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ORIGINAL ARTICLE

Field patterns of temporal variations in the light environment within the crowns of a Mediterranean evergreen tree (*Olea europaea*)

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Abstract

Key message **There are specific diurnal light variation patterns and negligible seasonal variation within tree crowns. Crown-mediated regulation of temporal light regimes can be important for whole plant function in Mediterranean evergreens.**

Abstract The light environment within a tree crown can be characterized by specific variation patterns arising from the structural features of the crown. Within-crown light variation patterns can be important for plant productivity, but this has yet to be assessed in natural settings. The spatio-temporal variations of direct and diffuse photosynthetic photon flux density (PPFD), their proportions and sunfleck frequency within the crowns of isolated adult wild olive trees (*Olea europaea* L.) were investigated. Trees growing in contrasting Mediterranean conditions (continental vs. coastal) at the same latitude were compared. Instantaneous diffuse and total PPFD were measured with sunshine sensors in three crown layers (outer-, middle- and inner-crown) in the south-facing part of the crown, at two points of the diurnal (mid-morning and midday) and seasonal (summer and winter) cycles. Direct PPFD and the proportion of direct to total PPFD vary diurnally within the crown as a result of an increase in sunfleck frequency during midday and in self-shading during mid-morning, in both summer and winter conditions. Conversely, the lack of seasonal variation in the three light attributes is better explained by a greater average crown transmittance in winter conditions. The interplay between crown architecture heterogeneity and varying solar position renders identifiable patterns of temporal variations in the light environment within tree crowns. These patterns suggest that trees can benefit from the light heterogeneity typical of Mediterranean environments by developing conservative architectural layouts.

Keywords Mediterranean evergreen trees · Direct and diffuse PAR · Sunflecks · Crown transmittance · Spatio-temporal light variation · Within-crown diurnal and seasonal light variation · *Olea europaea*

Introduction

Light interception by tree crowns alters some characteristics of the light transmitted to deeper crown layers and to the understory. The crown modifies the proportion of directional fractions of light. Leaves and branches intercept sunrays increasing the proportion of diffuse radiation and reducing the proportion of direct radiation inside the crown (Suzaki et al. 2003; Combes et al. 2007). The intensity of both radiation fractions decreases towards the interior of the crowns (Uemura et al. 2006; Valladares and Niinemets 2008; Larbi et al. 2015), while direct PAR usually has a greater extinction coefficient (Urban et al. 2007). Transient

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pulses of direct light of variable intensity (i.e., sunflecks sensu Chazdon and Pearcy 1991, but see Smith and Berry 2013) appear within the crown at different moments and positions (Roden and Pearcy 1993). These light modifications are relevant to plant function, since leaf light absorption differs under direct or diffuse PAR (Brodersen et al. 2008). Additionally, sunflecks can affect light use because light use efficiency at the tree level is greater under diffuse PAR (Roderick et al. 2001; Urban et al. 2007; Mercado et al. 2009) and multiple morphological and physiological traits acclimate to the light intensity gradients (Walcroft et al. 2002; Valladares and Niinemets 2008; Posada et al. 2009; García-Verdugo et al. 2010; Larbi et al. 2015). Consequently, both overall carbon gain and the temporal dynamics of photosynthetic responses (i.e., steady-state vs. non-equilibrium photosynthesis) are affected by sunfleck regimes (Pfitsch and Pearcy 1989; Pearcy et al. 1994; Way and Pearcy 2012).

The interaction between the tree crown and the incoming radiation leads to spatial heterogeneity across the crown (i.e., intra-canopy light gradients; Sack et al. 2006). However, due to the apparent motion of the sun, the spatial heterogeneity in the light environment across the tree crown is highly variable over time. The incident photosynthetic photon flux density (PPFD) and the directional fractions of light vary diurnally and seasonally, especially at mid-latitudes. As a consequence, isolated trees intercept light coming from a wide range of solar elevations and azimuth directions and forage for light in preferential directions during the growing season (Bazzaz 1991; Valladares and Pearcy 1998). This determines the heterogeneous architectures of adult tree crowns (i.e., non-random foliage distribution), both horizontally and vertically, affecting diurnal and seasonal light interception patterns (Baldocchi and Collineau 1994; Sarlikioti et al. 2011). As a result, the light environment within the tree crown is shaped by the interaction between solar trajectory and crown architecture if complex topography, neighboring trees, clouds, wind and other fine scale factors do not interfere (Myneni and Impens 1985; Chazdon et al. 1988).

The existence of specific light interception strategies suggests that the light environment within the crown can also have specific variation patterns arising from the structural features of the crown. In other words, tree crowns have the potential to modify the temporal distribution of light within the crown (Myneni and Impens 1985; Roden and Pearcy 1993; Baldocchi and Collineau 1994; Sarlikioti et al. 2011). Temporal variations in the within-crown light gradient have rarely been addressed in ecological and eco-physiological studies in the field. This is surprising since the spatio-temporal heterogeneity of light within the tree crown elicits the expression of distinct leaf attributes linked to plant performance, thus contributing to the total net photosynthesis of the crown (Gratani et al. 2006; Niinemets and Anten 2009; Granado-Yela et al. 2011; Way and Pearcy 2012). To gain insights into temporal light variation patterns within the crown, above- and within-crown light measurements over time are required (e.g., Génard and Baret 1994; Suzaki et al. 2003; Granado-Yela et al. 2011) including other time-related variables, such as diurnal changes in solar elevation and azimuth angles (Brantley and Young 2009; Ishii et al. 2012).

In the Mediterranean region, temporal heterogeneity in light conditions is particularly important for plant function. In summer, irradiance peaks occur concomitantly with high temperatures and low water availability at midday. These conditions may entail photoinhibition risk of the most exposed leaves of the crown (Tenhunen et al. 1981; Werner et al. 2001). Plasticity-mediated adjustments in the size or angle of sun leaves may control both their own exposure (Valladares and Pugnaire 1999; Larbi et al. 2015) and the environment experienced by shade leaves (Sack et al. 2006; Rubio de Casas et al. 2011; Granado-Yela et al. 2011). Structural avoidance of midday irradiance can be more critical than light interception enhancement of sun leaves (Valladares and Pearcy 1998; Valladares and Pugnaire 1999; Falster and Westoby 2003; Granado-Yela et al. 2011). This may increase the penetration of direct irradiance during midday (Uemura et al. 2006) maximizing light interception, and therefore self-shading, during the morning (Granado-Yela et al. 2011). In static-leaved plant models (i.e., models that do not incorporate leaf solar-tracking movements and leaf shedding), light interception efficiency can change seasonally as a result of changes in solar angles (Sarlikioti et al. 2011). Mediterranean evergreen trees use a conservative light interception strategy throughout the year, which may contribute to buffering seasonal variation in the within-crown light environment (Granado-Yela et al. 2011; Rubio de Casas et al. 2011; Larbi et al. 2015).

