

**Functional fingerprinting estimates renewal opportunities for tree species in a
mixed Turkey oak forest**

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Abstract: Maintaining and managing trees with different ecological plasticity under climate conditions aggravated by short-term variability are major challenges for foresters. Our aims were to investigate species-specific ecophysiological responses of canopy trees in a mixed Turkey oak forest during their early-phase regeneration. We measured plant carbon and water exchange with portable IRGA equipment under natural field conditions (canopy gap) and in a climate-controlled (standardized) environment. We analyzed variability and differences in plant gas exchange in relation to important abiotic site parameters and the species as factors. Assimilation, stomatal conductance, and intrinsic water use were applied as calibrating parameters for plant functional fingerprinting to detect carbon-to-water response performance of the saplings. The most favorable water economy during summer and seasonal maximum in carbon uptake during fall evolved as common response characteristics of the species in canopy gaps. Sessile oak (*Quercus petraea*) was found to be a water-regulated species due to the highest relative ratio of intrinsic water-use efficiency. In contrast, Turkey oak (*Q. cerris*) and manna ash (*Fraxinus ornus*) were identified as carbon-driven species presenting a gradual increase in assimilation during their seasonal dynamics. Consequently, we can predict a delayed regeneration of sessile oak and progressive growth of manna ash and Turkey oak in the renewing canopy compared to the initial forest stand. European hornbeam (*Carpinus betulus*) and wild service tree (*Sorbus torminalis*) certainly remain accessory elements due to their unfavorable carbon input ratio and poor water use economy. Explored knowledge on carbon-to-water response behavior of these forest-forming trees can provide a novel contribution to afforestation practices in adaptive forest management.

Key words: Carbon sequestration, canopy gap regeneration, mixed forest trees, functional fingerprinting, water use

1. Introduction

Tree regeneration in mixed deciduous forests is a current research challenge in terms of species performance, environmental heterogeneity, and their interactions both from theoretical and management aspects (Löf et al., 2018; Pach et al., 2018). Highly diversified renewal was detected in oak-dominated stands, especially during the early stage forest regeneration (Tinya et al., 2020). As a result, the species composition of post-renewal forest gaps can differ significantly from the intact canopy (Taylor and Lorimer, 2003). For these reasons, detailed studies are essential to reveal species-related characteristics of gap-phase regeneration considering the ecological response of the saplings (Di Filippo et al., 2010; Zhu et al., 2014; Kollár, 2017; Sebastiano et al., 2017; Elek et al., 2018; Löf et al., 2018; Tinya et al., 2020).

Depending on their resilience capacity, trees can tolerate environmental variability during their regeneration (Göttmark and Kiffer, 2014; Elek et al., 2018). Canopy gaps generally support plant renewal, as demonstrated by certain regeneration parameters such as abundance, density, or growth of individuals (Zhu et al., 2014). Renewal parameters of the saplings in small-to-medium canopy gaps in oak forests were primarily related to the level of illumination, with increased light intensity positively affecting growth and shoot thickness (Březina and Dobrovolný, 2011; Zhu et al., 2014; Kollár, 2017). This positive effect is particularly large at the initial stage of the gap when the area is at the maximum (Zhu et al., 2014; Tinya et al., 2020). The relative ratio between light intensity (i.e. low to high illumination) and plant functional trade-offs

may also be important for biomass production (Purina et al., 2015; Salamon-Albert et al., 2018). Reduction in water availability due to elevated temperature and high light intensity can induce contradictory and species-specific responses in carbon allocation and hydraulic properties (Gortan et al., 2009; Petit et al., 2016; Kiorapostolou and Petit, 2018). Depending on the biological properties of the plants, restricted growth or decreased abundance can be detected during regeneration despite favorable environmental conditions (Březina and Dobrovolný, 2011; Saniga et al., 2014), (Martínez-Vilalta et al., 2002; Ďurkovič et al., 2013; Thomas, 2017; Bednorz and Nowinska, 2018).

