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Shifts in Biomass Allocation and Trait Correlations Under the Combined Effects of Drought and Shade

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ABSTRACT

Biomass allocation in plants is mainly interpreted through two major theories: Allometric Partitioning Theory (APT) and Optimal Partitioning Theory (OPT). Under a specific environmental condition where drought and shade co-occur, biomass allocation can also be explained by trade-off, facilitation, and uncoupled hypotheses. These theories and hypotheses make contradictory predictions regarding the direction of biomass allocation to above- versus belowground organs. Because empirical support can be found for each of them, it remains unresolved which framework better explains biomass allocation strategies under combined effects of drought and shade. Moreover, we lack a unified understanding of how these frameworks may integrate. To test these five frameworks, we examined three Fagaceae species with contrasting tolerances: drought-tolerant *Quercus pubescens*, shade-tolerant *Fagus sylvatica*, and *Castanea sativa* with moderate shade and drought tolerance. We conducted a greenhouse experiment to detect seedling responses to simulated drought and shade using an experimental design controlling water-table gradients, light quality and quantity. We analyzed aboveground growth via LiDAR, aboveground/belowground biomass allocations, and resource acquisition strategies of these three species. We found that individual seedling responses were highly nuanced along continuous gradients, and no single theory and hypothesis adequately explained the observed biomass allocation. Moreover, we developed a novel decision chart that systematically links these disparate theories and hypotheses, rather than treating them as mutually exclusive frameworks.

1 | Introduction

How plants allocate biomass for growth and survival is a key aspect of plant strategies (Weiner 2004). Two major frameworks have been proposed to explain biomass plant allocation: Allometric Partitioning Theory (APT) and Optimal Partitioning Theory (OPT). APT is a mechanistic model that predicts consistent and universal biomass allocation patterns which are controlled by plant size and biophysical constraints. According to this theory, leaf biomass scales to the ¾ power of the combined biomass of stem and root, while stem biomass scales isometrically with root biomass (Enquist and Niklas 2002; McCarthy and Enquist 2007). Whereas, OPT offers a more flexible framework proposing that plant species allocate biomass dynamically to the organ that acquires the most limiting resource to minimize limitations (Bloom et al. 1985; Grime 1979). According to OPT, resource availability, rather than fixed allometric relationships, drives biomass allocation. OPT highlights the adaptive nature of plants in response to environmental variability and resource scarcity to maximize fitness (Stearns 1992; Shipley and Meziane 2002).

Evidence from literature supports both APT and OPT. Both allometric and optimal partitioning principles can be at play in determining how trees allocate biomass depending on climate and soil characteristics of habitat (Gargaglione et al. 2010) and immediate resource availability imposed by environmental conditions (Poorter et al. 2015; Puglielli et al. 2021). In some

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cases, allometric equations can predict biomass allocation patterns effectively (Enquist and Niklas 2002; Eziz et al. 2017; Liu et al. 2021; West et al. 1999) while in others, the immediate environmental context and resource limitations play a more decisive role (Dolezal et al. 2021; Moncrieff et al. 2011; Pretzsch and Dieler 2012). Therefore, it remains unresolved which theory ultimately govern plant allocation strategies when environmental conditions impose opposing resource demands.

Under a specific scenario when drought and shade co-occur, three hypotheses were proposed regarding biomass allocation patterns (trade-off, facilitation and uncoupled) and we propose that these hypotheses can be linked to the APT and OPT as an extension of these two major theories (Figure 1). When drought and shade co-occur, an allocation trade-off between aboveground and belowground is expected due to a zero-sum dynamic (McCarthy and Enquist 2007). That is, either light interception or water acquisition should be optimized. According to the "trade-off hypothesis" (Smith and Huston 1989), plants may prioritize either aboveground or belowground allocation, depending on the availability of resources, under combined effects of drought and shade. For example, increased allocation to roots is expected under drought due to resource limitations (such as carbon or water). Whereas the "facilitation hypothesis" (Holmgren 2000) suggests that shade may alleviate drought stress, as canopy shading can lower vapor pressure deficit (VPD) and reduce evapotranspiration, allowing plants to allocate more biomass into aboveground structures. Alternatively, an orthogonal effect has been proposed, where shade and drought act independently without significant interaction—"uncoupled hypothesis" (Sack 2004; Sack and Grubb 2002; Wang and Wang 2023).

Empirical support exist for each of these three hypotheses. Trade-off hypothesis was supported in *Pinus massoniana* (Deng et al. 2019), *Picea abies* (Schall et al. 2012), and various tropical tree species (Markesteijn and Poorter 2009) as plants allocated relatively greater proportions of biomass to organs capturing limited resources compared to the control. In dry Mediterranean habitats, shade has been shown to mitigate adverse effects of drought on *Quercus* species (Quero et al. 2006), supporting facilitation hypothesis. However, *Liriodendron tulipifera* (Holmgren 2000) and four *Quercus* species (Quero et al. 2006) expressed no significant trade-off between aboveground versus belowground allocation. Therefore, these varied responses highlight the complexity of plant responses to combined stress factors and underscore the importance of considering species-specific and environmental factors.

Research to date has not examined how these separate theories and hypotheses on biomass allocation may integrate. In this study, we interconnect APT, OPT, trade-off, facilitation and uncoupled hypothesis by developing a decision chart (Figure 1). For example, a significant deviation from fixed allometric relationships and a higher allocation to belowground structures at the expense of aboveground structures under drought would support the trade-off hypothesis and OPT. In a different scenario, if shade alleviates drought effects, allometric relationships may