Our main goal was to determine the patterns of variation of some biologically relevant characteristics of light (i.e., PPFD, the proportion of directional fractions and sunfleck frequency) within the crown. We chose isolated, adult trees of *Olea europaea* growing in two natural populations at the same latitude in Spain. This species has orthotropic sun leaves that show midday irradiance avoidance syndrome and plagiotropic shade leaves (Granado-Yela et al. 2011). We measured instantaneous total and diffuse PAR with sunshine sensors in three crown layers (outer-, middle- and inner-crown) during two periods of the day (mid-morning and midday), in 2 months (July and February) representing extreme yearly changes in the solar incidence angle. We posed the following hypotheses:

1. Light attributes change diurnally within the crown. As incident light is maximum during midday (Md) on cloudless days, we expect that direct PPFD, the proportion of direct to total PAR and sunfleck frequency are greater during Md than during mid-morning (Mm) within the crown. We tested this hypothesis by comparing these light attributes between periods of the day.
2. Direct PAR transmittance is enhanced during Md and diffuse PAR transmittance is enhanced during Mm. We expect that any temporal change in the light attributes is related to changes in crown transmittance. To test this hypothesis, we assessed crown transmittance (%) to direct and diffuse PAR in both periods of the day considered.
3. Extreme seasonal changes in the solar elevation angle do not result in light condition changes within the crown. For this purpose, we compared the three light attributes and crown transmittance between the time points considered.

Methods

Study species and populations

The wild olive tree (*O. europaea* L.) is a sclerophyllous evergreen species that occupies a wide variety of Mediterranean environments (Green and Wickens 1989; Granado-Yela et al. 2013). Adult trees of this species display sun and shade phenotypic syndromes in the same plant (Rubio de Casas et al. 2011; Granado-Yela et al. 2011). Sun leaves are orthotropic, shade leaves are plagiotropic and both sun and shade leaves are static (i.e., they do not track the apparent motion of the sun; Granado-Yela et al. 2011). The vegetative growth season is during spring (March–May) and leaves are fully expanded by July (García-Verdugo et al. 2010). Leaf life-span ranges from 1 to 3 years, without a clear leaf-shedding season (Diamantoglou and Mitrakos 1981; Gratani and Bombelli 2000a). To study comparable light environments, we used two natural wild olive populations located at the same latitude (i.e., with equivalent sun paths and day length) but differing in local environmental conditions (Tables 7 and 8 in Online Resource 1). Local conditions can play a role in leaf arrangement and crown structure, and therefore can influence light transmission throughout the crown (Valladares and Niinemets 2008). The Aldea del Fresno (AF) population grows in a continental Mediterranean climate in the central region of the Iberian Peninsula (Madrid, Spain) at 690 m.a.s.l. on a south-facing slope of ≈26°. At this location, minimal winter temperatures determine the thermal distribution limit for this species (Rubio de Casas et al. 2002; Granado-Yela et al. 2013). The San Luis (SL) population is located on a geographic island (Menorca, Balearic Islands, Spain) characterized by a coastal Mediterranean climate, at 50 m.a.s.l. on flat land (Table 1). To prevent shading from surrounding vegetation, we selected five isolated adult trees of similar size in each location. Individuals in AF were 3.48 ± 0.31 m high, with a maximum and minimum diameter of 6.75 ± 0.57 and 6.05 ± 0.53 m, respectively. In SL, they were 3.36 ± 0.21 m high, with a maximum and minimum diameter of 4.79 ± 0.25 and 4.43 ± 0.39 m, respectively. In AF the trees were growing on the same slope, and thus at equal aspects. The study was conducted on 27 July 2011 and 1 February 2012 in AF, and on 31 July 2011 and 23 February 2012 in SL. Climatic conditions during sampling were within the average normal values for both locations (Table 1, Tables 7 and 8 in Online Resource 1). Our objective was to capture spatio-temporal variation in light conditions across seasons. Therefore, we took all our measurements at two temporal points representing extreme yearly elevation angles. Specifically, we chose July and February because they provide adequate conditions to measure extreme solar elevation angles corresponding to summer and winter, respectively (≈65° at solar noon in July and ≈35° in February). Hereafter, we refer to the temporal windows in which measurements were taken as winter conditions (February) and summer conditions (July) and the temporal scale of variation will be referred to as season.

To investigate crown effects on both direct and diffuse PAR fractions in the absence of other sources of variation, sampling was performed on cloudless days to avoid the effects of clouds on the properties of the incident light. On overcast days, 100 % of incident light is diffuse, while partially cloudy days introduce huge spatio-temporal variability in both incident PPFD and in the proportion of directional fractions of light (Escobedo et al. 2009). Thus, these conditions were not desirable. Moreover, clear days are representative of the Mediterranean climate, with 2500–3000 annual hours of clear sky (Bolle 2003). Since wind strongly affects light penetration inside the crown (Roden and Pearcy 1993), sampling was performed under conditions of absent wind.

Light environment characterization

We characterized the light environment at three different crown layers: outer-, middle- and inner-crown layers, by measuring instantaneous total and diffuse photosynthetically active radiation (PAR) expressed as photosynthetic photon flux density (PPFD, µmol m^{-2} s^{-1}). All light measurements were performed using BF5 PAR sensors

Table 1 Coordinates, altitude and environmental variables for the two populations of *Olea europaea* during winter (February) and summer (July) sampling periods. Climate data were provided by the State Meteorological Agency of the Spanish 'Ministerio de Agricultura, Alimentación y Medio Ambiente; www.aemet.es)

Population	Location	Latitude	Longitude	Altitude (m.a.s.l.)	Year	Month	*T* (C°)	TM (C°)	Tm (C°)	*R* (mm)	*H* (%)	CD (days)	*I* (h)
AF	Aldea del Fresno	40°19′50″N	4°24′50″W	690	2012	February	6.1	9.7	2.6	37	71	8	148
	Madrid–Spain				2011	July	24.8	31.2	18.4	15	39	16	359
SL	San Luis	39°49′3″N	4°16′31″E	50	2012	February	10.7	14	7.5	59	77	3	148
	Menorca–Spain				2011	July	24.3	28.4	20.3	3	64	15	352

T mean temperature, *TM* average of the maximum temperatures, *Tm* average of the minimum temperatures, *R* total monthly rainfall, *H* mean relative humidity, *CD* number of cloudless days, *I* number of sunshine hours

(Delta-T Devices, Cambridge, UK) coupled with HOBO H22-001 dataloggers (Onset Computer Corp., Bourne, MA, USA). The BF5 sunshine sensor consists of seven photodiodes covered by an acrylic dome. A shading pattern within the dome allows measurement of diffuse irradiance without the need for an external shading ring. This is a desirable feature for measuring diffuse irradiance inside the crown (see Wood et al. 2003 for details). However, the BF5 sunshine sensor is a rather large device (120 mm × 122 mm × 95 mm). To avoid disturbance of measured irradiance by nearby leaves and branches, we carefully displaced any leaves and branches below the sampling point to make room for the sensor. For each instantaneous measurement, direct PAR was calculated according to Campbell and Norman (1998).

