Sunfleck properties from time series of fluctuating light

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ABSTRACT

Light in canopies is highly dynamic since the strength and composition of incoming radiation is determined by the wind and the Sun's trajectory and by canopy structure. For this highly dynamic environment, we mathematically defined sunflecks as periods of high irradiance relative to the background light environment. They can account for a large proportion of the light available for photosynthesis. Based on high-frequency irradiance measurements with a CCD array spectroradiometer, we investigated how the frequency of measurement affects what we define as sunflecks. Do different plant canopies produce sunflecks with different properties? How does the spectral composition and strength of irradiance in the shade vary during a sunfleck? Our results suggest that high-frequency measurements improved our description of light fluctuations and led to the detection of shorter, more frequent and intense sunflecks. We found that shorter wind-induced sunflecks contribute most of the irradiance attributable to sunflecks, contrary to previous reports from both forests and crops. Large variations in sunfleck properties related to canopy depth and species, including distinct spectral composition under shade and sunflecks, suggest that mapping canopy structural traits may help us model photosynthesis dynamically.

1. Introduction

Light is one of the most dynamic environmental factors in plant canopies. The arrangement of foliage and branches creates gaps through which light penetrates to the lower canopy. Thus, canopy architecture generates a patchy light environment composed of shade, partial shade (or penumbra), and full sunlight. The proportions of each depends on gap sizes, canopy height, and environmental factors, such as the Sun's position (Tang et al., 1988; Barradas et al., 1998), the movement of clouds, and the canopy itself dictated by the wind speed, duration and direction (Burgess et al., 2016). Patches of significantly higher irradiance than that of the surrounding shade in the lower canopy can make an important but highly variable contribution to the total incident irradiance reaching the lower canopy. This contribution may range from 4% to more than 80% in agricultural crops (Tang et al., 1988; Barradas

et al., 1998). Since photosynthesis does not respond instantaneously to fluctuations of irradiance, and that the relation between irradiance and photosynthesis is non-linear, these fluctuations will substantially affect plant function.

Few studies have investigated the effect of specific canopy structural traits, such as canopy height and leaf area (Barradas et al., 1998) or depth in the canopy (Pearcy et al., 1990) on the regime of light fluctuation in canopies (Way and Pearcy, 2012; Smith and Berry, 2013). Nevertheless, we know that shade tolerance affects species composition, abundance, location and coexistence in forest canopies (Gravel et al., 2010). Moreover, structural traits affecting light penetration in plant canopies will evidently influence the heterogeneous distribution of light through the canopy. For example leaf size, shape, orientation and clumping (Falster and Westoby, 2003), but also stand density, tree and crown height, and branching architecture make up the 3D structural

arrangement affecting how light is intercepted by leaves (Burgess et al., 2017). Beyond this, the mechanical properties of stems and branches that dictate their movements and propensity of leaves to flutter help to create the temporal signature of irradiance dynamics, according to canopy type (Burgess et al., 2016). In general, a high leaf area, implying a high probability of light interception, decreases the frequency of high irradiance events (Miyashita et al., 2012).

Researchers named these brief, intermittent periods of high irradiance, 'sunflecks' (McLean, 1919), 'sun patches' or 'sun gaps' depending on their irradiance, size, and duration although no consensus on nomenclature has been reached (Smith and Berry, 2013). Many studies define sunflecks as periods of irradiance over a chosen threshold based on the surrounding shade environment (*e.g.* > 70% of the above canopy irradiance in Barradas et al., 1998; or above 50 or 300 $\mu mol\ m^{-2}\ s^{-1}$ in Miyashita et al., 2012 and Roden and Pearcy, 1993, respectively). Although shade itself is dependent on canopy architecture and biophysical factors. Moreover, due to different research aims and technical limitations, measurements of irradiance are performed at diverse frequencies, usually from $0.2\ s^{-1}$ (Tang et al., 1988; Barradas et al., 1998) to $1\ s^{-1}$ (Pfitsch and Pearcy, 1989a; Vierling and Wessman, 2000) and rarely up to $20\ s^{-1}$ (Desjardins et al., 1973; Roden and Pearcy, 1993). Since light is measured by a detector collecting photons over a defined period of time (integration time), we can significantly improve the description of light fluctuations using discrete time-series of irradiance with a very short integration time. Correspondingly, a significant amount of information could be gained when calculating sunfleck frequencies, peak intensity and duration from measurements integrated over one second or less (Chazdon, 1988).

At first, most research centred on the effect of sunflecks in forests (Atkins and Poole, 1937; Evans, 1956) on understorey species such as shrubs or forest saplings (Pearcy, 1983; Chazdon and Field, 1987), and herbaceous species (Blackman and Rutter, 1946; Pfitsch and Pearcy, 1989b), and more rarely on crops (Norman et al., 1971) or orchard species (Lakso and Barnes, 1978). In recent years, heightened interest in improving carbon gain by optimizing photosynthetic processes in response to fluctuating light has shifted the focus towards crop species (Murchie et al., 2009; Kaiser et al., 2018; Slattery et al., 2018). The distinct structure and architecture of crop and forest canopies, such as a larger distance between canopy gaps and sunflecks creating more penumbra in forests, means that their sunfleck patterns are very different. Unlike forests, where the lignified stems that compose the trunk and branches of trees have more resistance to wind, in crops relatively large canopy movements of several centimetres within less than a second can be induced by a light breeze (Maitani, 1979). This wave-like motion of crop canopies is sometimes called "Honami" (Inoue, 1955), and will in turn generate a pattern of frequent, but short, sunflecks (Tong and Hipps, 1996).