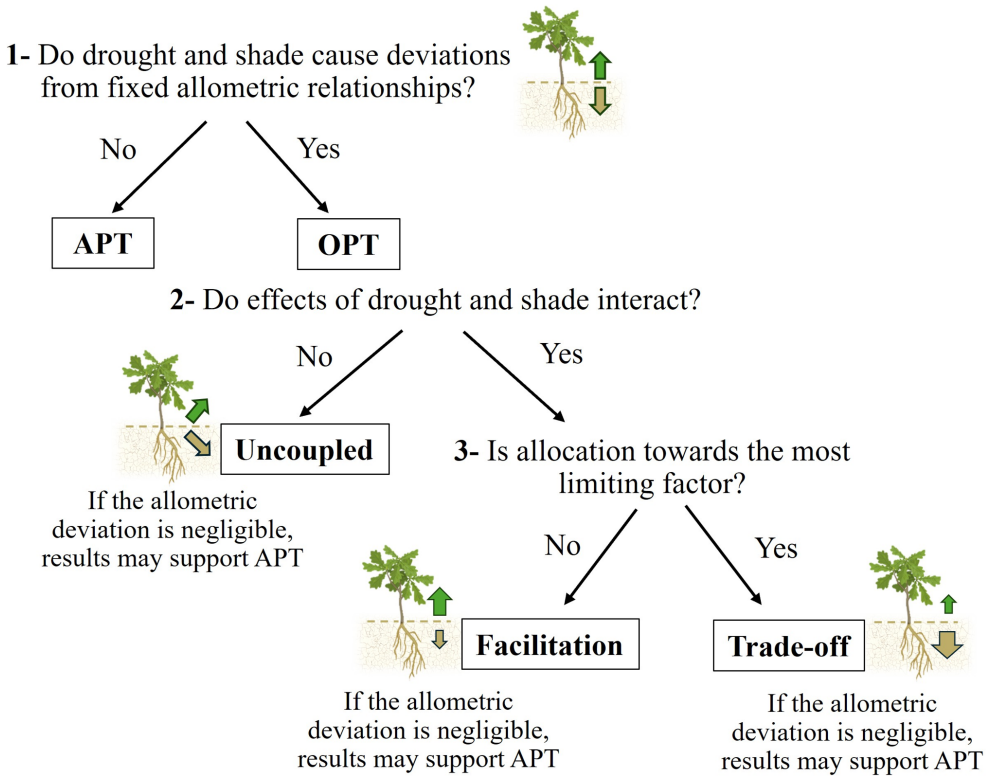

FIGURE 1 | A decision chart combining different theoretical frameworks on plant biomass allocation patterns under different scenarios of drought and shade. Green and brown arrows indicate allocation to shoot and root, respectively, and arrow sizes indicate relatively higher or lower biomass allocation. APT, Allometric Partitioning Theory; OPT, Optimal Partitioning Theory.

still be valid, and the facilitation hypothesis may be supported if aboveground allocation increases more than belowground allocation under the combined effects of drought and shade (Figure 1).

Biomass allocation and resource trade-offs in plants can be interpreted within the Plant Economics Spectrum (PES) that links trait variation to resource acquisition and conservation (de la Riva et al. 2016; Reich 2014). Reduced carbon assimilation during drought constrains biomass production, forcing plants to balance carbon allocation between organs involved in water uptake (roots) and carbon gain (leaves). This mass-balance trade-off determines whether a species allocates proportionally more to roots or shoots. Under drought, greater biomass allocation to roots does not necessarily enhance water uptake because thicker roots have lower absorptive surface area (Freschet et al. 2021). Thus, plants face trade-offs between acquisitive strategies characterized by rapid resource uptake and conservative strategies (Reich 2014). Species with fast acquisition strategies typically form thin, short-lived roots with high specific root length (SRL), which enhances rapid soil exploration but imposes a carbon maintenance cost. In contrast, species with thick, long-lived roots trade surface area for persistence, supporting drought tolerance or avoidance through conservative carbon use (Pérez-Ramos et al. 2013). Similarly, specific leaf area (SLA) reflects investment in light capture per unit leaf biomass, linking leaf morphology to resource-use efficiency. Together, root and leaf economic traits indicate how plants balance carbon costs and resource returns, thereby helping to explain variation in biomass allocation and performance under drought and shade.

There is no consensus on whether shade exacerbates or mitigates the effects of drought on tree growth and survival (Bachofen et al. 2019; Pardos and Calama 2022; Pretzsch et al. 2018). Experimental studies are necessary to evaluate seedling responses and how shade and drought interact to affect the growth performance and mortality of species with varying tolerances to these stressors. Although biomass allocation under combined effects of drought and shade has been studied in several European woody species (Holmgren 2000; Pardos and Calama 2022; Quero et al. 2006; Sack and Grubb 2002; Schall et al. 2012), these studies employed neutral-density shade cloths that exclusively reduce light quantity (photosynthetically active radiation—PAR), neglecting light quality (red-to-far-red light ratio, R:FR), which induce shade avoidance responses including increased allocation to elongation, apical dominance, and specific leaf area (SLA) (Ballaré et al. 1990; Fazlioglu et al. 2016; Gruntman et al. 2017). Using light filters instead of shade cloths can more accurately simulate the effect of foliar shade beneath the canopy (Petrella et al. 2022).

In this study, we selected three Fagaceae species with distinct levels of shade and drought tolerance (drought-tolerant *Quercus pubescens*, shade-tolerant *Fagus sylvatica*, and *Castanea sativa* with moderate shade and drought tolerance) to test the above-mentioned theoretical frameworks on biomass allocation under combined effects of drought and shade. Specifically, we addressed the following questions:

1. How do biomass allocation, resource acquisition, and growth impacted by drought, shade and their interaction change in three Fagaceae species?
2. Do individuals allocate biomass to build structures that adhere to fixed allometric equations (APT), or do shifting resource availability force plants to deviate from such equations (OPT)?
3. Does allocation to aboveground or belowground increase under combined effects of drought and shade, or are the effects of drought and shade independent (testing trade-off, facilitation, uncoupled hypotheses)?

2 | Methods

2.1 | Experimental Design

We developed a new experimental design to simulate drought and shade, Drought and Shade Modulator "DaSMod," based on previous methodologies (Fernández and Reynolds 2000; Marchin et al. 2020) (Figure 2 and Supporting Information Appendix Figure A1). We induced soil water deficiency by adjusting water-table depths and generated spectral shading using two light filters (LEE 124 Dark Green and LEE 130 Clear for control) at the greenhouse of the University of Bayreuth, Germany. In DasMod, commercially available foam bricks (Oasis Maxlife) allow steady water transport to seedlings via capillary action owing to their uniform conductivity and bulk density characteristics (Snow and Tingey 1985). The experimental seedlings were grown in sterilized natural sandy loam soil (79% sand, 15% clay, 6% silt) to facilitate root sample harvesting. Four 3 cm diameter holes were drilled at the bottom of 3 L rectangular pots (14 × 14 × 16 cm) to enhance soil-foam contact. Seedlings accessed water through capillary action facilitated by this contact area. A fine nylon mesh (25 μm) was placed between pots and foam blocks to prevent root penetration into the foam while allowing water uptake.

