mortality (Adams *et al.*, 2017), and some studies have addressed fire impacts on xylem vulnerability to embolism in surviving branches (Bar *et al.*, 2019, Hood *et al.*, 2018, Kavanagh *et al.*, 2010, Midgley *et al.*, 2011). However, studies jointly addressing how increasingly larger losses in hydraulic conductance, in addition to increasing levels of carbohydrate reserve depletion, may subsequently limit resprouting are more scarce.

Here, we report the results of an experiment that sought to disentangle the mechanisms affecting resprouting in potted oak seedlings experimentally exposed to three levels of water availability and two levels of light. Treatments were jointly imposed to generate a range in both stored NSC concentrations and losses of hydraulic conductivity.

The oak species (*Quercus ilex* L. and *Quercus faginea* Lam.) in this study are the dominant oaks in the drier parts of the oak expansion range in the Western Mediterranean basin. Regeneration of Mediterranean oaks heavily depends on resprouting because of high seed predation (Herrera, 1995). Understanding the limits to resprouting in these two species is thus important to improve estimates on potential species replacements under climate change. Furthermore, these species show contrasting life history strategies (Palacio *et al.*, 2018): *Q. ilex* is sclerophyllous and evergreen, whereas *Q. faginea* is deciduous and exhibits hydraulic segmentation (Peguero-Pina *et al.*, 2015).

Overall, we sought to elucidate whether: i) resprouting capacity (percent individuals resprouting) was controlled by hydraulic limitations, NSC limitations (that is, the depletion of NSC reserves) or their interaction; and ii) the growth of the resprouts exhibited a legacy effect due to previous impacts on hydraulic limitations, reserve availability or concurrent photosynthesis limitations.

We hypothesized that hydraulic limitations would control the percentage of plants that resprout, but subsequent growth of the resprouts would be dependent on NSC content and mobilization to grow the resprouting tissues. Because *Q. ilex* is more scleromorphic than *Q. faginea*, and leaf construction costs (in terms of g glucose g^{-1} dry matter) increase with schlerophylly, we expected that resprouting growth would be more dependent on NSC in *Q. ilex* than in *Q. faginea*. Finally, we hypothesized that imposed reductions of light and water availability would decrease concurrent photosynthesis as a source of C, which would additionally limit resprouting. However, we expected that this photosynthesis effect would be minor relative to that of sink (stored NSC) limitations.

Methods

Study site

The experiment was performed at the experimental field site at the School of Agrifood and Forestry Science and Engineering at the University of Lleida (Spain; 41.62 N, 0.59 E). We constructed a rain-out shelter that was covered by clear polyethylene plastic, as commonly used in greenhouse building. Half of the structure received natural solar radiation, and the other half was covered by dense shade cloth. Plants under ambient light (that is, under the polyethylene plastic) received a maximum PPFD of 1500 μmol m^{-2} s^{-1} and plants under the shade cloth received 2-3% (35-45 μmol m^{-2} s^{-1}) of full sun. The structure had openings on both sides to increase ventilation and minimise heat build-up. The temperature in the rain-out shelter was 3ºC higher than outside the shelter under ambient light, and 2.5ºC higher in the shade treatment (Fig. S1). The difference in vapour pressure deficit across sun and shade treatments was 0.1 kPa (Fig. S1)

For this study we obtained 2-year-old seedlings from local nurseries. The provenances originated from the mountain range of the Iberian System. Plants were grown in 11 L pots (20 cm × 20 cm × 27.5 cm). The rooting medium used was the commercial potting mix Humin Substrat N6 (Neihaus, Klasman-Deilmann GmbH, Geeste, Germany). Pots were regularly fertilized with a slow release NPK MgO fertilizer (17-09-11-2, Osmocote Universal, KB, Ecully, France) and daily watered to field capacity until treatment implementation.

The plants grew for 6 months (since February 2017) in the rainout shelter before experiment inception. They developed new leaves under the experimental light conditions, but there may have been legacy effects from the previous growing seasons in the nursery, which could not be quantified. The experiment began in the northern hemisphere summer (July) of 2017 and lasted for 2 years. We induced resprouting by removing the canopy by clipping above the root collar in July 2017, and then again in July 2018 (twice in total; details below).

Experimental treatments

We induced depletion of carbohydrate reserves and water stress by implementing two different light regimes: sun (ambient) and shade (35-45 μmol m^{-2} s^{-1}) in concert with three different levels of water stress. Light manipulations may alter additional aspects of plant physiology and morphology, but our experimental design was to mimic a comparison between seedlings growing in the understory of a forest or in an open woodland under different levels of water stress.

The three different watering treatments were set to achieve different values of percentage loss of conductivity (PLC); 0, 50 and 80% PLC (P_0, P_{50} and P_{80}, respectively), which represent different critical water stress thresholds and the potential for recovery in angiosperms (Resco *et al.*, 2009, Urli *et al.*, 2013). P_{50} represents moderate water stress in angiosperms and P_{80} represents severe stress, and potential mortality. During treatment implementation, we stopped watering and allowed plants to dehydrate and we measured midday stem water potential (Ψ_{md}) every other day in a subset of plants (n=5). Stem water potential was measured after introducing the cut stem in zip lock bag, and allowing it to equilibrate for 30 minutes in the dark at room temperature (PMS1000, PMS, Albany, OR). We then calculated the expected PLC based on Ψ_{md} from previously published vulnerability curves for our species and provenances (Esteso-Martínez *et al.*, 2006, Peguero-Pina *et al.*, 2014). Once plants reached the target PLC, we kept soil moisture constant at that level for two weeks. This was achieved by weighing a subset of pots (n=5 per each treatment) and adding back the water that had evaporated every day. After this 2 weeks period, we conducted the relevant measurements (PLC, $\Psi_{md,}$ photosynthesis) and sampling protocols (for biomass, leaf area, NSC and construction costs) and then induced resprouting. We could not always reach our target levels, but our approach allowed us to establish a gradient of PLCs which was the major goal (see Table 1, S1, Fig. S2). We repeated the same measurements over the two years of the experiment.

Sample size for this experiment was 360 plants: 30 replicates × 2 species × 3 water treatments × 2 light levels. Although all plants were inside the same shelter, we rotated them every fortnight to minimise the impact of microclimatic differences within the shelter on our experimental plants. We measured the basal diameter and height of all plants at the beginning of the experiment. We used a random number generator to assign plants to treatments. After assigning each plant to a treatment, we ensured there were no significant *a priori* differences in plant size across treatments (ANOVA, $P > 0.05$).

Resprouting

Plants were clipped above the root collar and the pots were then kept at constant weight (to maintain a constant water level) for two more weeks after clipping and, at that point, all pots were regularly watered to field capacity until the next growing season, when the experiment was repeated. That is, we clipped (and sampled) all the 360 plants twice: once in 2017 and then again in 2018. The only exceptions were: i) the plants that died during the experiment as a result of our treatments (i.e. a plant that did not resprout in 2017 was not treated again in 2018); and ii) the plants that were destructively harvested for NSC and construction costs analyses, as detailed below.

We monitored resprouting starting after the first re-watering, two weeks after clipping, by counting the number of resprouting individuals daily for the first two weeks, every two days for the next two weeks, and weekly for the next seven months (no resprouting occurred before re-watering). We quantified resprouting growth by measuring, nine months after clipping, the total length of the re-growing shoots (that is, the sum of the length of all the shoots within a plant), the basal diameter (above the point of clipping) and the volume (calculated from length and diameter assuming the branches formed a cylinder). Throughout the manuscript, resprouting capacity refers to the percentage of individuals that resprouted and resprouting growth relates to changes in length, diameter and volume of resprouting shoots. There was mortality during the experiment as a result of treatment implementation. The percentage of resprouting individuals was thus calculated relative to the total number of individuals alive (i.e. with stem and green leaves) per treatment before clipping on a given year.

PLC measurements

We tested whether the watering treatments had reached the target PLC levels by measuring native PLC in 5 plants per treatment. We measured PLC in both experimental years, and always immediately before the clipping. That is, we first measured PLC, then we induced clipping and monitored resprouting twice throughout the experiment (once in each year). We used stem PLC as a proxy of root PLC, an assumption that will be addressed in the discussion.