Next, we overview the most important previous findings on light-induced and moisture-related behavior of canopy tree species coexisting in a mixed Turkey oak forest. Under environmental water deficit, the regeneration of sessile oak (*Quercus petraea* (Matt.) Liebl.) is poor, demonstrating decreased carbon assimilation and conductivity (Bréda et al., 1993; Epron and Dreyer, 1993; Březina and Dobrovolný, 2011). Turkey oak (*Q. cerris* L.) is a light-reactive plant with an increased growth rate and moderate drought tolerance. Saplings of this species can reduce their growth and water output by down-regulating the stomatal conductance (Tognetti et al., 2007; Deligöz and Bayar, 2018). Manna ash (*Fraxinus ornus* L.) is a light-reactive species with an increased growth rate and drought flexibility supported by morphological and physiological features (Kalapos and Csontos, 2003; Gortan et al., 2008; Petit et al., 2016; Kiorapostolou and Petit, 2018). European hornbeam (*Carpinus betulus* L.) is a shade-tolerant tree that prefers longer yet moderate irradiation that promotes successful regeneration, even under a closed canopy (Boratyński, 1996; Sikkema et al., 2016; Salamon-Albert et al., 2018). The response of wild service tree (*Sorbus torminalis* (L.) Crantz) is variable; high

irradiation causes rapid early growth, while low irradiation can lead to long-term persistence in the seedling bank. Severe drought can cause xylem embolism in this species (Martínez-Vilalta et al., 2002; Rasmussen, 2007; Nicolescu et al., 2009; Pyttel et al., 2013; Thomas, 2017).

The aim of this study was to evaluate carbon-, and water exchange performance of canopy tree saplings considering species-specific ecophysiological drivers during the early-phase forest regeneration. We analyzed plant responses by using two measurement approaches, field canopy gap (target) and standardized experimental (reference) climate with their site-specific conditions. We evaluated 1) plant gas exchange variability, especially related to the relative importance of abiotic site factors and interspecific heterogeneity; (2) we selected the most susceptible gas exchange parameters to point out characteristics and differences in saplings responses; and (3) we constructed functional fingerprinting to present the carbon-to-water economy of the study species at their renewing process under canopy gap conditions. In summary, we estimate and discuss the carbon and water exchange-related regenerative opportunities of the trees and their consequences for the canopy composition.

2. Materials and methods

2.1. Experimental sites

To study plant carbon and water exchange behavior, we measured tree responses both in forest canopy gaps under variable field conditions as well as under climate-controlled and standardized greenhouse environments. The semi-dry mixed forest stand was located in a hilly landscape in mid-western Hungary near Zánka (N46°52'40.5" E17°39'24.7"). This community formed a moderately sparse (65-75% cover) canopy

with a co-dominance of Turkey oak and sessile oak (*Fraxino orno-Quercetum cerridis* Kevey et Sonnevend 2008) in the upper canopy and manna ash sparsely mixed with European hornbeam and wild service tree in the lower canopy (Kevey, 2008). The climate at his site is seasonally variable, with low annual precipitation (660 mm), moderate air humidity (74%), and a high annual mean temperature (12°C). The thin soil horizon (cambisol) was acidic brown forest soil with Permian sandstone parent material. At this site, we created three canopy gaps that contained the focal species and had ecologically comparable environmental parameters (Table 1). These artificial gaps were small (157, 188 and 198 m²), had no exposure, and had a medium to high level of total light availability throughout the day. Surface plant cover was medium (55-60%) in these locations, containing mainly regrowth individuals of canopy trees and some forest undergrowth. The regenerative abundance of the study species was the highest for *Q. cerris*, followed by *F. ornus*, *Q. petraea*, *C. betulus*, and *S. torminalis*.

We used an outdoor greenhouse at the Botanical Garden of University of Pécs (N 46° 4' 39.6" E 18° 12' 25.69") to grow the experimental plants for standardized measures. The mean temperature values were 11.8, 22.6, and 12.8 °C with 282, 117, and 170 mm of precipitation in the spring (April to May), summer (June to August), and fall (September to October), respectively. The 2-to-4-year-old saplings had been collected in a Turkey oak forest and were planted in 18×18×18 cm containers filled with soil:peat:sand mixture at a 6:2:2 ratio to optimize water retention and permeability of the planting medium. Plants received natural rainfall and were also watered twice a week using 5 liters of water for each container to prevent desiccation. Prolonged-release nutritional supplement (Osmocote Complete; 20 g per container) was provided once a year in March, prior to the growing period (April to October). Light conditions were

similar to those in the experimental canopy gaps; plants were exposed to total irradiation for half of the day.