Light filters induce shade avoidance response in plants by changing light quality and quantity (Fazlioglu et al. 2016; Gruntman et al. 2017). In previous studies, this method has been used on herbaceous plants. Dark green light filters can reduce the R:FR ratio to 0.04 (around 1.18 under full sun; Petrella et al. 2022) and PAR to 10% of daylight at 2 cm above the soil level (Gautier et al. 1999). In the context of natural environments, mature *Fagus sylvatica* presents a similar scenario: during the full foliation phase and clear sky conditions in July, the understory R:FR ratio and PAR can be as low as 0.06 and less than 1%, respectively (Leuchner et al. 2007, 2011). Therefore, the use of light filters, rather than the widely used shade cloths, provides more realistic shade conditions for seedlings.

Seedlings of the three species were commercially procured from a certified local nursery in Germany, specialized in forest seeds and seedling cultivation (www.die-forstpflanze.de). Species identification was confirmed by the supplier and by our own observations. 1-year-old *F. sylvatica* and *C. sativa* and 2-year-old *Q. pubescens* seedlings were placed in containers with a water

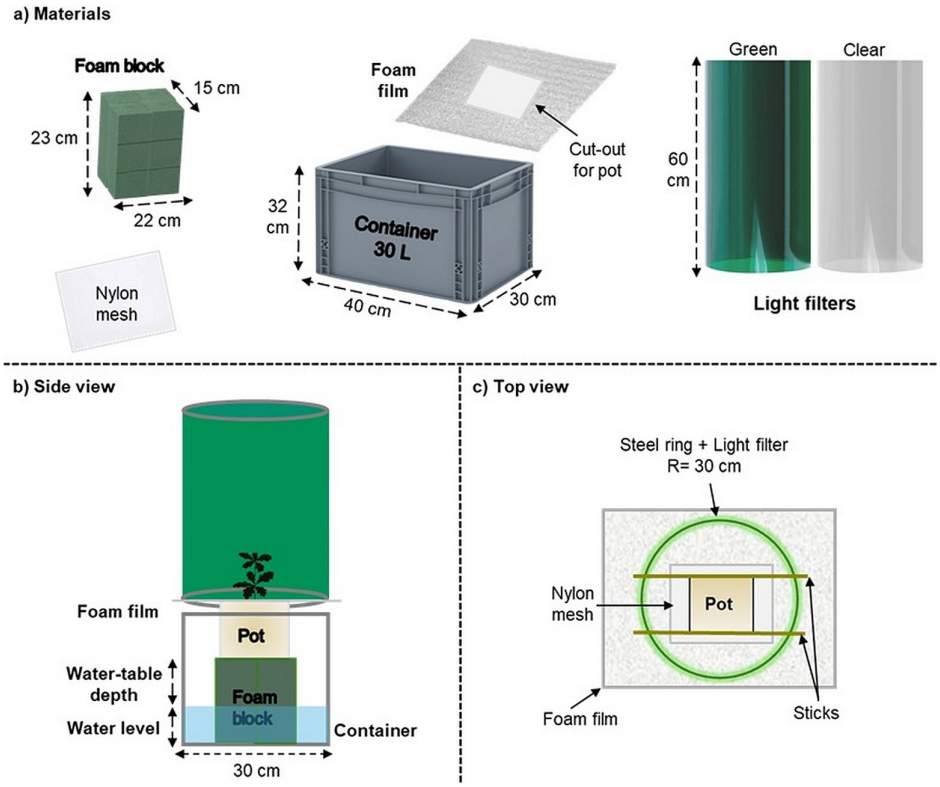

FIGURE 2 | Drought and Shade Modulator "DaSMod." (a) The main materials needed to construct DaSMod. (b, c) Views from the side and top, respectively. The foam film was illustrated as transparent in (c) for enhanced visualization and clarity of the design.

depth of 21 cm in April 2023. Similar-sized individual tree seedlings were randomly assigned to different treatments. We used a "gradient design" (Kreyling et al. 2018) to explore patterns in species responses to continuous and interacting drought and shade factors. Gradient design arranges experimental units along gradients without replication; they are particularly useful for characterizing the shape of responses to the stress gradient and when the definition of appropriate treatment levels is unknown. This design allows us to capture the maximum variation in the response variable of interest.

In total, 60 experimental units (60 seedlings) were used in the experiment (3 species × 2 light filters × 10 water-table depths). Therefore, this experiment included two main treatments: (a) drought alone treatment with 10 water-table depths ranging from 2 to 20 cm in 2 cm intervals under clear light filter and (b) combined effects of drought and shade using the same 10 water-table depths under green light filters. These water-table depths were maintained throughout the experiment by adding water to the containers when necessary. After the acclimatization period for the seedlings to capillary watering, the experiment began on June 28, 2023. Due to initial size differences among species, *Quercus*, *Castanea*, and *Fagus* were harvested after 48, 55, and 61 days of treatment, respectively.

2.2 | Measurements

Each container housed a single seedling in a pot. This approach had several advantages. Firstly, it prevented the seedlings from shading each other. Secondly, it allowed for the easy harvesting of the entire root system from each pot. We maintained 45 cm distance between containers to prevent green light filters from shading control treatment units. Thirdly, this arrangement also facilitated the separate scanning of each seedling using a crane mounted LiDAR system. For each LiDAR scan event, we removed the light filters allowing un-obstructed views of the experimental plants. The resulting 3D point data were used to estimate relative changes in height and upper crown volume of each individual throughout the experiment.

We used a capacitive soil moisture sensor (SoilWatch 10) at the harvest to detect soil moisture at a 10-cm depth in *Castanea* and *Fagus* seedlings (Supporting Information Appendix Table A1). These sensors were not used during the experiment to prevent damage to the root systems of the living seedlings.

2.3 | Growth Performance Traits

At the beginning of the experiment and at harvest, net assimilation (A_{net}, μmol of CO_2 $m^{-2}s^{-1}$), and transpiration (E, mmol $m^{-2}s^{-1}$) were measured at midday with LI-6800 with a fluorometer chamber. Instantaneous water use efficiency (WUE_i) was calculated as the ratio of A_{net} to E. Moreover, stomatal conductance and fluorescence of all individuals were monitored each week using LI-600 Porometer/Fluorometer by measuring two leaves per seedling. At the harvest, leaf turgor lost point (π_{TLP}, MPa) values of selected individuals were estimated using the vapor pressure osmometer method (Bartlett et al. 2012) as it can be used as a drought resistance indicator (Álvarez-Cansino et al. 2022).