We measured hydraulic conductivity in stems (50 mm long) before and after removing the air embolisms, as in Sperry *et al.* (1988). We cut the entire shoot, from the root collar, under water in the field. The stem was wrapped in wet paper towels inside zip lock bags in a 4ºC cooler and transported to the laboratory. The measured stems were then recut under water once in the laboratory. The procedure used for this study was the same that is detailed in Peguero-Pina *et al.* (2018). Briefly, we perfused distilled, degassed and filtered water (0.22 mm) with 0.005% (v/v) Micropur (Katadyn Products, Wallisellen, Switzerland) to prevent microbial growth. The hydraulic conductivity was measured at a pressure of 0.005 MPa and air embolism was removed at a pressure of 0.15 MPa for 60-90 s. The water flow was measured with a digital mass flowmeter (Liqui-Flow, Bronkhorst High-Tech, Ruurlo, The Netherlands) connected to a computer.

Leaf gas exchange measurements

We measured leaf gas exchange with a portable photosynthesis system (LI-6400XT, Li-Cor Inc., Lincoln, NE, USA) during the last round of growth measurements on 5 plants per treatment. Measurements were conducted between 10:00h and 14:00h local time, to minimize circadian effects and afternoon stomatal closure. We measured each plant under the two treatment levels of PPFD: 1500 (full sun) and 40 µmol m^{-2} s^{-1} (shaded) but here we only report values under growth (treatment) conditions. The other conditions in the chamber were set to 25.0ºC, 400 ppm, and 1.5 kPa for temperature, CO_2 and vapour pressure deficit, respectively.

Biomass, leaf area and non-structural carbohydrate analyses

Immediately prior to clipping, we randomly selected 5 individuals per treatment for destructive measurements. Fresh leaves were first scanned and leaf area and number were calculated with ImageJ for all the leaves in each individual (Schneider *et al.*, 2012). Samples were microwaved quickly after harvest for 30 seconds at 700W, to prevent enzymatic reactions. We then calculated dry biomass by harvesting and weighing the different plant parts (roots, stem, old leaves and new leaves) after drying (48h at 105ºC) and calculated leaf mass area (LMA). Roots were manually extracted and washed from the potting mix, carefully to minimize losses of root biomass.

We extracted soluble sugars and starch in roots following Palacio *et al.* (2007). After grinding the dried biomass with a mill (IKA A10, IKA-Werke, Staufen, Denmark), soluble sugars (sugar from now on) and starch were extracted separately. For sugar, we first added 10 ml of ethanol (80% v/v) to 50 mg of sample and waited for 30 minutes at 60ºC in a water bath. After this time, we centrifuged (NEYA 8, REMI ELEKTROTECHNIK LTD., Vasai, India) the sample for 10 minutes at 3,200 rpm. We then added 50 µl of supernate, 450 µl of ethanol (80%), 500µl of phenol (28%) and 2,500 µl of sulfuric acid (96%), mixed it and let it sit for 30 minutes. The third step was to read the absorbance at 490 nm with the spectrophotometer (Spectrophotometer UV-1600PC, VWR, Radnor, PA, USA) after removing the supernatant and drying the sample at 70ºC for 16 hours.

To measure starch content, we added 4 ml of sodium acetate (pH 4.5) to the dry sample and left it for 60 minutes in a 60ºC water bath. We then left it to cool and added 1ml of Amyloglucosidase (0.5% w/v), which was then incubated in the stove (16 hours at 50ºC). After the incubation, we added 50µl of supernatant to the sample, 450 µl of sodium acetate (pH 4.5), 500µl of phenol (28%) and 2500 µl of sulfuric acid (96%). We then mixed it and let it sit for 30 minutes, we measured again the absorbance at 490 nm with the spectrophotometer. NSC was calculated as the sum of starch and sugars. Unless otherwise noted, NSC refers to the concentration of stored non-structural carbohydrates in the roots.

Construction cost analyses

We estimated the leaf construction costs following previously developed methods (Nagel *et al.*, 2002, Poorter, 1994, Vertregt & Penning de Vries, 1987). We collected leaves from 5 more individuals per treatment (different to those used in NSC) and we measured ash content after exposing the sample to 400ºC for six hours (Nagel *et al.*, 2002). We analysed organic carbon and nitrogen contents as in Aspinwall *et al.* (2017) with a combustion elemental analyser (TruSpec Micro, Leco, St Joseph, MI, USA). Construction costs (CC) were then calculated using the formula from Poorter (1994) as:

$$CC = (-1.041 + 5.077\ C)\ (1-M) + (5.325N) \qquad \text{(eq. 1)}$$

where M, C and N indicate ash content and organic carbon and nitrogen concentrations, respectively.

Data analyses

We first tested whether our implementation of the water treatments had been successful with linear mixed-effects models (LMM), using Ψ_{md} and PLC at the time of inducing resprouting as dependent variables; with light and water treatments as well as species and their interactions as independent variables; and year as a random factor.

We tested for differences in percent resprouting with a generalized linear mixed model (GLMM), using a binomial distribution, where species, light, water treatments and their interactions were fixed factors and year was a random factor. Differences in NSC, construction costs, net assimilation (A_{net}) and growth were analysed with LMM, where species, light, water treatments and their interactions were fixed factors and year was a random factor.

We sought to understand whether resprouting capacity and growth were correlated using GLMM with a binomial distribution, where year was the random factor. In order to understand whether resprouting capacity was limited by hydraulics or by reserves, we used LMM where PLC and NSC and their interactions were the explanatory variables and year was included as a random factor. In order to understand whether growth was driven by hydraulics, reserves or photosynthesis, we additionally used LMM with PLC, NSC and A_{net} and their interactions as fixed factors and year as a random factor.

All statistical analyses were implemented in the R software environment (version 3.5.2; R development Core Team, 2018) using the "lme4" package for GLMM and LMM (Bates *et al.*, 2015), the "car" package for Wald tests in GLMM and LMM (Weisberg, 2019). Additionally, we performed model selection in all of the above cases using automated dredging procedures (Bartoń, 2018). We also calculated the marginal and conditional R^2 (R^2_m and R^2_c), which refer to the fixed or to the random and fixed components in mixed models, respectively, following Nakagawa and Schielzeth (2013).

Results

Water treatment implementation

Our water treatments were successful in that we managed to create different levels of water stress and, importantly, there were no significant differences across species (Table 1, Table S1, Fig. S1) or across years. However, we could not always reach the desired PLC levels for the following reasons. First, our seedlings were more vulnerable to cavitation than previously published values for the same species (Esteso-Martínez *et al.*, 2006, Peguero-Pina *et al.*, 2014). The value of PLC for a given value of Ψ_{md} was higher in our seedlings than in published values. Since we measured Ψ_{md} during our experiment to infer PLC from the published literature, this generated a higher experimental PLC under the P_{50}_sun treatment (between 65 and 68%) than our target value for the oaks (Table 1, Table S1, Fig. S1). The second issue was that our species were very resistant to cavitation and we could not reach the water potentials necessary to induce PLC over 80%, even after leaving the plants without water for two months. Consequently, measured PLC values under the P_{80}_sun treatment (between 69 and 72%) were lower than expected (Table 1, Table S1, Fig. S1). The third issue was that evapotranspiration was low in the shade treatment; consequently, PLC was consistently lower than in the full sun treatment. Indeed, PLC ranged between 28-41% in the P_{50}_shade treatment, and between 40-54% in the P_{80}_shade treatment (Table 1, Table S1, Fig. S2) in both species. Given this problem P_{50}_shade and P_{80}_shade in the second experimental year were merged under a single treatment (P_{50}_shade).

Resprouting capacity

Resprouting capacity was significantly affected by our experimental treatments. There were differences across species and water levels, and there were also significant interactions between light and water treatments and between species and light treatments (Table 2, Fig. 1).