Experimental design

We measured light in the middle- and in the inner-crown layers of each tree in the southern crown sector along an imaginary diagonal transect inclined 45° from the horizontal, from the geometric centre of the crown to the outer-crown layer (Fig. 1). Since a southerly orientation is the most irradiated at the latitude of the studied populations, we assumed that the strongest across-crown differences in the light environment would be found in the southern sectors of the crowns. The distances between sampling points were proportional to crown thickness. In a preliminary study, we found that approximately 50 % of total irradiance was lost within the first 0.5–0.8 m of the crown (unpublished data). The middle-crown layer was defined at approximately 0.8 m and the inner-crown layer was the innermost layer of leaves. The distances between the outer- and the middle-crown layer were 0.94 ± 0.12 m in AF and 0.77 ± 0.13 m in SL ($p > 0.05$). Between the outer- and the inner-crown layer the distances were 1.61 ± 0.1 in AF and 1.28 ± 0.14 in SL ($p > 0.05$). García-Verdugo et al. (2010) found no significant variations in incident irradiance among wild olives in similar topographic conditions, either by direct measurements or by estimations from hemispheric photographs. Thus, we measured the incident irradiance at the outer-crown layer for all trees by placing a single sensor in an open site at each location.

To evaluate the diurnal irradiance variations, light measurements were taken at two different periods of the day representing contrasting irradiance conditions: mid-morning (Mm; approximately 1 h after sunrise, with a lower irradiance than midday) and midday (Md; i.e., the period of maximum irradiance that comprises solar noon). To account for seasonal differences in day length, we set each period at 2 h for summer and 1 h and 20 min for winter. Since high variability was expected within periods of the day and among individuals, elapsed time between periods of the day (i.e., between Mm and Md) was set to be equal to the duration of the sampling periods. By proceeding in this manner, we reasonably expected that all sequences of measurements were more similar within each period than between periods, even if variance among individuals and/or sequences of measurements was high.

Outer-crown irradiance was continuously logged every 2 s during each period of the day. We could not, however, permanently set the light sensors within the crown because the middle sensors would have shaded the inner sensors. Therefore, we placed one sensor in the middle-crown layer of one individual and logged irradiance every 2 s during a time interval of 20 s, obtaining a sequence of 10 instantaneous measurements per interval. We immediately removed the middle-crown sensor and a sensor placed in the inner-crown began logging for 20 s. We then proceeded equally in another wild olive, sampling all five individuals per population in a sequential fashion. To obtain representative measurements of each period of the day (i.e., accounting for changes in solar elevation angles) in the five individuals, we repeated this procedure five times at each

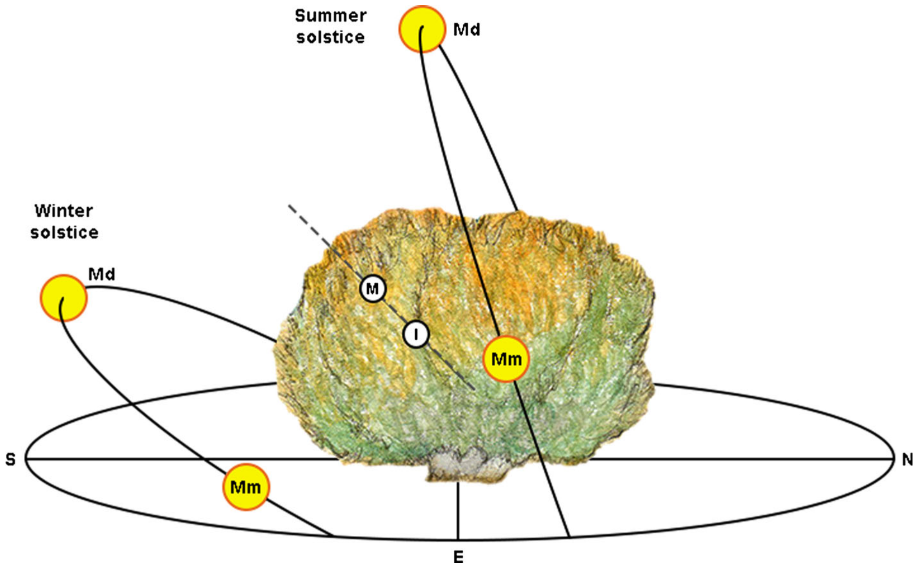

Fig. 1 Depiction of *Olea europaea* and the experimental design. Distribution of within-crown sampling points (*I* inner-crown layer, *M* middle-crown layer) along a diagonal transect (*dotted line*) in the southern crown sector. Solar trajectory in summer and winter solstices are shown. *Orange circles* represent approximate solar position during the sampled periods of the day, *Mm* mid-morning, *Md* midday. Compass directions relative to the tree are given. *E* East, *N* North, *S* South

period of the day (i.e., taking measurements for 20 s in all five individuals per population). Sampling all trees of each population during the same day was preferred over sampling the trees at the same hour on different days. This allowed us to ensure equal atmospheric conditions for all individuals and greatly simplified the field campaigns.

From these data, we extracted the contribution of direct to total PAR, the average and extreme direct and diffuse PPFD values, transmittance of direct and diffuse PAR and sunfleck frequency in each crown layer, period of the day and season in both populations.

Contribution of direct to total PAR

The contribution of direct to total PAR indicates the availability of this directional fraction relative to the total PAR available in each crown layer, period of the day and season. The percentage of total PAR not accounted for by the direct fraction corresponds to the diffuse fraction. For assessing the contribution of direct to total PAR, we obtained cumulative direct PAR for each sequence of instantaneous measurements and expressed it as a percentage of cumulative total PAR. We then averaged these values per period of the day, crown layer and season for each tree.

Direct and diffuse PPFD and crown transmittance

We calculated mean direct and diffuse PPFD per crown layer, period of the day and season by averaging instantaneous measurements over these factors. To identify whether any variation was accompanied by changes in extreme PPFD values we selected the maximum and minimum PPFD value measured per tree, crown layer, period of the day and season. Transmittance of directional fractions was calculated as the proportion of direct (or diffuse) PPFD reaching the middle- and inner-crown layers relative to incident direct (or diffuse) PPFD in the outer-crown, expressed in percentage. For estimating mean transmittance of direct and diffuse PAR per tree, crown layer, period of the day and season, we first averaged PPFD values for each sequence of instantaneous measurements and calculated transmittance for each sequence in the middle- and inner-crown layers. Finally, we averaged the transmittance values for each period of the day.

Frequencies of direct PPFD within the crown

We estimated sunfleck frequency per tree, crown layer, period of day and season from the raw instantaneous measurements of direct PAR. For this purpose, we classified the instantaneous measurements into classes above a given intensity by 100 µmol m^{-2} s^{-1}. For graphical purposes, we regressed the frequency of direct PPFD expressed in number of seconds against cumulative PPFD classes ordered by increasing intensity, in SigmaPlot 10.0 (Systat Software Inc. San José, CA, USA).