2.2. Sampling design and gas exchange measurements

We measured gas exchange in the forest canopy gaps and in the experimental containers during the growing period (May to October) in 2013-2014. We selected saplings for measurements that 1) were located in a typical canopy gap environment, 2) were in the same developmental stage, and 3) had intact and typical shoots with healthy leaves undamaged by animals or other factors. We measured fully expanded and mature leaves of seasonally developed shoots from 3-5 saplings per site. These saplings were 3-4 years in age and met the requirements listed above. We recorded the species-related gas exchange and location-specific microclimate data in the canopy gaps (Table 1). Using the standardized measurement approach, we collected 60 records per response under climate-controlled conditions.

We measured plant gas exchange from mid-May to early June (spring), from the end of July to early August (summer), and from late September to early October (fall). We used open system portable LCA-2 (for instantaneous data) and LCA Pro+ (for climate-controlled data) IRGA equipment (ADC BioScientific Ltd., United Kingdom). We recorded carbon dioxide input and water vapor output rates, which are independent from each other, but are synergistic via a shared stomatal pathway (Field et al., 1991). These measurement systems operate within the detection range of Photosynthetic Photon Flux Density (PPFD; 0-3000 $\mu\text{mol m}^{-2} \text{s}^{-1}$), air and leaf temperature (T, 0–50 °C), air carbon dioxide (C_a , 0-2000 ppm), and relative air humidity (RH, %). In the field experiment, the above-mentioned instantaneous climate parameters were also recorded near the focal plants. For measurements in the climate-controlled plot, parameters were gradually

changed as 0-2000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD (irradiation), 20 °C, 25 °C, 30 °C (leaf temperature), 12 mBar (air humidity), and 370 ppm (carbon-dioxide), according to our standardized measurement protocol. To increase measurement reliability, we recorded the data within the total range of irradiation in the canopy gaps as well as under the standardized conditions. To increase the detection accuracy of gas exchange rates, we conducted measurements from sunrise until the midday depression, when the plants were not exposed to significant abiotic stress. We calculated net assimilation (A , $\mu\text{mol CO}_2 \text{m}^{-2} \text{s}^{-1}$) as the degree of carbon input, transpiration (E , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) referring to water loss, and stomatal conductance (g_s , $\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$) that indicates relative level of gas exchange. Additionally, we calculated photosynthetic ($\text{pWUE} = A/E$) and intrinsic ($\text{iWUE} = A/g_s$) water-use efficiency to estimate plant carbon-to-water economy.

2.3. Data processing and statistical analyses

Focusing on instantaneous and standardized data, we established non-linear response curves for the experimental data by using a first-order exponential decay algorithm (Equation 1).

$$y = y_0 + A_1 \times e^{(-x/t_1)}, \quad (1)$$

where, y_0 is the offset as the upper limit of the function, i.e., the maximum rate of the parameter, A_1 is the amplitude as the lower limit of function, i.e., the minimum rate of the parameter, and t_1 is the decay constant, i.e. the inflection point of the response curve. To validate the statistical adequacy of the curve fitting, we calculated the adjusted chi-square-related probability (p). We defined the threshold point between light-dependent (low-irradiated) and light-saturated (high-irradiated) ranges, resulting in two functional subsets. We calculated species gas-exchange rates both for the canopy gaps and climate-

controlled datasets in the three functional light ranges as total, light-dependent, and light-saturated. Considering the standardized gas exchange responses, we used datasets recorded at seasonal temperatures relevant to the canopy gap environment: 15°C and 20°C in spring and fall, and 25°C and 30°C in summer. We employed the Origin 6.1 program (OriginLab Corporation, USA) to fit curves and calculate the light-response ranges. We used the Statistica 12.6 program (Dell Technologies Inc., USA) to estimate the variability in gas exchange responses related to the site parameters, i.e. measurement conditions, light intensity, seasonal variation, and the differences between the study species. We applied the Kruskal-Wallis test as a non-parametric analysis at $P < 0.05$ probability level. Finally, we constructed plant functional fingerprints by utilizing the carbon and water response patterns of the species under canopy gap conditions.