Taken in isolation, water scarcity had a more important effect on resprouting than light availability: the effect of water was significant ($P < 0.0001$), but light was not significant ($P > 0.05$). Indeed, mean resprouting was 68% in the shade and 63%

the sun (Fig. 1a, b), but resprouting significantly declined with water stress from 88% in P_0, to 57% in P_{50} and to 47% in P_{80} (Fig. 1a,c). There was however a significant interaction between the light and water treatments (Fig. 1c). Resprouting in the sun treatment declined from 97% at P_0, to 62% at P_{50} and to 31% at P_{80} (Fig. 1c). However, the effect of drought was highly variable in the shade treatment as resprouting varied from 80% in P_0, to 51% in P_{50} and to 79% in P_{80} (Fig. 1c).

Regarding the species, *Q. faginea* showed significantly higher (Table 2, Fig. 1a,b) resprouting (77%) than *Q. ilex* (54%). However, species effects depended on the interactions with light (Fig. 1b). Resprouting in *Q. faginea* was favored by the shade, as resprouting increased from 61% in the sun to 95% in the shade (Fig. 1b). However, shade exerted a negative effect on resprouting in *Q. ilex*, which declined from 65% in the sun to 45% in the shade (Fig. 1b).

Resprouting growth

Resprouting growth was affected by light, water, and their interaction and, in the case of total shoot length, treatment effects depended on the species (Table 2, Fig. S3, Fig. 2). Total shoot length, basal diameter and shoot volume were always higher in the sun than in the shade treatments (Fig. 2, Fig. S3). Total length was higher for *Q. ilex* in the shade, but differences across species vanished at high light (Fig. 2a). Total resprouting length in the sun declined from 61 cm to 30 cm to 26 cm as water stress increased from P_0 to P_{50} to P_{80}, respectively (Fig. 2b). Total resprout length in the shade showed a less marked declined from 21 cm to 14 cm to 15 cm as water stress increased from P_0 to P_{50} to P_{80}, respectively (Fig. 2b). A similar pattern was apparent for basal diameter, which decreased in the sun from 2.9 mm at P_0 to 2.5 mm at P_{50} and to 2.2 mm in P_{80} (Fig. 2c). In the shade, however, diameter was higher in P_{80} (1.85 mm) than in P_0 (1.4) or P_{50} (1.5) (Fig. 2c). Differences in volume followed the same trend as those in length (Fig. 2d).

Coordination between resprouting capacity and resprouting growth

We observed that the patterns of correlation between resprouting capacity and growth were highly contrasting across species (Fig. 3). On the one hand, percent resprouting in *Q. ilex* correlated positively with total length ($P < 0.0001$, $R^2_m= 0.28$) basal diameter ($P < 0.0001$, $R^2_m = 0.18$) and volume ($P < 0.0001$, $R^2_m = 0.32$). On the other hand, the correlation between percent resprouting and growth in *Q. faginea* was not significant for length ($P = 0.15$) and volume ($P = 0.5$), and negative in the case of diameter ($P < 0.0001$), although the power of the negative correlation was very low ($R^2_m = 0.08$).

Photosynthesis, carbohydrates and construction costs

Photosynthetic rates measured at ambient light varied across species marginally ($P < 0.1$), across light, water and their interaction significantly ($P < 0.05$) and across the interaction between light and species marginally ($P < 0.1$) (Table 2, Fig. S4). In particular, A_{net} in P_0_sun treatment for *Q. faginea* (13 μmol m^{-2} s^{-1}) was significantly higher than in the P_0_sun treatment for *Q. ilex* (9.5 μmol m^{-2} s^{-1}). Average A_{net} in all other treatments ranged between -0.7 and 2.8 μmol m^{-2} s^{-1} but they were not statistically significant, nor was year.

The concentration of root NSC ranged between 7.6-27% in *Q. faginea* and between 8-22% in *Q. ilex*. Consequently, the minimum value of root NSC concentration reached across species was not different (7.6% vs 8.0%) indicating that we reached similar levels of reserve depletion across species. However, *Q. faginea* showed a significantly higher capacity for accumulating NSC on average (18.5% in *Q. faginea* vs 14.2% in *Q. ilex;* Table 2, Fig. S5a).

There were also significant differences in NSC across light treatments (Table 2), with higher concentrations in the sun (20%) relative to the shade (13%) treatment (Fig. S5a, b). However, the effect of light depended on its interaction with the water treatment (Table 2, Fig. S5b). NSC in the shade was highest at the P_{80} treatment (15%) and lower at the P_{50} (10%) and P_0 (12%) treatments, while in the sun treatments, NSC was lower in the P_{80} treatment (18%) compared to the P_{50} (19%) and P_0 (22%) treatments. NSC concentrations reflected storage capacity as starch accounted for 71% of the total NSC pool across species. Importantly, year was not significant in the model.

We estimated construction costs on a mass and leaf area basis. On a mass basis, the construction cost of a *Q. faginea* leaf were significantly lower (1.28 g glucose g^{-1} dry matter) than for a *Q. ilex* leaf (1.44 g glucose g^{-1} dry matter) (Table 2, Fig. S6), indicating that leaf construction costs for *Q. faginea* were 11% lower than for *Q. ilex*. However, the leaf mass area (LMA) of *Q. faginea* (8.8 g cm^{-2}) was 39%

lower than *Q. ilex* (14.3 g cm^{-2}). Consequently, the construction costs of *Q. faginea* on a leaf area basis (0.011g cm^{-2}) were 45% lower than for *Q. ilex* (0.020 g cm^{-2}) (Fig. S6a,b). On a leaf area basis, construction costs were also affected by light, water and their interactions with species (Table 2, Fig. S6c, d, e). Leaf construction costs on an area basis were higher in the sun than in the shade (Fig. S6c), and they also increased with drought, particularly in P_{80} (Fig. S6d). The interaction between light and water meant that costs in P_{80} were constant regardless of light level (Fig. S6e).

Factors affecting resprouting capacity

We examined the correlation between resprouting capacity and PLC and NSC and we observed different patterns across species (Table 3, Fig. 4). Higher PLC had a negative effect on resprouting, which was significant in *Q. faginea* and *Q. ilex* ($P <$ 0.001, Table 3). We can examine the point where 50% resprouting occurs, as an analogy with epidemiological studies, which use LD_{50} as an indicator of the median lethal dose (or as an analogy with, P_{50} broadly used in plant hydraulics). In *Q. faginea*, resprouting was below 50% only when water stress was above P_{50} in all cases (Fig4b). For *Q. ilex*, resprouting was below 50% only when water stress was above P_{50} in all cases except for one point (lower left of Fig. 4a), indicating that NSC limitations may have played an additional role (Fig. 4c).

In *Q. ilex,* there was a significant (P >0.001, Table 3, Fig. 4c) and positive correlation between NSC and resprouting capacity, and an interaction between PLC and NSC (Table 3). Resprouting in *Q. faginea* was independent of NSC (Table 3). The R^2_m of our statistical models were 0.36 for both species (Table 3).

Factors affecting resprouting growth

Photosynthesis was the most important variable regulating growth of resprouts (Table 3, Fig. 5). The best model included A_{net} as the only significant parameter for total shoot length in *Q. faginea* ($P < 0.0001$; $R_m^2 = 0.43$) and *Q. ilex* ($P < 0.0001$; $R_m^2 = 0.76$) and for volume in *Q. ilex* ($P < 0.0001$; $R_m^2 = 0.77$). Photosynthesis alone ($P = 0.001$) and, to a minor degree, its interaction with NSC ($P = 0.01$) were significant drivers of volume in *Q. faginea* ($R_m^2=0.56$). NSC was an important predictor for diameter in *Q. ilex* ($P < 0.0001$; $R_m^2= 0.46$), but no variable was a significant predictor of diameter in *Q. faginea* ($P > 0.05$). It is worth noting that PLC did not show a significant correlation with any of the growth parameters (Table 3).

Discussion

We exposed seedlings of two naturally co-occurring oak species to contrasting light and water conditions for two years to understand the drivers of resprouting. We observed that hydraulic limitations on the capacity to re-sprout were present in both species, but that carbohydrate depletion only affected *Q. ilex*, which was the species with the highest leaf construction costs. Subsequent growth of re-sprouts was primarily driven by current photosynthesis, while stored carbon (NSC) played a significant but secondary role. The mechanisms affecting the capacity for re-sprouting (primarily hydraulics) differed from those affecting the growth of the re-sprouts (primarily C uptake), although additional differences were observed in two closely related and co-occurring oak species.