Statistical analyses

To test whether the light attributes differed diurnally, seasonally and across crown layers, we performed one-way Brunner–Dette–Munk (BDM) tests, a non-parametric test analogous to one-way ANOVAs. BDM allows for the estimation of a distribution-free statistic and the power is not reduced by small sample sizes (Brunner et al. 1997). We performed a separate analysis per factor. In every analysis, the dependent variable was treated as

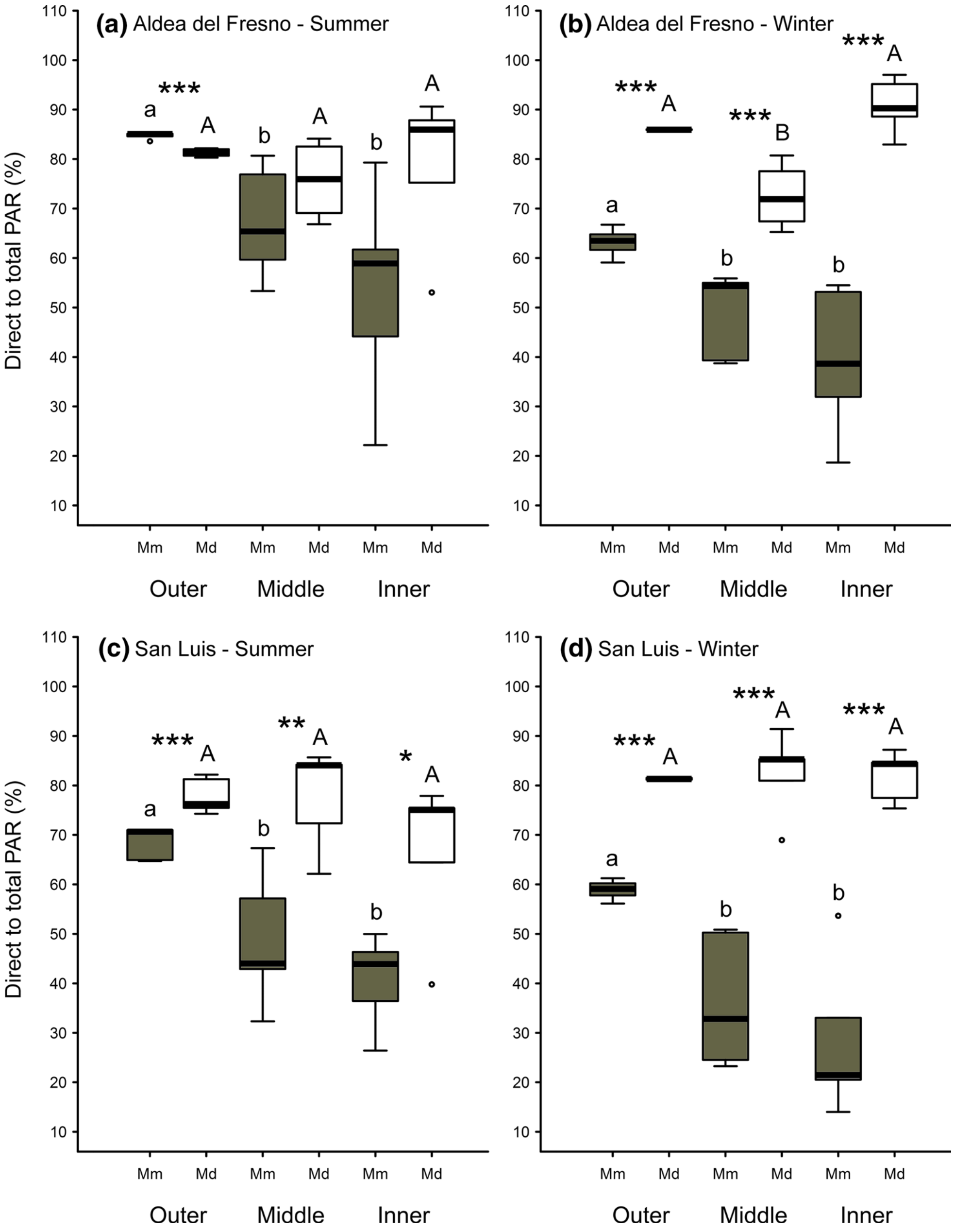

Fig. 2 Relative contribution of direct to total PAR in each crown layer and period of the day in Aldea del Fresno in summer (**a**) and winter conditions (**b**), and in San Luis in summer (**c**) and winter conditions (**d**). *Md* Midday, *Mm* mid-morning. *Boxes* represent data between the 25th and 75th percentile and whiskers the 5th and 95th percentiles. *Open circles* are outliers. *Lower-case letters* indicate contrasts between crown layers during Mm, *capital letters* indicate contrasts between crown layers during Md. *Asterisks* denote significant mean rank differences between periods of the day from BDM tests. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$. $N = 5$ trees

combinations of the levels of the remaining factors. For instance, when the factor was crown layer, four dependent variables were tested in four separate analyses: direct PAR in summer during Mm, direct PAR in winter during Mm, direct PAR in summer during Md and direct PAR in winter during Md. We performed all analyses with the BDM.test function of the asbio package (Aho 2015) in R v3.1.2 (R-Core Team 2014). In those analyses where the factor had more than two levels (i.e., crown layer), multiple comparisons were performed with the nparcomp function of the nparcomp package (Konietschke et al. 2015) in R. An *N* of five trees was used for all analyses. To assess whether direct and diffuse PAR had different transmittances, we performed BDM tests using the directional fraction as a factor. To investigate diurnal and seasonal patterns of changes in sunfleck frequency, we performed BDM contrasts for each intensity class. We plotted Figs. 2 and 3 with the Cairo package (Urbanek and Horner 2014) in R v3.1.2.

Results

Contribution of direct to total PAR

The crown affected the contribution of direct to total PAR differently during the two periods of the day (Fig. 2). In