Specific leaf area (SLA, $mm^2 g^{-1}$) and specific root length SRL ($mg\,mm^{-3}$) were measured in surviving individuals to represent the resource-acquisition strategies of plants. For SLA measurements, six fully grown leaf samples per individual were scanned using a portable leaf area meter and weighed after oven-drying (Pérez-Harguindeguy et al. 2013). SRL was calculated using these formulas: $SRL = 4/(\pi \times r^2 \times RTD)$ and RTD = Dry mass/volume (Freschet et al. 2021). Per individual, six samples of fine roots were scanned using a flatbed scanner. RhizoVisionExplorer v.2.0.3 software was used to compute variables from root images and to calculate SRL (retrieved from https://www.rhizovision.com). We also calculated leaf, stem, and root mass fractions (LMF, SMF, and RMF in $g\,g^{-1}$) in all individuals to analyze plant biomass allocation patterns (Poorter and Sack 2012).

At the whole-plant level, we calculated total biomass at harvest. Moreover, relative growth rate (RGR) of seedlings was calculated based on the relative change in height (cm) and crown volume (cm^3) from the start of the experiment to the harvest using 3D point data from LiDAR.

2.4 | Data Analyses

2.4.1 | Point Cloud Processing

We analyzed point cloud data from LiDAR to detect relative changes in seedling height and crown volume and calculated the relative growth rate (RGR) as a measure of growth performance (research question 1). This method allows a non-destructive way to quantify relative growth changes and account for initial size (crown volume) differences in the experiment when analyzing trait data using a fixed effects model.

Raw point cloud data gathered from different directions in the greenhouse were cleaned with the Statistical Outlier Removal (SOR) tool in CloudCompare software (v.2.13.2, http://www.cloudcompare.org). Later, each individual seedling was detected and analyzed using a combination of point cloud processing and voxel-based analysis (cf. modified from Dietrich et al. (2025)). That is, point data were voxelized at a resolution of 3 mm, and the crown volume was estimated as the product of voxel count and voxel size. We thereby estimated the RGR of seedlings at multiple time points in the experiment. RGR was calculated as the difference between the initial size and the size at the end of the experiment, divided by the number of days until the harvest. Therefore, RGR based on crown volume = (Volume Final − Volume Initial)/days and RGR based on height = (Height Final − Height Initial)/days.

2.4.2 | Fixed-Effects Model

The presence of shade changes how sensitive the seedling is to the drought. To explore such an interactive effect of drought and shade, we compared the slopes under drought versus drought and shade. A significant change in slope under drought and shade compared to drought treatment would indicate the interactive effect. Therefore, we examined slope divergences in a regression-based gradient framework.

We used a fixed-effects model for a direct interpretation of species-specific responses and the interaction of drought and shade while accounting for the effect of plant initial size:

$$Y \sim \text{Water} \times \text{Light} \times \text{Species} + \text{Initial size}$$

where Y = trait value, Initial size = initial crown volume calculated by LiDAR, Water = different water-table depths representing the drought stress, and Species = three study species. These models were fitted into the complete dataset ($N = 60$, df = 48). For RGR based on height and crown volume, the same model was used without the effect of initial size as this factor was already accounted for while calculating RGR.

2.4.3 | Correlation Analyses

To examine the relationships between biomass allocation, resource acquisition traits, and growth performance (research question 1), we used Spearman's rank correlation analysis, as it is effective for non-normally distributed continuous data and relatively robust to outliers. Pairwise correlation matrices were constructed, showing correlation coefficients between every pair of selected traits (RGR, biomass at harvest, SLA, SRL, LMF, RMF) in several data subsets (excluding the highest water level, where the soil volumetric water content equals the soil field capacity). In total, six matrices were constructed for (a) *Quercus* under drought, (b) *Quercus* under drought & shade, (c) *Fagus* under drought, (d) *Fagus* under drought & shade, (e) *Castanea* under drought, and (f) *Castanea* under drought & shade.

2.4.4 | Standardized Major Axis (SMA)

We used the Standardized Major Axis (SMA) bivariate line-fitting method to examine different theoretical frameworks on plant biomass (Figure 1 and research questions 2 and 3). The first question can be tested using the SMA line-fitting method by applying the slope test for 0.75 in leaf versus stem and root, and the slope test for 1.0 in stem versus root. The second question can also be tested with SMA by comparing slopes in shoot versus root under drought versus the combined effect of drought and shade. If slopes are not different, the effects can be additive (no slope interaction). The third question can be analyzed by comparing the magnitudes of the slopes. If the shoot versus root slope increases under the combined effect of drought and shade relative to drought alone, the result would support the facilitation hypothesis, as shade may have mitigated the drought effects. A lower slope would support the trade-off hypothesis.

We used the sma function in the "SMATR" package to fit bivariate lines and construct confidence intervals for the true slope (Warton et al. 2012). We also tested robustness using Huber's M estimation method which provides robustness to outliers in slope estimation. Specifically, slope.test function was used (y, x, data, log = "xy," method = "SMA," slope.test = 0.75, robust = T, type = "shift") between leaf versus root and leaf versus stem. Similarly, slope test = 1.0 was applied for stem versus root. Later,

allometric exponents (slopes), confidence intervals, and *p*-values were extracted to detect biomass allocation patterns across species and treatments.

3 | Results

3.1 | Biomass Allocation–Resource Acquisition–Growth Interplay

Ten water levels (water-table depths) inside containers of Drought and Shade Modulator "DaSMod" effectively generated a gradient of decreasing soil moisture as indicated by soil volumetric content and leaf turgor loss point (π_{TLP}) values (Supporting Information Appendix Tables A1 and A2). At the end of the experiment, 40 of 60 individuals survived (based on electron transport rate $>0.4\,\mu$mol electrons $m^{-2}s^{-1}$). Mortality rates were 30%–35% in each species. Mortality in *Quercus* and *Castanea* occurred primarily at the lowest water levels (3–5–7 cm), independent of being under clear or green light filter (Supporting Information Appendix Figure A1). Crown volume at harvest (cm^3) calculated from point cloud data from LiDAR was highly correlated with aboveground biomass at harvest in surviving individuals (Supporting Information Appendix Figure A2). Therefore, crown volume at the beginning of the experiment can be used as a good predictor of initial above ground biomass.