3. Results

3.1. Gas exchange variability and site conditions

We focused on three site parameters to evaluate their relative importance in gas exchange performance of the study species both in canopy gaps and under climate-controlled conditions (Table 2). Regarding the total irradiation, we detected the highest variability in assimilation, photosynthetic, and intrinsic water use efficiency based on the light response ranges. Large seasonal differences were found in transpiration and stomatal conductance of tree species as well as in gas exchange functions under light-dependent and light-saturated conditions. Comparing tree species responses, the largest variability in carbon uptake, stomatal conductance, and intrinsic water use efficiency were observed both at low and high irradiation. Saplings also differed in their photosynthetic water use efficiency in canopy gaps, with large seasonal variation under

standardized conditions. In conclusion, species-related stomatal conductance, intrinsic water use efficiency, and carbon uptake along the light response ranges seemed to be the most important for further analyses.

3.2. Plant responses under contrasting environments

Here we present and compare species responses under field and standardized conditions along the functional light ranges and the seasons, using the three important gas exchange parameters indicated in the previous section (Figure 1). Saplings generally showed higher assimilation under standardized climate compared to field conditions. In contrast, Turkey oak and manna ash showed equal or higher carbon input rate in canopy gaps than under climate-controlled conditions during fall. Stomatal conductance proved to be the most differentiating parameter between the two measurement environments. In general, species presented significantly lower levels of this parameter in canopy gaps compared to those under the standardized climate. In contrast, European hornbeam, manna ash, and wild service tree showed increased and season- or irradiation-dependent conductivity in canopy gaps. Regarding the intrinsic water use efficiency, tree saplings presented significantly lower values in canopy gaps than under standardized conditions. A particularly high level of water use was detected in canopy gaps in the case of Turkey oak during summer and fall at both low and high irradiation, and for sessile oak under all conditions.

3.3. Functional fingerprinting for carbon-to-water economy

We developed the functional response patterns of the species to illustrate their in-situ (canopy gap-related) performance by using the three responsive gas exchange parameters (Figure 2). Under total irradiation, carbon input increased continuously along the seasons, with the exception of sessile oak, which had a summer maximum, and wild

service tree, which had a summer minimum. The relative ratio of this function was high for the two oak species and manna ash, and low for hornbeam and wild service tree. Stomatal conductance also increased along the seasons, presenting a spring minimum and a fall maximum. In general, the relative ratio of this function was high for wild service tree, medium for Turkey oak and manna ash, and low for hornbeam. Distinctly, the wild service tree presented a summer minimum in this parameter. Intrinsic water use efficiency generally displayed summer maximum with different relative levels for each species. The highest relative ratio was detected in sessile oak, followed by Turkey oak and manna ash. European hornbeam and wild service tree presented permanently depressed intrinsic water use efficiency.

Analyzing plant responses under low (light-dependent) and high (light-saturated) irradiation, carbon sequestration increased from spring to fall for most species. Persistently high assimilation rates were detected in Turkey oak and manna ash in both functional light ranges. Sessile oak presented moderate carbon sequestration with a continuous increase under light-saturated conditions. European hornbeam presented a medium to low level of carbon uptake, and wild service tree had a particularly low assimilation ratio with opposite seasonal trends in the two light ranges. In general, stomatal conductance increased from spring to fall in European hornbeam, which was the opposite of the wild service tree with its significant summer decline. Wild service tree and manna ash presented a high level of stomatal conductance, while this ratio was medium for the oak species and low for hornbeam. Intrinsic water use efficiency varied to a large degree depending on the light response ranges and the species. Sessile oak showed a persistently high ratio and a declining trend from spring to fall, while hornbeam was characterized by a medium level and summer maximum. Turkey oak and

mannan ash presented a summer maximum with a wide ratio range at low irradiation. The wild service tree showed opposite trends in parameter dynamics even in the two functional light ranges.

4. Discussion

Presently, one of the most intensively studied topics in forest science, improved silviculture requires species-specific and resilience-based knowledge on trees (Elek et al., 2018; Löf et al., 2018; Tinya et al., 2020). In oak-dominated mixed forests, structural changes with variable growth intensity have been detected among or within the vertical layers (Taylor and Lorimer, 2003; Löf et al., 2018; Tinya et al., 2020). Considering plant response strategies, ecological plasticity and resistance to disturbance may regulate the process and success of regeneration (Göttmark and Kiffer, 2014; Saniga et al., 2014). In our study, we developed plant functional fingerprints as an analytical tool to characterize tree regeneration dynamics based on their carbon-to-water economy under canopy gap conditions. Below we discuss species-specific functional drivers and limitations and estimate canopy changes for subsequent forest succession.