Factors affecting resprouting capacity

The resprouting literature in woody species has traditionally discussed the role of stored carbohydrates and nutrients as the main drivers of re-sprouting (Clarke *et al.*, 2013, Pate *et al.*, 1990). Only a handful of studies have documented water limitations, as indicated by predawn water potential (Cruz *et al.*, 2003), as a potential factor affecting resprouting. However, to the best of our knowledge, this is the first study directly demonstrating that the degree of losses in hydraulic conductance before the perturbation that induces resprouting will limit subsequent resprouting capacity in woody species. Hydraulic limitations were more severe in *Q. faginea* than in *Q. ilex*, even though *Q. faginea* shows a higher degree of hydraulic segmentation (Peguero-Pina *et al.*, 2015), which is often considered advantageous for recovery after water stress is relieved because runaway cavitation is isolated (Tyree & Zimmerman, 2002).

Our results were only partly consistent with the hypothesis that NSC limits re-sprouting capacity. We observed a correlation between re-sprouting and NSC only in *Q. ilex*, but the mechanistic reason underlying this relationship remained puzzling after examining differences in leaf construction costs and the amount of reserves, across species. The lowest NSC concentrations in *Q. ilex* roots were 8.1% at the P_{50}_shade treatment which, multiplied by total root weight, adds up to 0.67 g of NSC.

The construction costs of a *Q. ilex* leaf at the P_{50}_shade treatment were 0.01 g glucose cm^{-2}. These reserves should thus have been enough to build 67 cm^2 of leaves, which is equivalent to 16 leaves in the P_{50}_shade treatment, and to 37% of total leaf area grown within one season. In addition to building new leaves, basal resprouters also need to rebuild the stem (which has lower construction costs than the leaf, (Poorter, 1994)) and support respiratory costs. However, these numbers indicate that the amount of NSC left would have been enough to resprout and recover canopy photosynthetic capacity.

This apparent contradiction could be partly explained by interactions with hydraulic impairment, which could have limited NSC remobilization (Table 2). *Q. ilex* often showed low re-sprouting (<50%) when NSC and PLC were low (<10%) and high (>50%), respectively. The opposite pattern was also true, as we observed a number of cases in the shade treatment with high re-sprouting rates (>50%) despite NSC being below 10% (Fig. 4c), and this coincided with PLC being <50% (Fig. 4a).

However, and contrary to this hypothesis, PLC was only 20% in the P_{50}_shade treatment for 2018, when re-sprouting was 0% and NSC was 8.1% (Fig. 4a, c). A plausible, but speculative, explanation for this observation is that the root seedlings were disconnected from the soil in the P_{50}_shade treatment. That is, in conditions of low water and shade, the plant may have encountered disruption in the soil-root continuum such that hydraulic constraints occurred, although they could not be picked up by our PLC sampling scheme which focused on main stems. This could also explain why PLC values in the shade were lower than in the sun, also VPD differences across treatments were only minimal. Further studies on the mechanisms addressing resprouting should thus address the disconnection between roots and soils. To our knowledge, this is the first study indicating this could be a possibility.

Differences between *Q. ilex* and *Q. faginea* in resprouting further supports the hypothesis that NSC may only limit resprouting if accompanied by hydraulic impairment. Resprouting in *Q. faginea* was not limited by NSC reserves, although it reached lower NSC concentrations than *Q. ilex*, and this could be because low NSC did not co-occur with high PLC in *Q. faginea*. That is, the lowest NSC concentrations in *Q. faginea* were 7.6% in the P_{50}_shade treatment, which multiplied by total root weight, equals 0.24 g of NSC. Construction costs were 0.006 g glucose cm^{-2}, which indicates that reserves were sufficient to build 40 cm^2 of leaves (or 27% of total leaf area after one growing season). The potential to build new material in *Q. faginea* was thus lower than in *Q. ilex* (which was of 67 cm^2 of leaves, as stated above) because of the lower NSC content. However, we did not observe NSC limitations in this species, which we attribute to the fact that PLC was never above 50% in this species. That is, low NSC alone was not enough to induce reserves limitation in *Q. faginea*. Additional processes, such as bud limitation, could account for some of the explained variation.

Factors affecting resprouting growth

We observed that resprouting growth was not driven by the same mechanisms as resprouting capacity. One of the differences was that hydraulic limitations developed before the perturbation did not exert any carry-over effects over the growth of the resprouts. This contrasts with drought responses, where hydraulics have been documented to affect plant growth for some years after the drought (Anderegg *et al.*, 2015, Ogle *et al.*, 2015). This difference is likely driven by the fact that we focused on basal resprouting, where new tissue that is free from embolisms is grown. We thus cannot discard a role for hydraulics limiting the growth of epicormic sprouts, particularly for species that maintain their xylem functional for many years. We note that one could have encountered drought legacies if the period between clipping and re-watering had been longer than in this experiment.

Another difference between the drivers of re-sprouting growth and capacity was that net photosynthesis appeared to correlate best with growth. Photosynthesis was the sole correlate of height in both species and of volume in *Q. ilex*, indicating that source rather than sink limitations control resprouting in these species. This is perhaps not surprising considering the strong reductions in C uptake imposed by both our shading and drought treatments.

The potential role of NSC as a driver of growth was overall weak. NSC correlated with secondary growth in *Q. ilex* and, along with photosynthesis, it affected volume in *Q. faginea*. Such a weak role of NSC may be puzzling, considering the wealth of literature supporting a role of carbohydrates as major drivers of re-sprouting (Pausas & Keeley, 2014, Zeppel *et al.*, 2015). However, our results are consistent with the drought literature, where overall, NSC concentrations seldom limit plant survival or growth in angiosperms (Adams *et al.*, 2017, Korner, 2003).

Our results indicate that source limitations to growth were the most common under the different stresses, but sink processes also played a role. Following (and simplifying) the model from Huang *et al.* (2019) and Gessler and Grossiord (2019), under source limitation we should observe that photosynthetic declines lead to a decline in root reserves. This pattern of source limitation is consistent with our results in the shade treatment, where photosynthetic rates and root NSC concentrations were lower than in the P_0_sun. Our temporal design does not allow us to determine the precise moment when NSC concentrations declined, but most likely it occurred during the first few months after treatment implementation because we did not observe differences across years at the moment prior to clipping.

Similarly, there were significant declines in NSC concentration as water stress increased in the sun treatments, further indicating source limitations to growth in the sun across drought treatments. However, we observed that NSC concentrations in P_{80} treatments were higher than in P_0 treatments in the shade, a pattern that is consistent with sink limitations. That is, Huang *et al.* (2019) and Gessler and Grossiord (2019) propose that when sink limitations occur, a decline in root metabolic activity leads to an increase in metabolite accumulation. This pattern was consistent with the results obtained after imposing the double stress of shade and drought, indicating that multiple stress responses and metabolic limitations co-occur.

The evolutionary role of NSC reserves requires further assessment since NSC constituted significant portions of plant dry mass in the roots and yet exhibited a limited role in regulating re-sprouting capacity and primary growth.

Limitations on the use of stem PLC as a proxy for root PLC

We need to acknowledge that a limitation of this study was the use of stem PLC as a proxy for root PLC. Previous studies have indicated how this proxy can be problematic when there is substantial hydraulic segmentation (Johnson *et al.*, 2016) because roots have sometimes (Tyree & Zimmerman, 2002), but not always (Wu *et al.*, 2020), been documented to be more vulnerable to embolism than stems. Although the existence of hydraulic segmentation was formulated long ago (Zimmermann, 1978), it is still unclear how prevalent it is across species (Wu *et al.*, 2020).

For the two species of concern here, we could not find any study addressing whether hydraulic segmentation occurs in seedlings. Previous studies conducted with adult trees (Peguero-Pina *et al.*, 2015), however, observed that leaves of *Q. subpyrenaica* (the hybrid between *Q. faginea* and *Q. pubescens*) withered prematurely as leaf water potentials dropped below -3MPa, which indicates hydraulic segmentation between leaves and stems. The same study did not find vulnerability segmentation between leaves and stems in *Q. ilex*.