Growth performance traits, such as biomass at harvest and relative growth rate (RGR) calculated using crown volume (cm^3/day) and height (cm/day) were decreased under drought and the combined effects of drought and shade, except for *Fagus* (Figure 3 and Supporting Information Appendix Table A3). When only surviving individuals were analyzed, we observed a typical shade avoidance response as mean height and SLA were greater under green light filters compared to clear light filters (Supporting Information Appendix Table A4). Mean instantaneous water use efficiency (WUE_i) at the end of the experiment

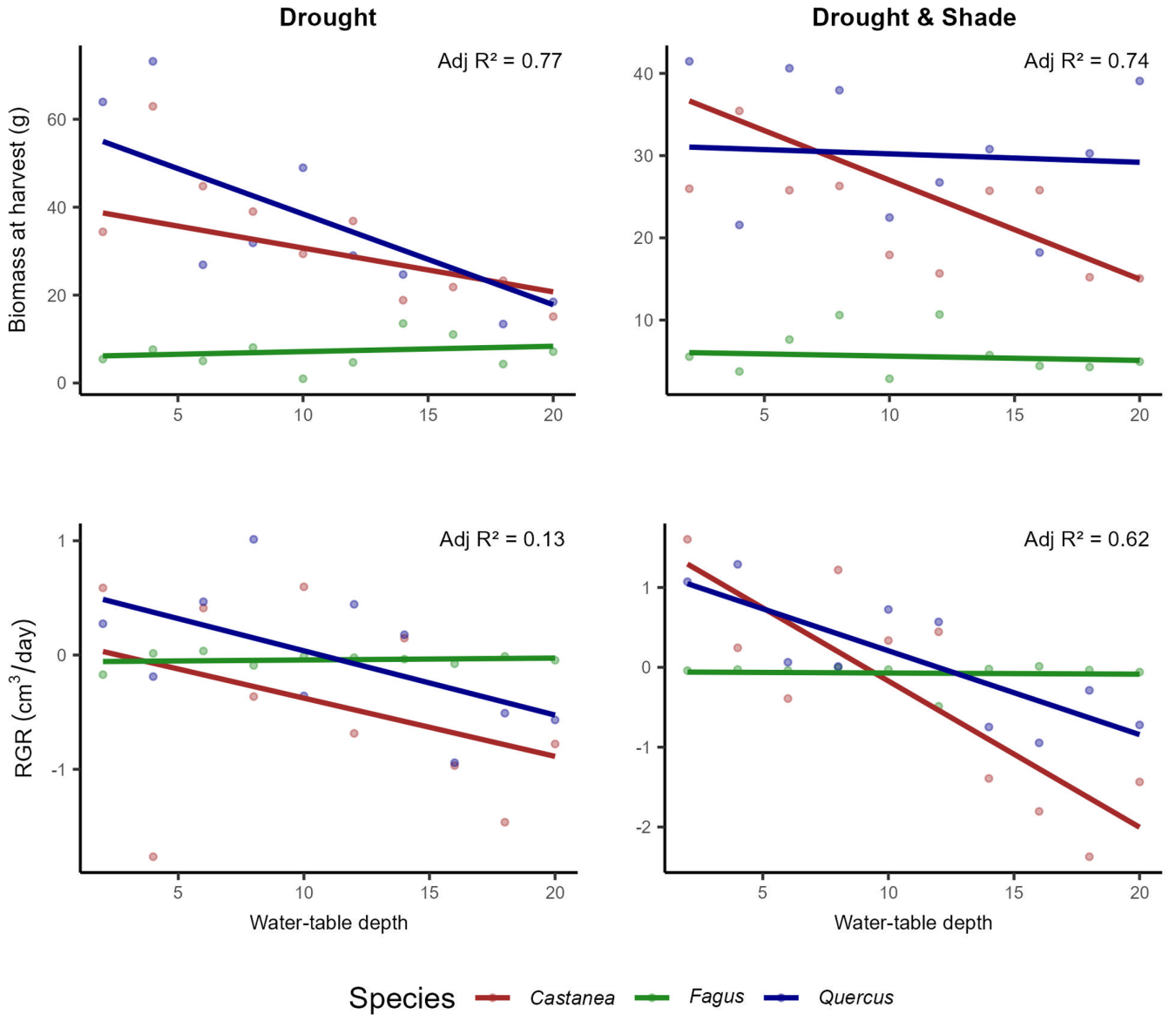

FIGURE 3 | Biomass at harvest (g) and relative growth rate (RGR) calculated by crown volume (cm^3/day) in response to drought (left panel) and to combined effects of drought & shade (right panel) for three species. Species-specific lines were derived from fixed-effects linear models.

was lower in *Fagus* and *Quercus* under drought and shade compared to drought treatment (Supporting Information Appendix Figure A3). Reduced WUE_i stemmed from higher transpiration rates, larger SLA, and lower VPD (more humid air) under shade (Supporting Information Appendix Table A4). That is, plants produced larger and thinner leaves while keeping stomata open as they could afford to lose more water while maximizing photosynthesis (increased A_{net}).

Species-specific fitted slope values were detected based on the fixed-effect model (Supporting Information Appendix Table A3). Responses of *Quercus* and *Castanea* mainly showed negative slopes, indicating significant treatment effects, whereas *Fagus* was the least affected species probably due to its small initial size (Figure 3). In *Quercus*, the slope in relative growth rate based on height change (RGR – Height) was relatively stable—such a conservative response may be in accordance with a drought-tolerant strategy (Supporting Information Appendix Table A3). The model explained only a very limited proportion of the variance in stem and root mass fractions. Overall, drought- and shade-induced changes in growth and biomass fractions were species-specific.