Oak species are reported to exhibit different or even contrasting water and carbon use patterns related to their biological features and physiological plasticity (Tognetti et al., 2007; Deligöz and Bayar, 2018), which affects their spatiotemporal growth during regeneration (Taylor and Lorimer, 2003; Tinya et al., 2020). Nevertheless, functional coordination of water vapor output and carbon input can further enhance growth success of *Quercus* species (Tognetti et al., 2018) beyond the theoretical considerations of stomatal behavior. Among our study species, sessile oak has the highest ecological and economical value (Bobiec et al., 2018). As a light-demanding species, sessile oak grows dynamically and abundantly under spatially and temporally heterogeneous light

conditions (Taylor and Lorimer, 2003; Březina and Dobrovolný, 2011; Saniga et al., 2014); however, low-to-medium irradiation were found to be optimal for regeneration density (Březina and Dobrovolný, 2011). In our study, medium carbon uptake and low stomatal conductance led to the most efficient intrinsic water use. Based on these findings, balanced and mixed illumination can be considered the most favorable for sessile oak. These results reinforce the importance of the position-induced light environment in canopy gaps for sufficient regeneration of this species (Březina and Dobrovolný, 2011). Sessile oak also showed water-driven renewal performance, aiming to maintain its water economy at the cost of carbon sequestration. Due to the high stomatal down-regulation of sessile oak, the relative biomass and abundance of this species may decline more than in other stand-forming trees in native forest stands (Taylor and Lorimer, 2003; Di Filippo et al., 2010; Göttmark and Kiffer, 2014; Saniga et al., 2014). For Turkey oak, stomatal conductance has been reported to be high under drought stress, resulting in a less effective water economy (Tognetti et al., 2007; Deligöz and Bayar, 2018). In our experiment, this species showed moderate stomatal conductance, increased carbon assimilation, and medium level water-use efficiency. These response functions may result in more extensive growth and abundance in canopy gaps, similar to those found in the Mediterranean populations (Tognetti et al., 2007). As Turkey oak can utilize less than 60% of incident light energy for photochemical electron transport (Valentini et al., 1995), increased irradiation seems to be essential for its successful regeneration. This species can be considered both water and carbon driven, with high functional plasticity. This allows the species to be temporarily successful in forest stands with sparse canopies and under variable humidity conditions (Danielewicz et al., 2016), and even despite the high ratio of non-photochemical energy dissipation

(Valentini et al., 1995). Manna ash, mentioned as smaller trees and shrubs in the lower vertical layers, presents intensive growth during colonization around the open and disturbed areas (Caudullo and de Rigo, 2016). This tree had the most favorable carbon input among the study species, definitely confirming the early phase regeneration success (Tinya et al., 2020). Unexpectedly, medium-high conductivity results in seasonally balanced and moderate water use in the canopy gaps; this may be a functional consequence of high water storage capacity of root branches (Caudullo and de Rigo, 2016). Manna ash saplings were successful in carbon input both in ecologically limited (summer) and accumulation-related (fall) periods. Due to the hydraulic properties of the species and its carbon economy associated with the xylem safety (Petit et al., 2016; Kiorapostolou and Petit, 2018), responsive gas exchange functions lead to a high regenerative ability. Manna ash was found to be a carbon-driven species, especially during the second half of the growing period, providing the opportunity for rapid biomass increase within the renewing canopy. European hornbeam had the lowest gas exchange rates with progressive dynamics in carbon assimilation and stomatal conductance resulting in a seasonally balanced water economy. Since the regeneration of hornbeam saplings is stimulated by low-level and diffused irradiation, and their biomass production can be increased under short-duration and high light intensity (Purina et al., 2015), temporally variable photon flux density could be optimal for renewal. Beyond the direct effects of local climate, ecological trade-offs can further constrain in-situ regeneration of this species (Salamon-Albert et al., 2018). European hornbeam was found to be a mainly water-driven species with medium-to-low responsive functions. Limited carbon input negatively affects the short-term biomass increase of the saplings in canopy gaps (Purina et al., 2015; Salamon-Albert et al.,