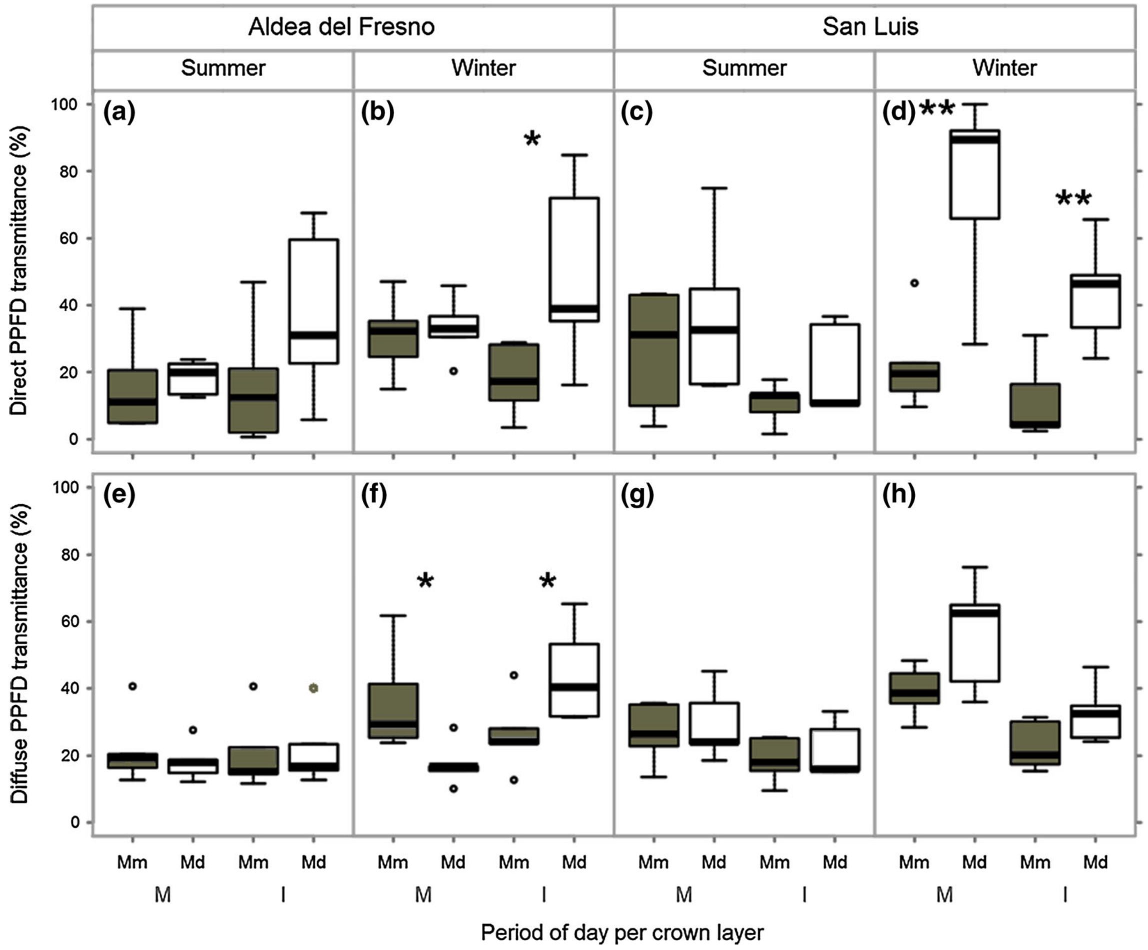

Fig. 3 Crown transmittance to direct (**a**–**d**) and diffuse (**e**–**f**) PPFD in Aldea del Fresno (**a**, **b**, **e**, **f**) and San Luis (**c**, **d**, **g**, **h**). *M* middle-crown, *I* inner-crown; *Md* midday, *Mm* mid-morning. *Boxes* represent data between the 25th and 75th percentile and whiskers the 5th and 95th percentiles. *Open circles* are outliers. *Asterisks* indicate significant mean rank differences between periods of the day from BDM tests. $^*p < 0.05$; $^{**}p < 0.01$. $N = 5$ trees

general, it was similar across the three crown layers during Md (70–90 % of total PAR; Fig. 2) and was reduced from the outer- to the middle- and inner-crown during Mm (20–65 % of total PAR). Diurnal differences in the contribution of direct to total PAR were significant in all crown layers (Fig. 2b–d). When they were non-significant in the middle- and inner-crown (Fig. 2a), it was due to an inverted diurnal variation pattern in the outer-crown.

In general, the contribution of direct PAR varied across seasons in the outer-crown (Fig. 2; Table 2) and did not vary significantly in the middle- and inner-crown.

Direct and diffuse PPFD

In both populations, direct PPFD significantly decreased from the outer- to the middle- and inner-crown layers. Direct PPFD in the three crown layers was significantly higher during Md than during Mm. Within the crown, Md values varied between 290 and 800 μmol m^{-2} s^{-1} and Mm values were below 216 μmol m^{-2} s^{-1} (Mean direct PPFD in Table 3). Maximum direct PPFD values decreased significantly from the outer- to the middle- and inner-crown layers only during Mm, while during Md they were similar in the three crown layers (Maximum direct PPFD in Table 3).

In both populations, diffuse PPFD significantly decreased from the outer- to the middle- and inner-crown layers (Mean diffuse *PPFD* in Table 4). Diffuse PPFD in the outer-crown was significantly higher during Md than during Mm in both populations and seasons, but in the middle- and inner-crown we did not find a unique pattern. In general, both maximum and minimum diffuse PPFD values decreased from the outer- to the middle- and inner-crown layers (Table 4).

Mean direct PPFD was higher in summer than in winter conditions in the outer-crown (Seasonal contrasts in Table 3), but in the middle- and inner-crown there were no significant seasonal differences. Similar results were

Table 2 Seasonal contrasts for the contribution of direct to total PAR. AF: Aldea del Fresno; SL: San Luis; O: outer-crown layer; M: middle-crown layer; I: inner-crown layer; Mm: mid-morning; Md: midday

Population	Crown layer	Period of day	BDM tests for seasonal contrasts			
			DF1	DF2	*F**	*P* (*F* > *F**)
AF	Outer	Mm	1.00	8.00	25.00	0.001
		Md	1.00	8.00	25.00	0.001
	Middle	Mm	1.00	7.50	6.22	0.039
		Md	1.00	7.81	0.51	0.498
	Inner	Mm	1.00	7.32	2.06	0.192
		Md	1.00	8.00	3.00	0.122
SL	Outer	Mm	1.00	7.99	25.64	<0.001
		Md	1.00	6.34	1.38	0.283
	Middle	Mm	1.00	7.97	1.38	0.275
		Md	1.00	7.98	0.51	0.497
	Inner	Mm	1.00	6.15	2.06	0.200
		Md	1.00	8.00	6.22	0.037

DF1 degrees of freedom of the factor (summer vs. winter), *DF2* degrees of freedom of the whole model, *F** non-parametric ANOVA-type F

$P(F > F^*)$: p value; $\alpha = 0.05$

$N = 5$ trees

obtained for mean diffuse PPFD (Seasonal contrasts in Table 4).

Transmittance of direct and diffuse PPFD

Transmittance (%) of direct PPFD did not differ significantly from transmittance of diffuse PPFD in almost all cases (Table 5).

In summer conditions, direct PAR transmitted to the middle- and inner-crown layers did not vary diurnally (Fig. 3a, c) while in winter conditions it was significantly higher during Md than during Mm (Fig. 3b, d).

Diffuse PAR transmittance did not differ significantly between periods of the day (Fig. 3e, g, h), except in AF in winter conditions (Fig. 3f), with opposite trends in the middle- and inner-crown layers. In general, transmittance of direct and diffuse PAR did not vary significantly between seasons (Fig. 3a vs. b; c vs. d; Table 6).

Sunfleck frequency

In both populations, low direct PPFD pulses were the most frequent. In fact, there was an exponential decrease in pulse frequency as PPFD increased (Fig. 4, Fig. 5 in Online Resource 2). In general, during Md there were more events of all intensity classes than during Mm except in the middle-crown of AF in summer conditions (Fig. 4, Fig. 5 in Online Resource 2). This was the tendency in both seasons.

Remarkably, the frequency of PPFD values classified as greater than 10 µmol m^{-2} s^{-1} was on average 22 and 45.5 % lower during Mm than during Md in summer and in winter conditions, respectively. Of an average sample of 10 instantaneous measurements, the percentage falling below 10 µmol m^{-2} s^{-1} was 26 % in summer (Fig. 4a, c, Fig. 5a, c in Online Resource 2) and 48 % in winter (Fig. 4b, d, Fig. 5b, d in Online Resource 2) during Mm, and less than 1 % during Md in both seasons. These diurnal differences were significant in almost all cases.