Correlation analysis of biomass allocation, resource acquisition and growth traits revealed distinct patterns of trait coordination across species and treatments (Figure 4). Across all three species,

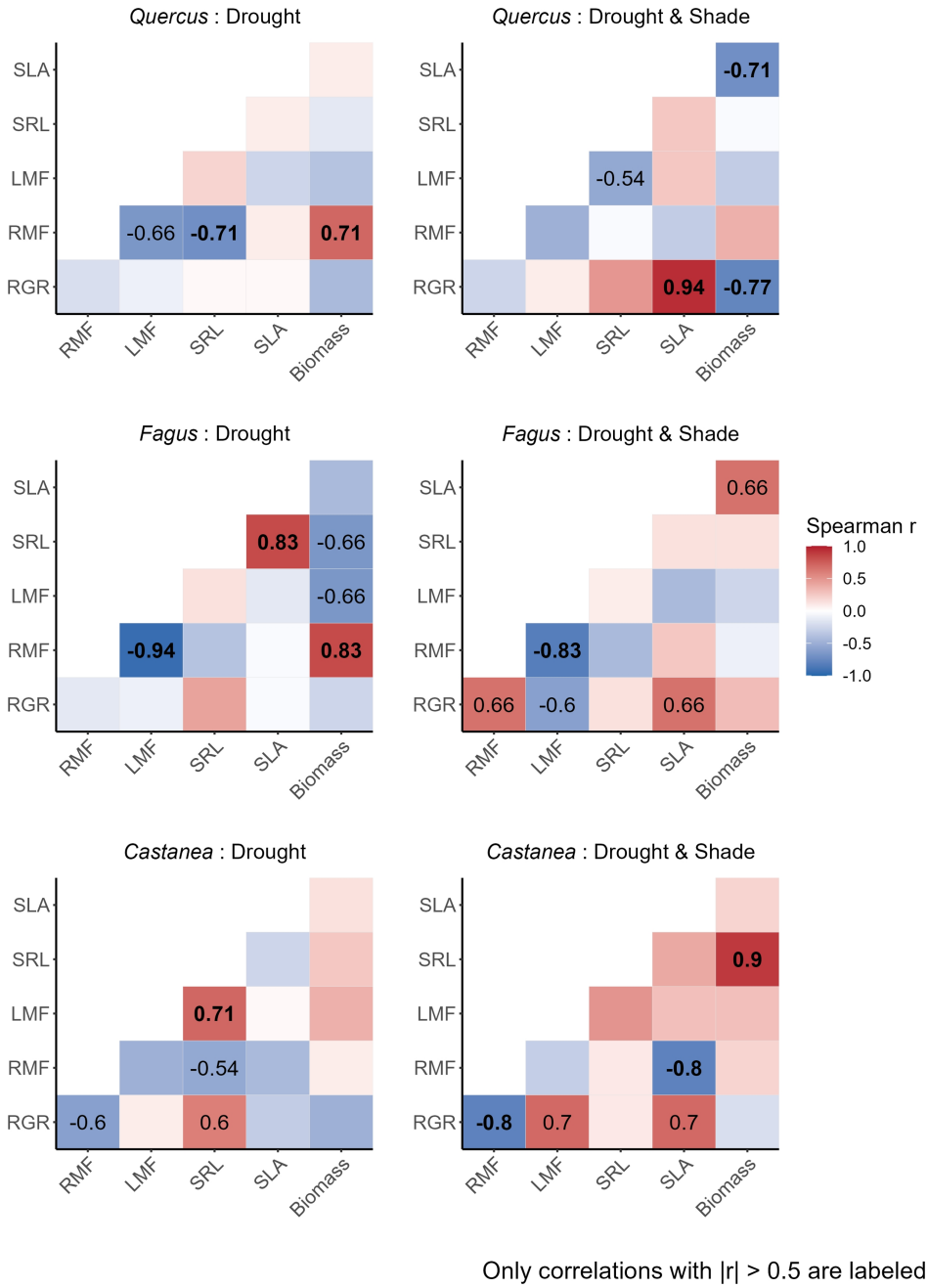

FIGURE 4 | Spearman correlation coefficients between biomass allocation, resource acquisition traits and growth for surviving seedlings. LMF, leaf mass fraction; RGR, relative growth rate based on crown volume (cm^3/day); RMF, root mass fraction; SLA, specific leaf area; SRL, specific root length.

correlations between relative growth rate (RGR) and specific leaf area (SLA) were significantly positive under the combined effects of drought and shade (Figure 4). However, high SLA was negatively correlated with total biomass in drought-tolerant *Quercus*, whereas in shade-tolerant Fagus, it was positively correlated with biomass. In *Quercus*, drought treatment was characterized by strong positive correlations between biomass and root mass fraction (RMF), indicating that root allocation was tightly coupled with growth performance. Resource acquisition traits such as SLA and specific root length (SRL) showed weak associations with growth under drought. By contrast, under combined drought and shade, RGR was tightly coupled with SLA and moderately with SRL, while biomass was negatively correlated with both RGR and SLA (Figure 4). This shift suggests a transition toward resource acquisition efficiency as a compensatory mechanism under the combined stress of drought and shade, but at the expense of total biomass accumulation.

Shade-tolerant *Fagus* showed the most substantial trait divergence across treatments. Under drought, biomass was strongly driven by RMF but was negatively correlated with SLA and SRL. This suggests that root allocation supports biomass accumulation, albeit at the expense of resource acquisition efficiency. An extreme negative correlation between RMF and LMF further highlights a strong trade-off between root and leaf allocation under drought stress. Under combined drought and shade, RGR became positively associated with both RMF and SLA, and biomass showed moderate positive correlations with SLA. However, strong negative correlations between RMF and LMF persisted (Figure 4). In *Castanea*, trait correlations were more stable across treatments. Under drought alone, RGR was positively associated with SRL, and biomass showed moderate positive correlations with both LMF and SRL, reflecting a balanced reliance on fine-root traits and leaf allocation. SLA was only weakly related to growth, indicating limited importance under drought-only conditions. Under the combined effects of drought and shade, *Castanea* maintained strong root–biomass linkages, with SRL highly correlated with biomass. At the same time, RGR became positively associated with both LMF and SLA (Figure 4), suggesting that shade introduced additional reliance on resource acquisition and leaf allocation to sustain growth.

3.2 | APT Versus OPT

Results of allometric analysis of three species, using a Standardized Major Axis (SMA) bivariate line-fitting method, under drought alone and drought & shade treatments indicated that the null hypothesis (APT) was not rejected nor supported due to large confidence intervals around slope estimates (Table 1). Only under drought and shade, leaf mass versus stem in *Castanea* shifted significantly from the expected APT slope and supported OPT ($p = 0.04$).