2018). While the shade tolerance of wild service tree has been reported to be variable (Maděra et al., 2013; Welk et al., 2016), individuals easily colonize well-illuminated areas (Thomas, 2017). For this species, we found low-moderate assimilation and extremely high stomatal conductance, with the lowest intrinsic water use efficiency. This response phenomenon may be explained by drought tolerance (Welk et al., 2016; Thomas, 2017) coupled with the high carbon and water storage capacity of root suckers (Schüte, 2001), which is especially promoted by the local groundwater excess in canopy gaps (Muscolo et al., 2014). Since xylem embolism can occur in *S. torminalis* (Martínez-Vilalta et al., 2002), individuals can optimize water use by increasing water input and transpiration. In our experiment, wild service tree exhibited a carbon-driven regeneration strategy with persistently low carbon uptake and water utilization. These functional traits generate low population density (scattered individuals) in forest stands (Hemery et al., 2009) and maintain the species as a constant vegetation component at both the landscape and community levels (Hemery et al., 2010; Maděra et al., 2012, 2013; Duda and Całka, 2013; Bednorz and Nowinska, 2018).

Conclusions

A functional response approach for tree regeneration can provide a novel interpretation of stem-wise dynamics in young mixed stands. Species-specific results are very important in tree-oriented silviculture, especially in the case of multispecies and highly diverse Turkey oak forests. We found different functional regeneration dynamics in water-driven (sessile oak), mixed (Turkey oak), and carbon-driven (manna ash) stand-forming trees as well as some additional species under persistent functional constraints (hornbeam and wild service tree). Saplings must encounter adequate abiotic conditions

within the microenvironments of a canopy gap. In addition, a small-sized opening can provide natural renewal options for a limited number of individuals. Exhibited plant functions and site characteristics can explain the slow and protracted regeneration process in semi-dry oak forests. Consequently, forest managers and practitioners should aim to find sites with optimal abiotic conditions for the trees during afforestation. Detailed knowledge about the species-specific carbon exchange and water economy can make early-phase regeneration more predictable.

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Table 1. Climate conditions with ¹regional climatic data and ²microclimatic ranges during the measurement period of 2013-2014 (section 1); number of sampling plots (N) and measurement data record (n) for study species (section 2) in the canopy gaps

Climate variable/species	Spring (May-Jun)	Summer (Jul-Aug)	Fall (Sept-Oct)
¹ Temperature (mean; °C)	11.6	22.4	11.8
¹ Precipitation (sum; mm)	180	213	74
¹ Relative air humidity (mean; %)	72	62	76
² Photon flux density ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	0 - 2999	0 - 2465	0 - 2355
² Leaf temperature (°C)	14.6 - 31.3	21.4 - 37.3	12.6 - 32.0
² Carbon-dioxide (ppm)	318 - 410	319 - 388	353 - 412
² Relative air humidity (%)	13.5 - 48.1	10.4 - 36.0	16.3 - 45.3
<i>Quercus petraea</i> (N = 7)	n = 257	n = 231	n = 333
<i>Quercus cerris</i> (N = 7)	n = 219	n = 225	n = 321
<i>Fraxinus ornus</i> (N = 7)	n = 196	n = 263	n = 202
<i>Carpinus betulus</i> (N = 5)	n = 387	n = 175	n = 281
<i>Sorbus torminalis</i> (N = 3)	n = 197	n = 207	n = 169

Table 2. Variability in gas exchange (A to iWUE) under canopy gap (GAP) and standardized (STD) climate conditions and the light response ranges (total to light-saturated) by site parameters. PPFD = photosynthetic photon flux density (df = 1), SPEC = species (df = 4), SEAS = seasons (df = 2). H values from Kruskal-Wallis test, ***P < 0.001, **P < 0.01, *P < 0.05, ns = non-significant, -- = invalid case.

Gas exchange	Site parameter	Total light		Light-dependent		Light-saturated	
		GAP	STD	GAP	STD	GAP	STD
A	PPFD	***1817.49	***2757.78	--	--	--	--
	SPEC	***341.67	***167.50	***94.80	***22.40	***836.94	***663.46
	SEAS	***251.40	***85.98	**10.80	***18.21	***1108.45	***157.37
E	PPFD	***687.54	***459.82	--	--	--	--
	SPEC	***613.75	***538.54	***302.75	***307.69	***648.37	***351.35
	SEAS	***1576.82	***1046.95	***619.38	***465.09	***1556.07	***761.56
pWUE	PPFD	***2005.24	***1995.45	--	--	--	--
	SPEC	***359.92	***76.20	***120.32	*13.16	***622.98	***97.75
	SEAS	***153.23	***762.50	*8.22	***59.39	***483.68	***1316.26
gs	PPFD	***636.68	***588.94	--	--	--	--
	SPEC	***1164.90	***1032.98	***422.33	***548.35	***979.73	***819.98
	SEAS	***952.43	***180.31	***345.88	99.25	***935.27	***135.59
iWUE	PPFD	***2057.92	***2154.36	--	--	--	--
	SPEC	***523.83	***342.66	***102.41	***33.24	***1038.30	***633.31
	SEAS	***76.97	***33.75	***27.82	ns 0.63	***475.51	***78.85