For adult trees of *Q. ilex*, (Martínez-Vilalta *et al.*, 2002) documented that roots were more vulnerable to cavitation than stems. The differences in the relationship between applied pressure and PLC across tissues were particularly high as PLC increased above 50%. That is, while there were no statistical differences in the P_{50} of roots and stems, roots became increasingly more vulnerable to cavitation than stems at higher water potentials (Martínez-Vilalta *et al.*, 2002).

We thus cannot discard the possibility that root PLC in the P_{80}_sun treatment for *Q. ilex* would have been larger than the one measured for stem PLC. A similar response may also have occurred in *Q. faginea,* if this species also displays vulnerability segmentation between roots and stems. That is, stem PLC may have underestimated root PLC, and the differences in PLC across organs would have been more accentuated at higher PLCs. If this is the case, we can speculate that the slope of the relationship between PLC and resprouting capacity would have been steeper than reported here (Fig. 4, Table 3).

We must acknowledge also the possibility that stem PLC in our species is not indicative of root PLC at all. Under this scenario, our results would indicate that stem PLC before clipping, and not root PLC, controls basal resprouting after clipping. However, there is no known mechanism to explain this relationship and we thus consider it unlikely.

Quercus resilience

Overall, our results indicated that oak seedlings were more resilient to clipping in the shade than in the sun. That is, light and water limitations (shade and drought) induced a higher level of resprouting than water limitations (drought) under no light limitation (sun). However, there were differences in PLC across treatments, which were substantially higher in the sun than in the shade. Indeed, comparisons on drought responses across different light treatments were affected by the different severities of drought. It should thus be noted that in the field, shady sites may sometimes be drier than sunny sites because of increased plant-plant competition for water (Valladares *et al.*, 2016). Under these circumstances, when shady environments are drier than sunny sites, we would thus expect a lower re-sprouting capacity in the shade than in the sun.

Previous studies assessing the recovery from drought in angiosperms indicate that lack of recovery may occur when PLC>80% (Resco *et al.*, 2009, Urli *et al.*, 2013). Our results on this regard are still tentative, and limited as they are based on stem PLC (and not root PLC), but they allow us to hypothesize that re-sprouting may become particularly limited when PLC is below 50%. Hence, resprouters are more susceptible to stress and disturbance, than to stress alone. It should be noted that we induced resprouting by clipping, to ensure homogeneity in treatments, but fire exerts an additional thermal stress (Casals & Rios, 2018). It is thus feasible that the hypothesized PLC threshold of 50% for limiting resprouting may be lower in burned plants.

It should also be noted that our results are limited to basal resprouting and further studies will need to address potential limitations in epicormic and other types of resprouting. In particular, the role of hydraulic legacies may be more important in epicormic resprouters. There are an increasing number of studies indicating increased intensity of forest fires under global warming, resulting from higher temperatures and drought intensities (Boer *et al.*, 2016, Jolly *et al.*, 2015, Nolan *et al.*, 2020). Our results offer new mechanistic insights and hypotheses to be tested in further experiments that may be used to improve model predictions. We thus hope this study serves as a starting point for more studies on this area to further clarify outstanding issues.

Acknowledgements

The present study has been supported by the National Natural Science Foundation of China (No. 31850410483), the talent funds of Southwest University of Science and Technology (No.18ZX7131), the MICINN (AGL2015-69151-R), INIA (RTA2015-00054-C02-01) and Generalitat de Catalunya (SGR2017-1518), Spain. We acknowledge technical support from MJ Pau, MP Sopeña, A Cunill, J Hedo, B Lavaquiol and C Maier. This manuscript benefited from the insightful comments provided by two reviewers and the Associate Editor and from statistical advice by JG Alday.

Authorship statement

VRD conceived the project with input from CA, JJPP, DSK, WS, DGW, MMB, JV, JMM, DTT and EGP; CA, EGP, JJPP and DSK cultivated the plants; CA, VRD, EGP, JJPP, DSK, OKZ, DTT and HQ performed measurements; CA prepared the data files; VRD analyzed the data and wrote the manuscript and all co-authors contributed to edits to the manuscript.

Conflict of interest

The authors declare no conflict of interest

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Supporting information

Table S1: results of linear mixed models analyses on differences across realized PLC values. Fixed factors were species, light and water treatments and their interactions and year was included as a random factor.

Figure S1: Differences in mean daily air temperature (T_{air}) and mean daily vapour pressure deficit (VPD) between sun and shade treatments (a, b) and in T_{air} between treatments and ambient (c,d). Data in the shelters were collected between June and July 2017 with a PCE-HT 71N (PCE Ibérica, Tobarra, Spain) logging automatically every 5 minutes. Ambient T_{air} data was downloaded from station number 9771C, from the Spanish Metorology Agency (www.aemet.es, 21st February 2020), which is placed inside the campus (<1 Km from the shelter).

Fig. S2: Realized values of percent loss of hydraulic conductance (PLC) and midday water potential (Ψ_{md}) at the time of inducing resprouting in *Q. ilex* (a,b) and *Q. faginea* (c,d). The target values were 0, 50 and 80% PLC (P_0,P_{50} and P_{80}, respectively). Values indicate mean and standard error.

Fig. S3: Changes in resprouting growth as a function of species, water and light levels. The species are *Quercus ilex* (Qi) and *Q. faginea* (Qf). The water levels refer to target levels of PLC (P_0, P_{50} or P_{80}, but see Table 1 for actual values). Sun or shade indicate whether the plants received either ambient, or 2-3% of ambient radiation, respectively. Values indicate mean and standard error.

Fig. S4: Changes in net assimilation rate across species, light and water treatments. To more clearly depict significant effects, we only include significant interactions (but note that the interaction in c is marginal). The water levels refer to target levels of PLC (P_0, P_{50} or P_{80}, but see Table1 for actual values). Sun or shade indicate whether the plants received either ambient, or 2-3% of ambient radiation, respectively. Values indicate mean and standard error.

Fig. S5: Changes in non structural carbohydrates (NSC) across species, light and water treatments. To more clearly depict significant effects, we only include significant interactions. The water levels refer to target levels of PLC (P_0, P_{50} or P_{80}, but see Table1 for actual values). Sun or shade indicate whether the plants received either ambient, or 2-3% of ambient radiation, respectively. Values indicate mean and standard error.

Fig. S6: Construction costs on a mass basis (a) and on a leaf area basis (b-e) as a function of experimental treatments. To more clearly depict significant effects, we only include significant interactions. The water levels refer to target levels of PLC (P_0, P_{50} or P_{80}, but see Table 1 for actual values). Sun or shade indicate whether the plants received either ambient, or 2-3% of ambient radiation, respectively. Values indicate mean and standard error.

Table 1: Target midday water potential (Ψ_{md}) to reach the desired PLC according to Esteso-Martínez *et al.* (2006) for Q. *faginea* and to Peguero-Pina *et al.* (2014) for *Q. ilex*, and actual values. Mean (and SE) actual values are presented. The letters in "Actual PLC" indicate the results of post-hoc analyses (Tukey HSD).