3.3 | Trade-Off Versus Facilitation

To address the third research question, SMA regression between aboveground and belowground biomass was performed. A significantly higher or lower slope between aboveground versus belowground biomass under combined effects of drought and shade compared to drought alone treatment support the facilitation or trade-off hypothesis, respectively. If the slopes are statistically not different, drought and shade does not interact and

TABLE 1 | Results of Standardized Major Axis (SMA) slope tests to test for Allometric Partitioning Theory (APT) and Optimal Partitioning Theory (OPT).

Species and treatment	Leaf vs. root: Slope test for 0.75	Leaf vs. stem: Slope test for 0.75	Stem vs. root: Slope test for 1.0
Quercus under Drought	Slope: 0.77 CI: 0.44–1.32 *p*-value: 0.93	Slope: 1.22 CI: 0.70–2.13 *p*-value: 0.07	Slope: 0.77 CI: 0.53–1.12 *p*-value: 0.14
Quercus under Drought & Shade	Slope: 0.89 CI: 0.46–1.70 *p*-value: 0.56	Slope: 0.69 CI: 0.44–1.09 *p*-value: 0.56	Slope: 1.25 CI: 0.65–2.42 *p*-value: 0.45
Fagus under Drought	Slope: 0.63 CI: 0.30–1.34 *p*-value: 0.60	Slope: 0.99 CI: 0.37–2.60 *p*-value: 0.53	Slope: 0.82 CI: 0.47–1.42 *p*-value: 0.39
Fagus under Drought & Shade	Slope: 1.09 CI: 0.57–2.08 *p*-value: 0.21	Slope: 0.79 CI: 0.46–1.34 *p*-value: 0.84	Slope: 1.15 CI: 0.72–1.84 *p*-value: 0.49
Castanea under Drought	Slope: 1.08 CI: 0.51–2.29 *p*-value: 0.29	Slope: 1.16 CI: 0.60–2.26 *p*-value: 0.17	Slope: 0.88 CI: 0.45–1.73 *p*-value: 0.67
Castanea under Drought & Shade	Slope: 0.84 CI: 0.38–1.88 *p*-value: 0.73	Slope: 1.38 CI: 0.77–2.46 *p*-value: **0.04**	Slope: 0.74 CI: 0.32–1.74 *p*-value: 0.43

Note: CI represents lower and upper limits of confidence intervals. Mean slope estimates and CIs were calculated using robust line fitting with Huber's M estimation. Bold *p*-value indicates a significant difference in the slope test.

TABLE 2 | Results of Standardized Major Axis (SMA) slope tests to compare biomass allocation to aboveground and belowground under drought and combined effects of drought and shade.

Species and treatment	Leaf + stem vs. root
Quercus under Drought	Slope: 0.78 CI: 0.59–1.03
Quercus under Drought & Shade	Slope: 1.01 CI: 0.51–2.02
Fagus under Drought	Slope: 0.73 CI: 0.42–1.25
Fagus under Drought & Shade	Slope: 1.00 CI: 0.65–1.54
Castanea under Drought	Slope: 0.96 CI: 0.53–1.73
Castanea under Drought & Shade	Slope: 0.74 CI: 0.34–1.65

Note: CI represents lower and upper limits of confidence intervals. Mean slope estimates and CIs were calculated using robust line fitting with Huber's M estimation.

results support uncoupled hypothesis. Due to large confidence intervals around slope estimates, results remained inconclusive (Table 2).

4 | Discussion

Species-level responses to drought and the combined effects of drought and shade diverged strongly, reflecting potential allocation trade-offs and adaptive shifts in the plant's economic spectrum. Drought-tolerant *Quercus* exhibited strong coupling of root mass fraction (RMF) with biomass under drought but weak correlations between growth and acquisitive traits (e.g., SLA and SRL which are often used to identify acquisitive strategies). However, under combined effects of drought and shade, *Quercus* shifted its strategy toward resource acquisition, as shown by higher correlations between relative growth rate (RGR) based on crown volume, SLA, and SRL. However, this shift came at the cost of reduced total biomass which might be due to increases in tissue maintenance costs under combined effect of drought and shade. Under drought, relative growth rate of shade-tolerant *Fagus* was positively correlated with SRL. Under the combined effects of drought and shade, relative growth rate of *Fagus* was positively correlated with SLA and RMF. In contrast, *Castanea* exhibited a more balanced strategy: even under stress, it maintained strong associations between fine-root traits (SRL) and leaf allocation (LMF) and biomass, reflecting stability without extreme shifts in root versus shoot allometry.

Species-specific trait coordination modes may control how traits interact to maintain growth under combined stresses. *Quercus* prioritizes root allocation under drought, *Fagus* relies on high SLA under shade, while *Castanea* integrates allocation and resource acquisition flexibly depending on the environment. In general, SRL is more labile and rapidly responsive, while RMF is more conservative/structurally constrained. Negative correlations between SRL (thinner and longer roots) and RMF in three species suggest an acquisitive strategy that boosts soil exploration efficiency while saving carbon allocation to roots. When biomass allocation to roots is limited due to limited C-assimilation from shade, seedlings may compensate via morphological traits (e.g., higher SRL or SLA). Especially, SLA was positively correlated with RGR under the combined effects of drought and shade. Such a response would be adaptive under stress.

Plant biomass allocation responses to drought should reflect drought tolerance, with drought-tolerant species showing the least reduction in plant biomass when drought occurs. Drought-tolerant species often display higher RMF than drought-intolerant species (Puglielli et al. 2021). Here, mean RMF values in *Quercus* exceeded those in *Castanea* but remained lower than in shade-tolerant *Fagus* (Supporting Information Appendix Table A3). Moreover, a very small change in relative growth rate (RGR) based on crown volume in *Quercus* across treatments suggests an adaptive and conservative response to increasing drought stress. *Quercus* seedlings expressed positive correlations between RGR and resource-acquisition traits (although a greater replication is needed to confirm statistically significant correlations). Therefore, maximizing resource acquisition (fast end of economics spectrum) might explain such drought-driven vegetation shifts in *Quercus*. Although shade-tolerant and drought-intolerant species are expected to be very sensitive to dry conditions (Holmgren et al. 2012), *Fagus* seedlings expressed an adaptive response, and high SLA might have allowed persistence across the stress gradient. In accordance with a global synthesis on biomass allocation (Puglielli et al. 2021), shade-tolerant *Fagus* exhibited a lower mean LMF than shade-intolerant deciduous broadleaf species.