In winter, the maximum PPFD value for a given sunfleck was below 400 µmol m^{-2} s^{-1} during Mm reaching up to 1300 µmol m^{-2} s^{-1} during Md. In this season, the frequency differences between periods of the day were significant throughout the range of PPFD classes up to 900–1300 µmol m^{-2} s^{-1} (Fig. 4b, d, Fig. 5b, d in Online Resource 2). Seasonal differences in sunfleck frequency were non-significant in almost all cases (Tables 9 and 10 in Online Resource 2).

Discussion

Our results highlight a marked pattern of diurnal variations of the light environment within the crowns of wild olive trees. The contribution of direct PAR within the crowns is on average during Md 70–90 % and during Mm 20–40 %, indicating that the diffuse PAR fraction is predominant

Table 3 Descriptive statistics of Direct PPFD

Population	Season	Crown layer	Diurnal and across-layers contrasts					
			Maximum direct PPFD		BDM§	Mean direct PPFD		BDM§
			Mm	Md	$P(F > F^{*})$	Mm	Md	$P(F > F^{*})$
AF	Summer	Outer	1309.27 ± 10.65	1864.32 ± 2.65	***	1011.36 ± 21.94 a	1674.66 ± 26.33 a	***
		Middle	683.21 ± 141.08	1284.55 ± 161.55	**	155.27 ± 59.64 b	307.62 ± 38.92 b	*
		Inner	725.97 ± 271.87	1519.94 ± 233.89	*	191.27 ± 94.43 b	620.77 ± 191.52 b	n.s.
	Winter	Outer	357.75 ± 8.97 a	1054.21 ± 1.14	***	187.17 ± 9.9 a	1018.94 ± 1.92 a	***
		Middle	292.79 ± 38.4 ab	1009.68 ± 107.69	***	72.24 ± 13.89 b	338.69 ± 41.45 b	***
		Inner	214.32 ± 38.83 b	1047.9 ± 150.39	***	48 ± 15.07 b	505.43 ± 128.81 b	***
SL	Summer	Outer	1012.08 ± 7.23 a	1589.45 ± 9.37	***	760.07 ± 11.69 a	1428.24 ± 19.17 a	***
		Middle	685.23 ± 175.41 b	1273.33 ± 90.65	***	216.53 ± 68.71 b	524.08 ± 156.65 b	n.s.
		Inner	347.79 ± 73.69 b	1089.15 ± 264.79	*	93.32 ± 24.96 b	289.5 ± 87.4 b	*
	Winter	Outer	416.28 ± 7.63 a	1238.64 ± 4.92	***	250.81 ± 10.09 a	1138.87 ± 5.97 a	***
		Middle	272.6 ± 27.58 b	1176.19 ± 61.16	***	61.22 ± 15.8 b	803.32 ± 135.85 b	***
		Inner	176.48 ± 65.54 b	1089.03 ± 74.38	***	32.02 ± 15.08 b	488.91 ± 78.89 b	***

Population	Season	Crown layer	Diurnal and across-layers contrasts			Seasonal contrasts					
			Minimum direct PPFD		BDM§	Maximum PPFD		Mean PPFD		Minimum PPFD	
			Mm	Md	$P(F > F^{*})$	Mm	Md	Mm	Md	Mm	Md
AF	Summer	Outer	561.98 ± 21.12 a	1294.14 ± 85.28 a	***	**	**	**	**	**	**
		Middle	3.91 ± 2.98 b	23.21 ± 13.12 b	n.s.	**	*	n.s.	n.s.	n.s.	n.s.
		Inner	1.26 ± 1.26 b	27.75 ± 15.79 b	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Winter	Outer	28.38 ± 5.96 a	968.17 ± 2.98 a	***						
		Middle	0.13 ± 0.13 b	32.16 ± 23.89 b	***						
		Inner	0 b	63.45 ± 55.05 b	**						
SL	Summer	Outer	437.86 ± 23.71 a	1091.8 ± 77.68 a	***	***	***	***	***	***	n.s.
		Middle	4.79 ± 2.01 b	76.7 ± 53.00 b	*	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
		Inner	0.12 ± 0.13 b	18.92 ± 15.94 b	***	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Winter	Outer	73.29 ± 10 a	1026.96 ± 3.18 a	***						
		Middle	0 b	248.76 ± 127.83 b	**						
		Inner	0.25 ± 0.25 b	57.77 ± 36.15 b	*						

Average ± SE of the maximum, minimum and mean instantaneous direct PPFD and BDM contrasts between crown layers, periods of the day and seasons

Lower-case letters indicate BDM results between crown layers

The right end of the table indicates BDM results between seasons

AF Aldea del Fresno, *SL* San Luis, *Mm* mid-morning, *Md* midday

§ BDM tests for diurnal differences

$P(F > F^{*})$: p value for ANOVA-type F; $\alpha = 0.05$

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s.: $p > 0.05$

$N = 5$ trees for all contrasts

Table 4 Descriptive statistics of Diffuse PPFD

Population	Season	Crown layer	Diurnal and across-layers contrasts					
			Maximum diffuse PPFD		BDM§	Mean diffuse PPFD		BDM§
			Mm	Md	$P(F > F^*)$	Mm	Md	$P(F > F^*)$
AF	Summer	Outer	192.02 ± 0.97 a	437.12 ± 8.03 a	***	172.39 ± 1.05 a	380.18 ± 2.44 a	***
		Middle	47.33 ± 9.59 b	88.96 ± 10.81 b	*	37.85 ± 8.54 b	69.09 ± 9.52 b	n.s.
		Inner	47.45 ± 10.32 b	101.7 ± 21.07 b	*	36.22 ± 9.16 b	81.79 ± 18.30 b	*
	Winter	Outer	115.07 ± 1.86 a	172.59 ± 0.63 a	***	80.78 ± 2.45 a	166.43 ± 0.35 a	***
		Middle	51.49 ± 8.81 b	48.34 ± 6.79 b	n.s.	31.58 ± 6.32 b	29.14 ± 4.96 b	n.s.
		Inner	38.75 ± 8.06 b	88.33 ± 11.62 c	**	22.89 ± 4.65 b	73.92 ± 10.97 c	***
SL	Summer	Outer	377.33 ± 8.57 a	566.04 ± 24.29 a	***	302.81 ± 5.08 a	453.3 ± 6.7 a	***
		Middle	104.47 ± 17.54 b	151.9 ± 20.87 b	n.s.	80.74 ± 12.21 b	131.73 ± 20.18 b	*
		Inner	77.1 ± 11.44 b	130.84 ± 18.93 b	n.s.	56.81 ± 8.78 b	96.66 ± 15.83 b	n.s.
	Winter	Outer	197.7 ± 2.73 a	268.71 ± 1.14 a	***	150.94 ± 3.22 a	260.73 ± 0.79 a	***
		Middle	90.22 ± 9.77 b	211.19 ± 16.97 b	***	60.49 ± 6.24 b	146.77 ± 19.43 b	***
		Inner	48.84 ± 6.42 c	97.534 ± 12.41 c	***	35.25 ± 5.57 c	85.1 ± 10.59 c	***