Species	Light treatment	Water treatment	Target Ψ_{md} (MPa)	Target PLC (%)	Actual Ψ_{md} (MPa)	Actual PLC (%)
Q. ilex	Sun	P_0	> -4	< 20	-1.3 (0.20)	11.9 (2.3)$^{\mathbf{c}}$
		P_{50}	-6	50	-5.4 (0.54)	64.7 (6.87)$^{\mathbf{a}}$
		P_{80}	-8.9	80	-6.4 (0.62)	69.1 (7.56)$^{\mathbf{ab}}$
	Shade	P_0	> -4	< 20	-0.8 (0.14)	12.3 (2.84) $^{\mathbf{c}}$
		P_{50}	-6	50	-2.9 (0.77)	41.2 (10.9)^{abc}
		P_{80}	-8.9	80	-4.4 (0.56)	54.3 (10.69)^{ab}
Q. faginea	Sun	P_0	> -2.8	< 20	-1.1 (0.22)	15.6 (2.73)$^{\mathbf{c}}$
		P_{50}	-3.9	50	-3.9 (0.28)	53.2 (8.04)^{ab}
		P_{80}	-5.5	80	-4.2 (0.30)	66.1 (9.89)$^{\mathbf{a}}$
	Shade	P_0	> -2.8	< 20	-0.7 (0.12)	7.5 (1.35) $^{\mathbf{c}}$

	P_{50}	-3.9	50	-1.1 (0.21)	27.9 (9.86)^{bc}
	P_{80}	-5.5	80	-2.6 (0.51)	39.8 (13.0)^{abc}

Table 2: Results of a fitting a generalized linear mixed effects model (GLMM) on resprouting capacity, a linear mixed effects model (LMM) on length, diameter, volume, net assimilation (A_{net}) and non-structural carbohydrate concentrations (NSC), and an ANOVA on leaf construction costs on a mass (CC) and an area (CC_area) basis. The explanatory variables were in all cases species, light, water and their two- and three-way interactions included. We applied dredging techniques for automatic model selection and only the variables selected are included. Year was included as a random factor in GLMM and LMM models. ANOVA was performed for CC and CC_area because only data for 2018 was available. Values indicate either the $\chi 2$ (GLMM and LMM) or the F-values (ANOVA) and stars indicate the significance level.

	Resprouting capacity	Length	Diameter	Volume	A_{net}	NSC	CC	CC_area
Species	26.6***				3.1 ·	9.58**	46.3***	1299***
Light		157***	155***	154.9***	108***	50.1***		165.1***

Water	86***	67.7***	43.8***	43.9***	91.7***			699.5***
Light ×Water	64.4***	34.2***	52.9***	52.9***	88.7***	0.01**		206.6***
Species × Light	67.4***	7.8**			3.2·			67.7***
Species × Water								24.7***
Species × Water × Light								38.6***

Significance levels: *** <0.001; **<0.01; *<0.05; ·<0.1.

Table 3: Effects of PLC and NSC over resprouting capacity and additionally of net photosynthesis (A_{net}) over shoot total length, basal diameter and volume. Resprouting capacity was fitted with generalized additive mixed model (GAMM) and growth with a linear mixed-effects model (LMM). We applied dredging techniques for automatic model selection and only the variables selected in the best model are included. Values indicate the χ^2 and stars indicate the significance level. Values are also provided for the marginal R^2 (R^2_m) for each model.

	Resprouting capacity	Length	Diameter	Volume
Q. ilex;	$R^2_m = 0.36$	$R^2_m = 0.76$	$R^2_m = 0.46$	$R^2_m = 0.77$
PLC	43.2***			
NSC	29.2***		16.7***	
PLC × NSC	14.9***			
A_{net}		34.5***		25.9***
Q. faginea	$R^2_m = 0.36$	$R^2_m = 0.43$		$R^2_m = 0.56$
PLC	92.8***			
NSC				
A_{net}		19.3***		10.77***
A_{net} × NSC				6.1*

Significance levels: *** <0.001; **<0.01; *<0.05; ·<0.1.

Figure legends

Figure 1: Changes in resprouting capacity as a function of species, water and light levels (a) and significant interactions (b, c) The species are *Quercus ilex* (Qi) and *Q. faginea* (Qf). The water levels refer to target levels of PLC (P_0, P_{50} or P_{80}, but see Table 1 for actual values). Sun or shade indicated whether the plants received either ambient, or 2-3% of ambient radiation, respectively. Values indicate mean and standard error.

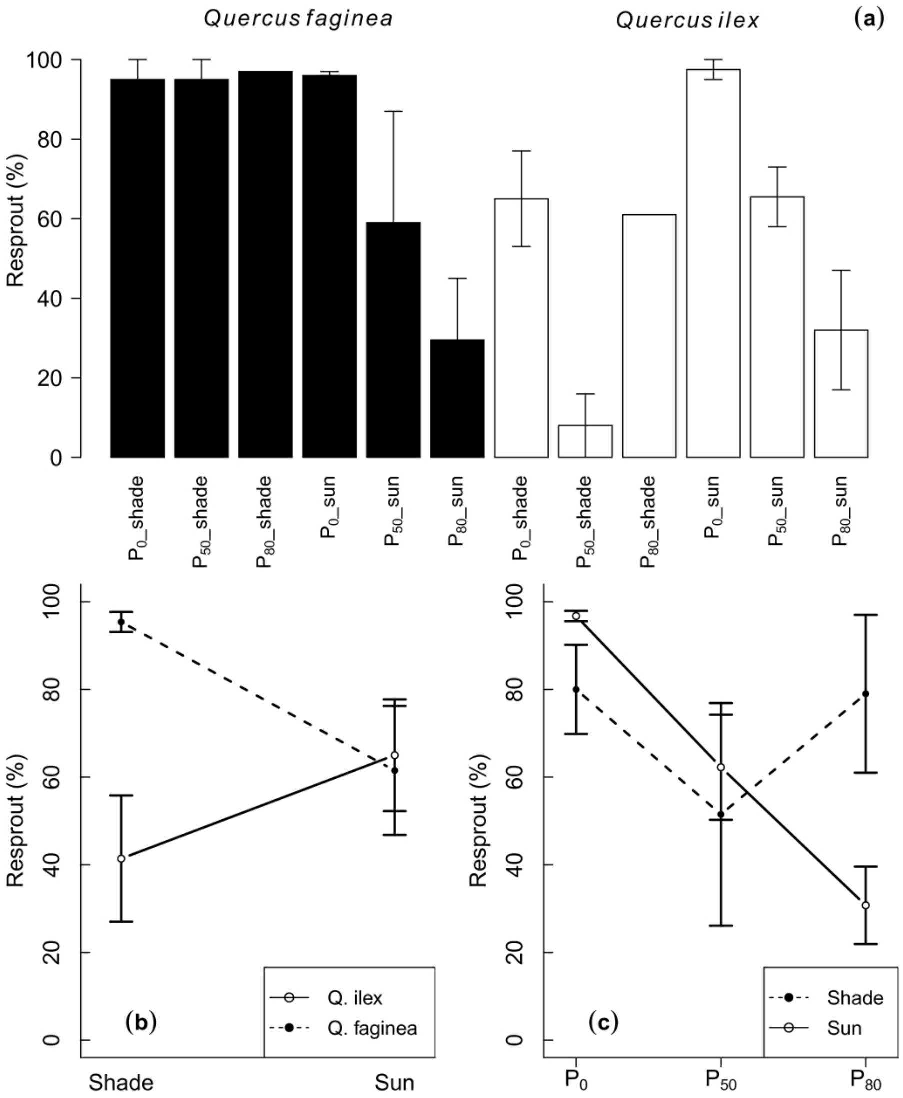
Figure 2: Changes in total length, basal diameter and volume across species, light, water treatments and their interactions. Only significant interactions are included. The water levels refer to target levels of PLC (P_0, P_{50} or P_{80}, but see Table 1 for actual values). Sun or shade indicated whether the plants received either ambient, or 2-3% of ambient radiation, respectively. Values indicate mean and standard error.