In this study, biomass allocation patterns in drought-tolerant *Quercus* and shade-tolerant *Fagus* partially supported APT and the facilitation hypothesis according to SMA slope tests. That is, broad-scale allometric predictions (i.e., ¾ power scaling between leaves and roots or stems) held under stress. *Castanea* supported OPT and the trade-off hypothesis (Tables 1 and 2). Juvenile and mature plants may exhibit different allocation patterns, with mature individuals often adhering to APT, while younger plants may align more closely with OPT (Smith-Martin et al. 2020). However, tree seedlings and saplings might also express these fixed allometric scaling relationships (Enquist et al. 2007). In our study, APT was mainly supported even in the seedling stage of tree species. Thus, basic allometric relationships (APT) may set the stage as a baseline "null" expectation, species-specific deviations (e.g., OPT) may reveal how plants may prioritize resources or coordinate allocation to maximize survival under complex environmental stresses.

Our results suggest that OPT might align closely with the trade-off hypothesis, both predicting resource-driven shifts in biomass allocation, such as increased root allocation during drought. Although APT does not inherently predict resource-driven shifts, it may align with the facilitation hypothesis where allocation remains consistent with size-based scaling relationships. As shade by green light filters can reduce drought effects (e.g., lower vapor pressure deficit in this study), individuals may not deviate from expected allometric relationships under the combined effects of drought and shade (Figure 1). In scenarios

where effects of drought or shade act independently on plants (uncoupled hypothesis), plant responses may align with OPT in case treatments indeed force individuals to deviate from expected allometric relationships (Enquist et al. 2007).

Several methodological limitations should be acknowledged when interpreting the results of this experiment, particularly due to differences in initial plant size and the limited replication within the two main treatments (drought alone and combined effects of drought and shade). To account for initial size differences across species (e.g., 2-year-old and 1-year-old seedlings), we used 3D point data from LiDAR to track aboveground growth during the experiment and included initial size as a covariate in the model while analyzing species responses. Using a gradient design without replications reduced the generalization of our findings on SMA regression due to wide confidence intervals resulting from low sample size ($n = 6$–7 surviving individuals per species in drought and in combined effects of drought and shade) and highly variable individual seedling responses. Therefore, slope tests in SMA regression neither rejected nor supported the null hypothesis regarding APT. Despite these limitations, simulated drought and shade treatments significantly decreased survival, biomass, and relative growth rates (Supporting Information Appendix Table A3).

Our findings suggest that APT, OPT, trade-off, facilitation, and uncoupled hypotheses can be linked as in the decision chart (Figure 1) and tested with the bivariate line-fitting method (Tables 1 and 2). The new experimental design, Drought and Shade Modulator "DaSMod," can be used to examine individual seedling responses to different scenarios of simulated drought and shade. Understanding how drought and shade interact to shape the growth and biomass allocation of seedlings is a key challenge as climate change continues to impact plant communities (e.g., drought events or increased canopy). Examining species-specific responses of European temperate forest species to various drought and shade scenarios can refine predictions about the regeneration potential of these species under climate change and may guide managers' decisions on species selection for reforestation and management practices (e.g., matching species to local light–moisture regimes or managing canopy cover to optimize survival and growth).

In conclusion, while the current findings offer valuable preliminary insights, they remain ambiguous whether the observed plant responses to concurrent light and water limitations follow the APT or OPT due to limited sample size and high individual variability. Therefore, further validation from empirical studies with larger sample sizes is needed. Drought-tolerant *Quercus*, shade-tolerant *Fagus*, and *Castanea* with moderate tolerance to shade and drought expressed distinct biomass allocation strategies and were positioned differently in trait correlations. These contrasting strategies underscore the importance of incorporating both trait variation and environment-specific covariance among traits into models of seedling establishment and forest regeneration under climate change.

Author Contributions

Fatih Fazlioglu: conceptualization (lead), data curation (lead), formal analysis (lead), methodology (lead), project administration (lead), visualization (lead), writing – original draft (lead), writing – review and editing (lead). **Steven Higgins:** conceptualization (supporting), data curation (supporting), formal analysis (supporting), funding acquisition (lead), methodology (supporting), project administration (supporting), resources (lead), visualization (supporting), writing – original draft (supporting), writing – review and editing (supporting).

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data gathered and analyzed in this study are included in the Appendix. Dataset, R, and Python codes are included as Supplementary files.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Dataset. **Data S2:** Python codes. **Data S3:** R codes. **Supporting Information Appendix Figure A1:** Photographs taken during the experiment. Panel (a) shows the acclimatization period for capillary watering in April 2023. Panel (b) shows the experimental design—Drought and Shade Modulator "DaSMod" in July 2023. Panel (c) shows some dead *Quercus* individuals at the harvest in August 2023. **Supporting Information Appendix Figure A2:** Crown volume at harvest (cm^3) calculated by point cloud data from LiDAR versus aboveground biomass in surviving individuals. **Supporting Information Appendix Table A1:** Soil moisture measurements of *Castanea sativa* and *Fagus sylvatica* at the harvest. **Supporting Information Appendix Table A2:** Leaf turgor loss point (π_{TLP}) values of selected individuals. These individuals were selected to represent low-medium-high water levels under clear and green light filters. **Supporting Information Appendix Table A3:** Species-specific mean slopes with *p*-values indicating if slopes are significantly different from zero (if water stress has significant effect). **Supporting Information Appendix Table A4:** Trait mean ± SE values of surviving individuals under drought and combined effects of drought & shade ($N = 6–7$ per species and treatment). Relative growth rate (RGR) was calculated using change in height and crown volume. A_{net}, net assimilation; E, transpiration rate; VPDleaf, vapor pressure deficit at leaf temperature. **Supporting Information Appendix Figure A3:** Instantaneous water use efficiency (WUE_i) of all seedlings at the harvest. $WUE_i = A_{net}/E$. Gray lines inside boxplots represent the median (the 50th percentile) and black dots represent mean values. Green dots represent individual data.