Population	Season	Crown layer	Diurnal and across-layers contrasts			Seasonal contrasts					
			Minimum diffuse PPFD		BDM§	Maximum PPFD		Mean PPFD		Minimum PPFD	
			Mm	Md	$P(F > F^*)$	Mm	Md	Mm	Md	Mm	Md
AF	Summer	Outer	147.87 ± 2.84 a	301.89 ± 7.63 a	***	***	***	***	***	***	***
		Middle	27.14 ± 8.00 b	54.14 ± 9.11 b	n.s.	n.s.	**	n.s.	**	*	***
		Inner	21.47 ± 8.88 b	56.92 ± 19.79 b	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
	Winter	Outer	40.26 ± 3.60 a	160.86 ± 0.25 a	***						
		Middle	9.48 ± 3.42 b	11.25 ± 2.53 b	n.s.						
		Inner	7.72 ± 1.98 b	64.61 ± 10.45 c	**						
SL	Summer	Outer	223.05 ± 6.49 a	395.11 ± 3.77 a	***	***	***	***	***	***	***
		Middle	58.93 ± 8.32 b	104.22 ± 22.06 b	n.s.	n.s.	n.s.	n.s.	n.s.	**	n.s.
		Inner	35.85 ± 6.83 b	71.93 ± 20.96 b	n.s.	*	n.s.	*	n.s.	n.s.	n.s.
	Winter	Outer	99.05 ± 4.6 a	250.3 ± 0.83 a	***						
		Middle	29.42 ± 1.9 b	127.56 ± 17.94 b	***						
		Inner	18.95 ± 3.01 c	73.57 ± 10.75 c	***						

Average ± SE of the maximum, minimum and mean instantaneous diffuse PPFD and BDM contrasts between crown layers, periods of the day and seasons

Lower-case letters indicate BDM results between crown layers

The right end of the table indicates BDM results between seasons

AF Aldea del Fresno, *SL* San Luis, *Mm* mid-morning, *Md* midday

$N = 5$ trees for all contrasts

§ BDM tests for diurnal differences

$P(F > F^*)$: p value for ANOVA-type F; $\alpha = 0.05$

*** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$; n.s.: $p > 0.05$

Table 5 One-way BDM tests for differences in crown transmittance between light directional fractions

Population	Season	Crown layer	Period of day	BDM tests for directional fractions			
				DF1	DF2	*F**	*P*(*F* > *F**)
AF	Summer	Middle	Mm	1.00	6.77	0.88	0.381
			Md	1.00	7.98	0.09	0.773
		Inner	Mm	1.00	6.47	0.68	0.438
			Md	1.00	6.95	1.11	0.327
	Winter	Middle	Mm	1.00	7.98	0.04	0.848
			Md	1.00	8.00	14.54	0.005
		Inner	Mm	1.00	7.45	0.68	0.435
			Md	1.00	7.16	0.09	0.775
SL	Summer	Middle	Mm	1.00	5.97	0.01	0.925
			Md	1.00	6.72	0.01	0.924
		Inner	Mm	1.00	7.83	4.31	0.072
			Md	1.00	5.12	0.25	0.638
	Winter	Middle	Mm	1.00	6.66	4.31	0.078
			Md	1.00	6.15	2.06	0.200
		Inner	Mm	1.00	6.68	2.53	0.158
			Md	1.00	7.34	0.88	0.377

AF Aldea del Fresno, *SL* San Luis, *Mm* mid-morning, *Md* midday, *DF1* degrees of freedom of the factor (direct *vs.* diffuse PAR), *DF2* degrees of freedom of the whole model

*F**: non-parametric ANOVA-type F

P(*F* > *F**): *p* value; $\alpha = 0.05$

$N = 5$ trees

Table 6 Seasonal contrasts of direct and diffuse PAR transmittance

Directional fraction	Population	Crown layer	Period of day	BDM tests for seasonal contrasts			
				DF1	DF2	F*	P(F > F*)
Direct PAR	AF	Middle	Mm	1.00	7.22	3.03	0.124
			Md	1.00	7.68	7.71	0.025
		Inner	Mm	1.00	6.98	0.37	0.564
			Md	1.00	7.91	0.87	0.378
	SL	Middle	Mm	1.00	7.65	0.00	1.000
			Md	1.00	7.80	4.35	0.071
		Inner	Mm	1.00	7.54	0.04	0.847
			Md	1.00	8.00	4.35	0.070
Diffuse PAR	AF	Middle	Mm	1.00	7.07	5.23	0.056
			Md	1.00	7.97	0.16	0.699
		Inner	Mm	1.00	8.00	1.39	0.272
			Md	1.00	7.72	7.62	0.026
	SL	Middle	Mm	1.00	7.98	7.62	0.025
			Md	1.00	7.99	7.71	0.024
		Inner	Mm	1.00	7.80	0.51	0.497
			Md	1.00	7.97	3.66	0.092

AF Aldea del Fresno, *SL* San Luis, *Mm* mid-morning, *Md* midday, *DF1* degrees of freedom of the factor (summer vs. winter), *DF2* degrees of freedom of the whole model