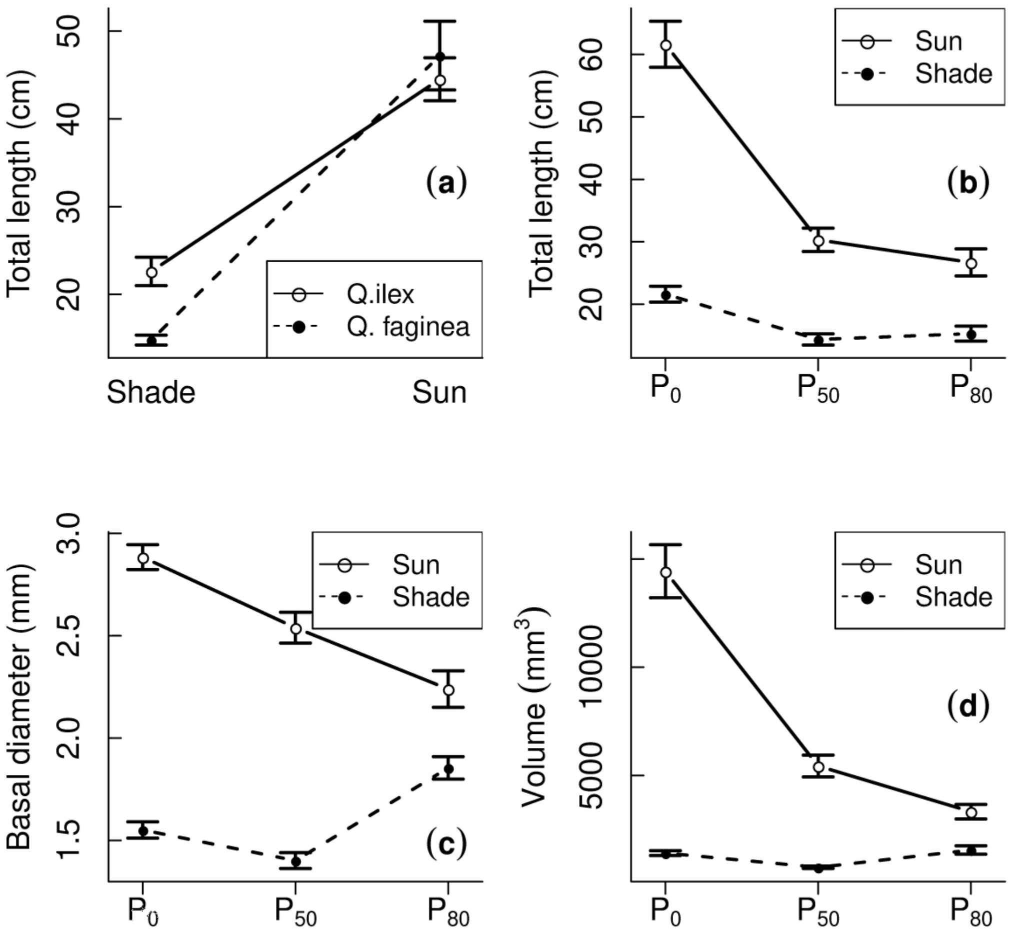
Figure 3. Correlations between % resprouting and the three growth variables (total length, basal diameter and volume) in *Q. ilex* (left) and *Q. faginea* (right). Best fit lines indicate the results of simple regression rather than the full model and they are included only for visualization purposes. Dashed lines indicate that the full model was not significant. Each point is a treatment mean.

Figure 4: Effects of NSC and PLC over resprouting capacity in *Q. ilex* (left) and *Q. faginea* (right). Best fit lines indicate the results of simple regression rather than the

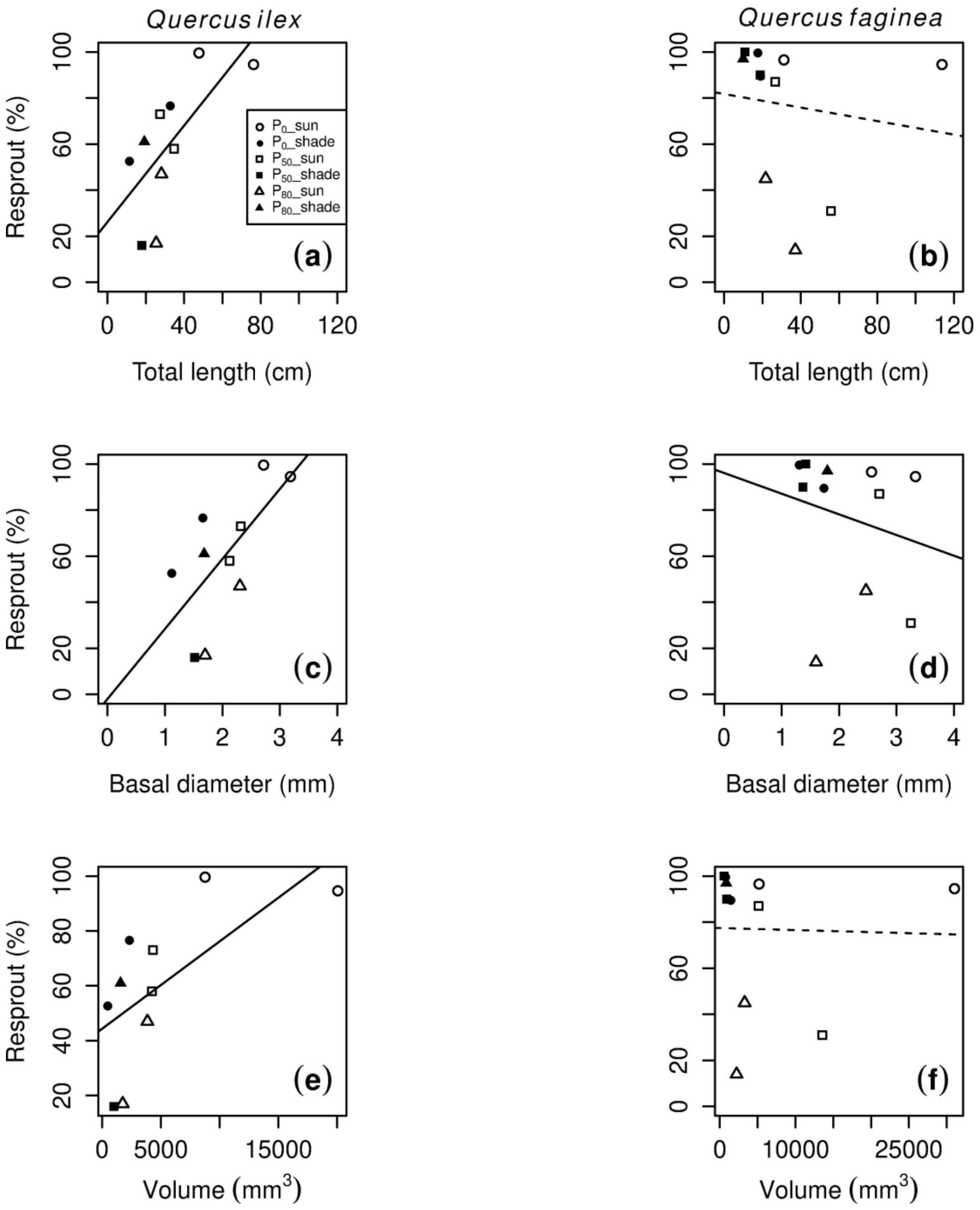
full model and they are included only for visualization purposes. Dashed lines indicate that the full model was not significant. Each point is a treatment mean.