Figure 1. Gas exchange dynamics of study species under canopy gap (color symbols) and standardized (black symbols) conditions along the light response ranges (total to light-saturated) and the seasons (spring to fall). (a-c) assimilation (A), (d-f) stomatal conductance (gs), (g-i) intrinsic water use efficiency (iWUE). Mean \pm 0.95 confidence interval, *p<0.05; **p<0.01; ***p<0.001; ns = non-significant. Responsive cases are indicated with colored asterisks.

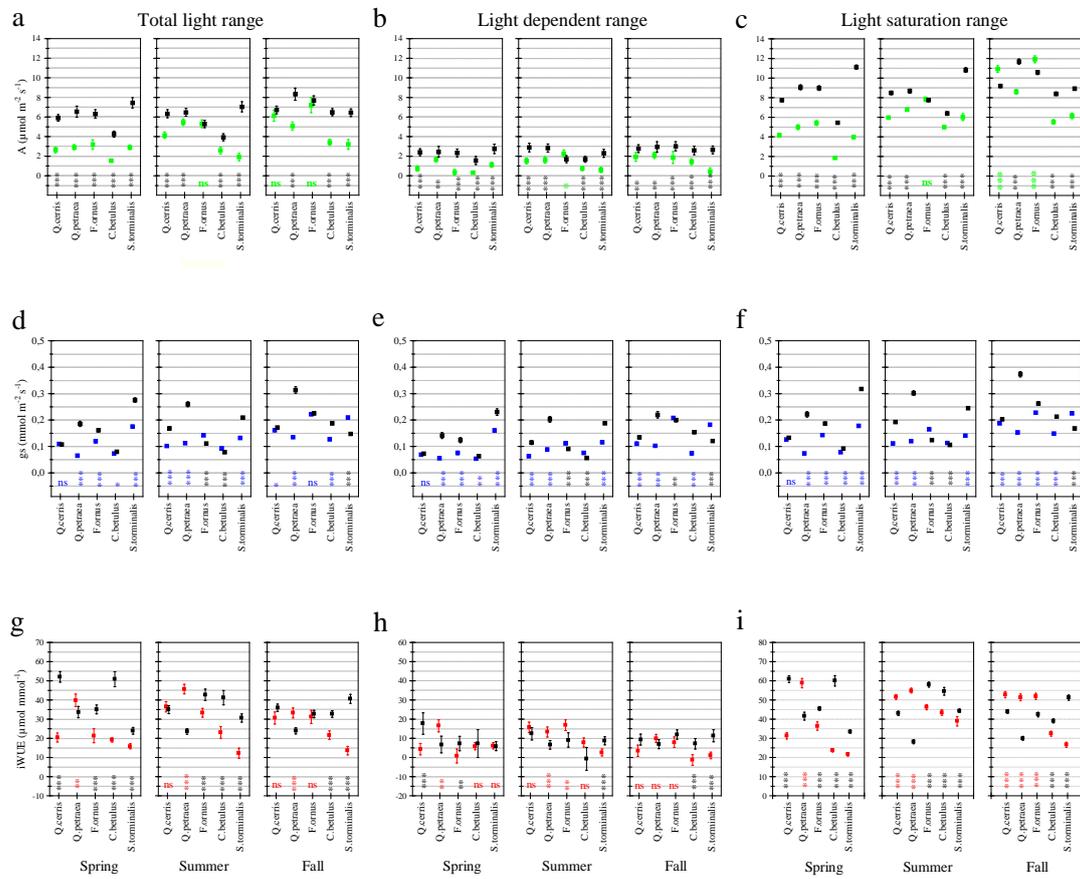


Figure 2. Functional fingerprints of the study species in canopy gaps along the light response ranges (total to light saturated) with assimilation (green), stomatal conductance (blue) and intrinsic water use efficiency (red). Relative gas exchange refers to standardized mean considering all cases of the given parameter.