*F**: non-parametric ANOVA-type F

P(*F* > *F**): *p* value; $\alpha = 0.05$

$N = 5$ trees

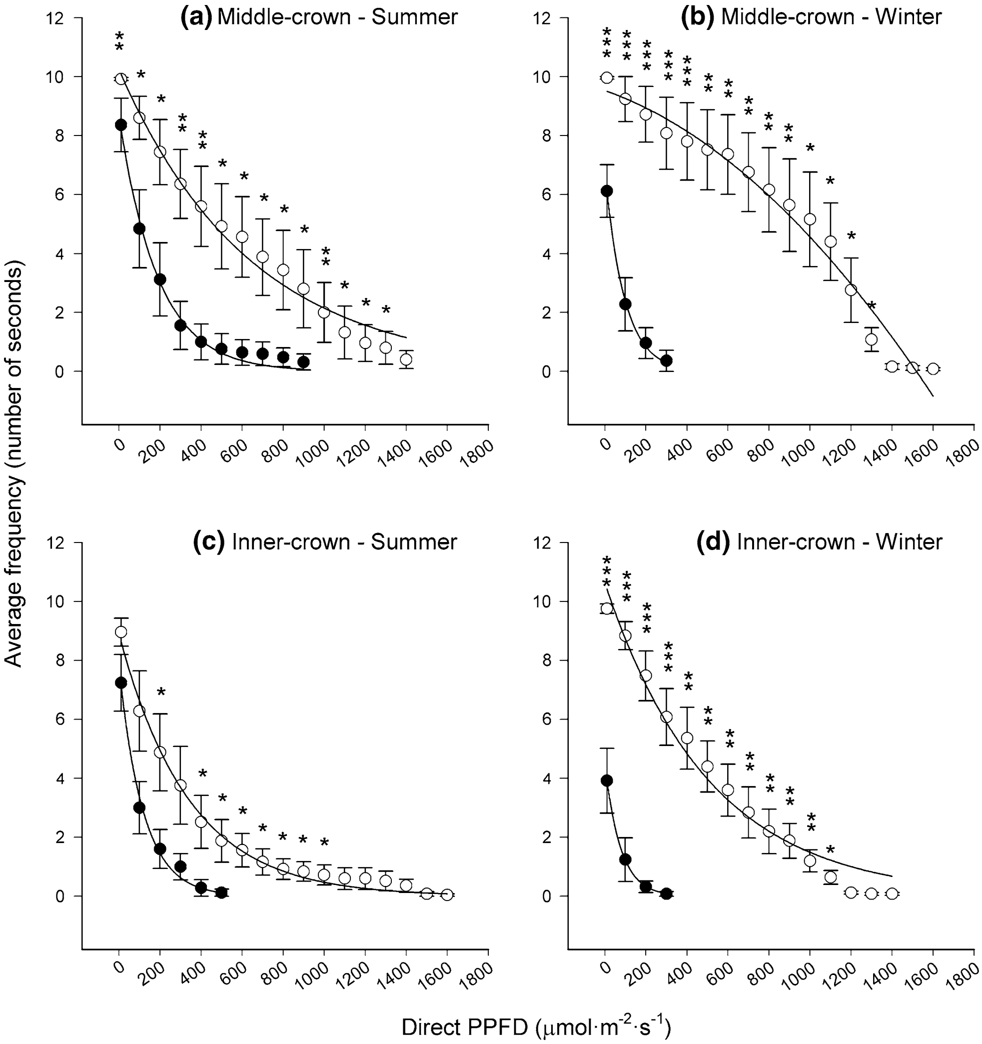

Fig. 4 Sunfleck frequencies (number of seconds) as a function of classes of cumulative direct PAR per period of the day in San Luis in the middle-crown in summer (**a**) and winter conditions (**b**), and in the inner-crown in summer (**c**) and winter conditions (**d**). *Closed circles* mid-morning; *open circles* midday. *Asterisks* indicate significant mean rank differences between periods of the day for each PPFD class from BDM tests. $*p < 0.05$; $**p < 0.01$; $***p < 0.001$; $N = 5$ trees

during the early hours of the day. Sunfleck frequency is higher during Md than during Mm in both seasons and populations in spite of the markedly contrasting environmental conditions.

The pattern of diurnal variations of direct PAR and average PPFD within the crown is similar to that occurring in the outer-crown, increasing from Mm to Md. However, the crown plays a role in modifying the relative contribution of both fractions during Mm as attested to by the higher PAR during Mm than during Md in the outer-crown. In turn, an inversion of the diurnal variation pattern in the outer-crown results in non-significant diurnal variations in the contribution of direct PAR within the crown, although the tendency towards diurnal differentiation is conspicuous.

The diurnal differentiation of the light environment within the crown is mediated by diurnal changes in the frequencies of sunfleck of different intensity. During Md there are more sunflecks falling above 10 µmol m^{-2} s^{-1} and sunflecks of different intensity last longer than during Mm. This result suggests that outer-crown layers cast more shade on subtending layers during Mm and enhance direct light penetration during Md (Falster and Westoby 2003; Uemura et al. 2006) across the two populations and seasons. Thus, the Md light environment within the crown seems to be important in determining the structure and function of Mediterranean evergreens. Light is a major driver of the expression of intra-individual plasticity in trees. Predictable light variation patterns drive the direction of light interception and Mediterranean evergreens can adjust the layout of within-crown layers to maximize light interception during midday (Gratani and Bombelli 2000b; Pearcy et al. 2005; Gratani et al. 2006; Sack et al. 2006; Granado-Yela et al. 2011).

On clear days, both direct and diffuse PAR are transmitted in the same proportions across the crowns of the studied trees according to the results of Génard and Baret (1994) in peach tree crowns in France. This can be important for plant productivity assessments in ecosystems with a high annual number of cloudless days (Bolle 2003). Remarkably, while maximum, mean and minimum direct PPFD actually vary throughout the day, diffuse PPFD within the crown can either be higher during Md or similar between periods, suggesting that the temporal distribution of diffuse PAR tends to be more homogeneous than that of direct PAR on clear days. Indeed, our raw data indicate high variability in instantaneous direct PAR within the crown, as shown by Cai et al. (2009) and negligible variability of diffuse PAR. It is timely to incorporate both PAR fractions explicitly in plant productivity research because: (1) light use efficiency depends both on the proportions of directional fractions and on their intensities (i.e., PPFD); (2) direct and diffuse PAR use efficiency vary as a function of sky conditions (Roderick et al. 2001; Gu et al. 2002); and (3) direct PPFD has a more marked temporal variation than diffuse PPFD within tree crowns.

The diurnal direct and diffuse PPFD variation pattern within the crown arises from a lack of differences in transmittance between periods of the day in summer conditions and by differences in transmittance in winter conditions. This highlights that the light measurements reflect the outcome of a crown-mediated filtering process that operates at several spatial scales (i.e., from the leaf to the whole crown; Cescatti and Niinemets 2004; Niinemets and Sack 2006; Niinemets and Anten 2009). For instance, a crown characterized by vertical sun leaves enhances the penetration of direct PAR, while a high leaf density reduces direct PAR transmittance and sunfleck frequency. Similarly, two crown types with an equal leaf density may differ in the size, number and distribution of openings, thus altering the intensity and frequency of direct PAR within the crown while maintaining a similar average transmittance (Smith et al. 1989; Wang and Jarvis 1990; Baldocchi and Collineau 1994; Cescatti and Niinemets 2004; Brantley and Young 2009). Diurnal and seasonal changes in solar position may play a double role in shaping the within-crown light environment, by eliciting the expression of crown architectural heterogeneity (Valladares and Pearcy 1998) and raising apparent changes in crown architecture due to geometrical effects (Smith et al. 1989; Mariscal et al. 2000).

In agreement with our hypothesis, there was a general lack of seasonal variations in the three light attributes within the crown. The whole plant may benefit from seasonal changes in solar position typical of mid-latitudes by developing a consensus architectural layout that allows a deeper light penetration at low solar elevation angles (i.e., winter; Valladares and Pearcy 1998; Falster and Westoby 2003) while preventing the middle- and inner-layers from receiving excessive light intensities at high solar elevation angles (summer; Howell et al. 2002; Pearcy et al. 2005). Our results unveiled a possible relevant role for winter light in whole plant function, since extreme sun elevation angles do not result in a significantly different light environment within the crown.

In this study, we found specific diurnal light variation patterns within the crown that match the known light interception patterns in wild olives and other Mediterranean evergreens (Werner et al. 2001; Gratani et al. 2006; Granado-Yela et al. 2011; Rubio de Casas et al. 2007; 2011). Our study highlights that light attributes display identifiable patterns of temporal variability within the crown. Temporal light variation is an important component of the light environment and can differ between direct and diffuse PAR fractions.

Author contribution statement All authors designed the study. ABVL, AGER, MDJ and CGY gathered the data. ABVL and CGY performed data analyses. ABVL, JAD, RRC, MDJ and LB wrote the manuscript.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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