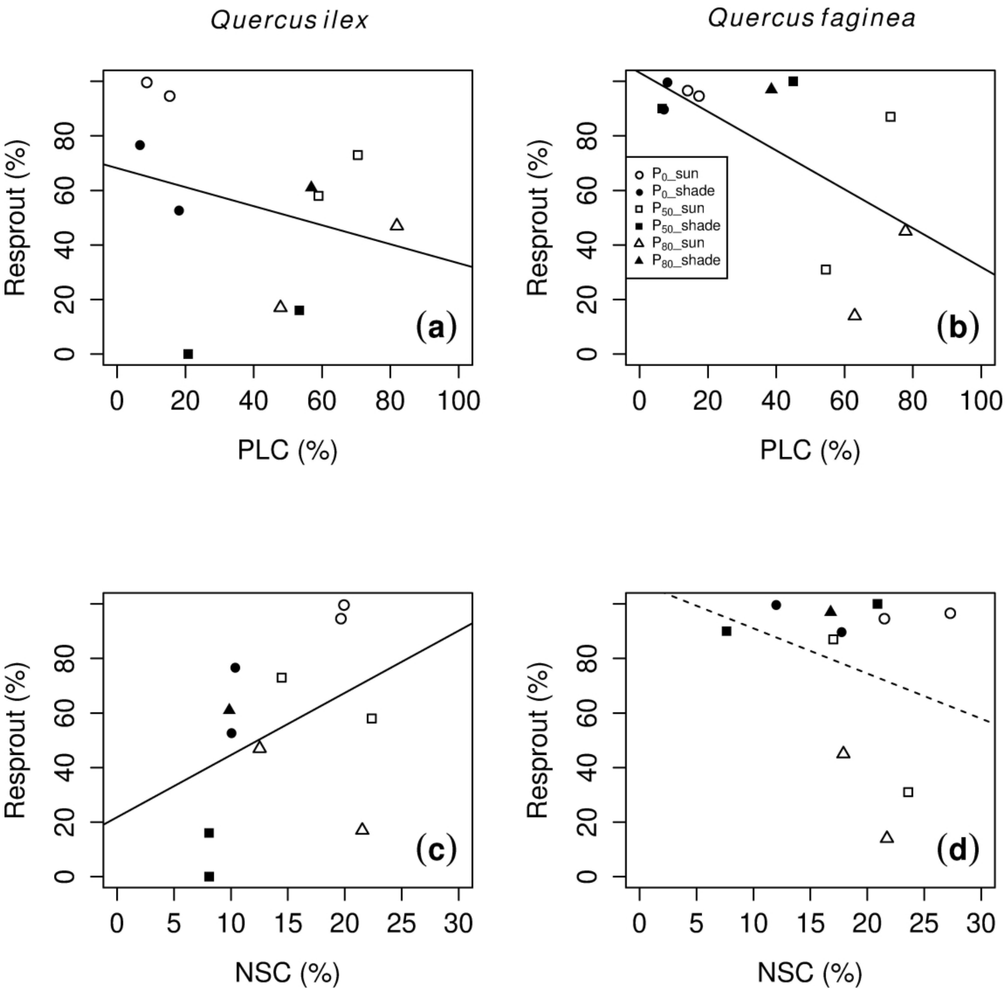
Figure 5: Correlates of growth across species. Photosynthesis (A_{net}) correlated with length and volume in both species. NSC only correlated with diameter in *Q. ilex* and its interaction with A_{net} in volume of *Q. faginea*. Best-fit lines indicate the result of simple regression, not of the ful model, and are included for visualization purposes only. Dotted lines indicate marginal relationships. Each point is a treatment mean.

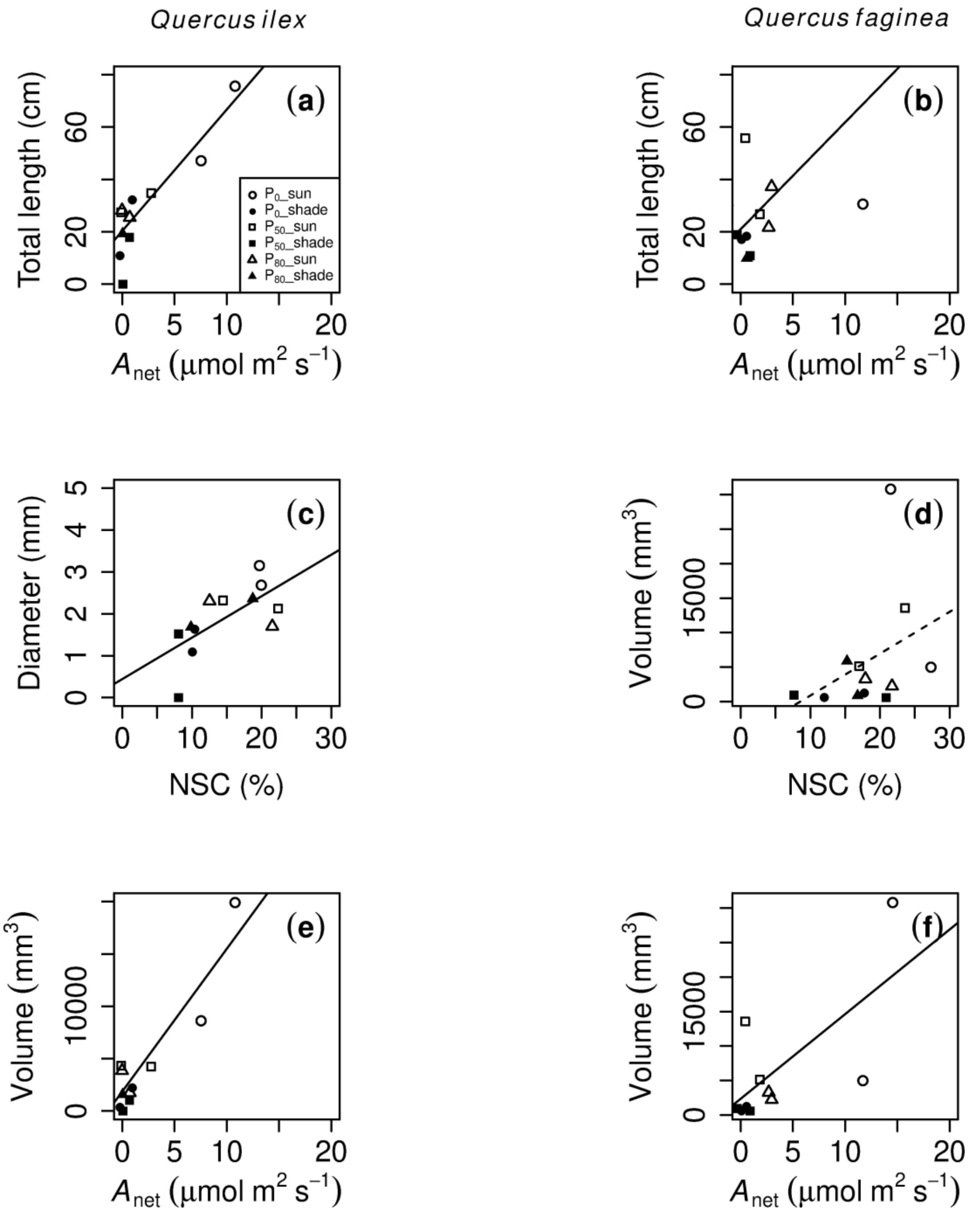

Quercus faginea
Quercus ilex
(a)
Resprout (%)
100
80
60
40
20
0
P_0_shade
P_{50}_shade
P_{80}_shade
P_0_sun
P_{50}_sun
P_{80}_sun
P_0_shade
P_{50}_shade
P_{80}_shade
P_0_sun
P_{50}_sun
P_{80}_sun
Resprout (%)
(b)
Q. ilex
Q. faginea
Shade
Sun
Resprout (%)
(c)
Shade
Sun
P_0
P_{50}
P_{80}



Total length (cm)
50
40
30
20
(a)
Q.ilex
Q. faginea
Shade
Sun
Total length (cm)
60
50
40
30
20
Sun
Shade
(b)
P0
P50
P80
Basal diameter (mm)
3.0
2.5
2.0
1.5
Sun
Shade
(c)
P0
P50
P80
Volume (mm3)
10000
5000
Sun
Shade
(d)
P0
P50
P80


Quercus ilex
Quercus faginea
Resprout (%)
Total length (cm)
Basal diameter (mm)
Volume (mm^3)
P$_0$_sun
P$_0$_shade
P$_{50}$_sun
P$_{50}$_shade
P$_{80}$_sun
P$_{80}$_shade
(a)
(b)
(c)
(d)
(e)
(f)
0
20
40
60
80
100
120
1
2
3
4
5000
10000
15000
25000


Quercus ilex
Quercus faginea
Resprout (%)
PLC (%)
NSC (%)
0
20
40
60
80
100
0
5
10
15
20
25
30
(a)
(b)
(c)
(d)
○ P_0_sun
● P_0_shade
□ P_{50}_sun
■ P_{50}_shade
△ P_{80}_sun
▲ P_{80}_shade


Quercus ilex
Quercus faginea
(a)
(b)
(c)
(d)
(e)
(f)
Total length (cm)
0
20
60
Diameter (mm)
0
1
2
3
4
5
Volume (mm^3)
0
10000
15000
A_{net} (μmol m^2 s^{-1})
0
5
10
20
NSC (%)
0
10
20
30
○ P_0_sun
● P_0_shade
□ P_{50}_sun
■ P_{50}_shade
△ P_{80}_sun
▲ P_{80}_shade