How photosynthesis adjusts to rapid fluctuations in light is complex because it involves several interacting processes with markedly different response times (Way and Pearcy, 2012). The delay of reaching full induction of photosynthesis hinders efficient use of a sunfleck by a leaf emerging from a long (> 5 min) period of shade (Kobza and Edwards, 1987; Sassenrath-Cole and Pearcy, 1992). A low stomatal opening can especially hinder the capacity to exploit sunflecks when the stomatal conductance in the shade is low (Allen and Pearcy, 2000). After the light-dependent reactions of photosynthesis, including absorption of light by chlorophylls, electron transport, and synthesis of NADPH and ATP which occur in less than half a second, the induction of the light-independent reactions limits the rate of CO_2 assimilation (A_n) in response to a sunfleck. This generally proceeds in three phases: first, residual metabolite pools, previously activated enzymes, and light activation of enzymes involved in RuBP regeneration allow A_n to increase in less than half a second following illumination (Sassenrath-Cole and Pearcy, 1992). Second, a buildup of photosynthetic metabolic pools allows for sustained CO_2 fixation which continues for several seconds post illumination (McAlister, 1939; Laisk et al., 1984). Especially in

short sunflecks (Pons and Pearcy, 1992), post-illumination CO_2 fixation can contribute a large proportion of the total carbon gained due to a sunfleck (Way and Pearcy, 2012). Third, processing of a residual pool of photorespiratory metabolites can induce a CO_2 burst in longer sunflecks (> 1 min), partially offsetting CO_2 assimilation (Vines et al., 1983; Pearcy, 1990). Other competing dynamic processes such as non-photochemical quenching can also reduce the energy directed to photosynthesis and thus affect sunfleck use (Murchie and Ruban, 2020).

Most current models do not take into account the dynamics of processes involved in photosynthetic induction and relaxation under fluctuating environmental conditions, despite steady-state models substantially overestimating carbon assimilation when compared with dynamic models (Naumburg and Ellsworth, 2002; Way and Pearcy, 2012). Improving models of photosynthesis is especially important in light of ongoing concerns over the increase in global demand for food (Ort et al., 2015), and the impact of global change on crop productivity (Asseng et al., 2014), both driving the need to improve crop performance. Therefore, a better understanding of patterns in light fluctuations among different crop canopies is crucial, if we want to elucidate the physiological dynamics of plant response to sunflecks (Murchie et al., 2018).

In order to describe sunfleck properties and dynamics in crop canopies, we developed an algorithm capable of detecting sunflecks, defined here as periods when photosynthetic photon flux density (PPFD) is higher than 5% or 5 $\mu mol\ m^{-2}\ s^{-1}$ relative to the background light environment, in time-series of PPFD. We used an array spectroradiometer measuring at very high frequencies (up to $100\ s^{-1}$), to achieve high enough resolution to adequately detect the rapid fluctuation of irradiance in crop canopies. We aimed to: (1) investigate how the frequency of measurements affects our estimation of sunfleck properties; (2) assess the variability in sunfleck frequency and properties in three different crop canopies; (3) evaluate differences in sunfleck properties at different canopy depths; and (4) examine how the spectral composition of radiation is modified during a sunfleck.

2. Material and methods

2.1. Study site and plant material

The experiment was conducted at the Viikki Experimental Farm and Viikki Field Plots, University of Helsinki, Finland (60.227 N, 25.018 E, 10 m above sea level) in three separate fields of oats (*Avena sativa*, L.), barley (*Hordeum vulgare*, L.) and broad bean (*Vicia faba*, L.). The varieties used were "Meeri", "Harbinger" and "Kontu" and were planted on May 25th, May 8th, and May 27th for the oat, barley and bean, respectively. The planting density was 500 seeds per m^2 for the oat and barley fields, and 70 seeds per m^2 for the bean field. Fertilization was applied as 350 kg ha^{-1} of BioA Nitrogen-Potassium 26%−2% fertilizer (BioA, Kotka, Finland) in the oat field, and 180 kg ha^{-1} of Premium Nitrogen 27% fertilizer (Belor Agro Oy, Salo, Finland) in the barley field. Farmyard manure was applied at a concentration of 17 and 25 $m^3\ ha^{-1}$ in the barley and bean field, respectively. The soil was a clay loam in the oat field, a fine-sandy moraine in the barley field, and intermediate between the two soil types in the bean field with a 2% slope at most (North-South orientation). At the time of measurement, the plant height was 85 cm, 65 cm and 55 cm in the oat, barley, and bean fields, respectively (see Table 1 for a list of canopy structural traits). The wind speed was recorded every 5 s and integrated into an hourly average by a sensor (WXT520, Vaisala, Vantaa, Finland) two meters above the ground located less than five meters away from the oat field, and 700 m away from the barley and bean fields (Fig. A1). We chose an hourly time step instead of a minute because the wind patterns, honami (small gusts of wind coming from any cardinal direction and lasting from a few second up to a minute) in the field were so localized that they may not reflect what sensors a few metres away record. In other words, we chose a more accurate low-resolution measurement rather than an inaccurate high-

Table 1

Summary of canopy structural traits for *Avena sativa, Hordeum vulgare* and *Vicia faba*. Values are means ± standard deviation when available. Values from similar experiments were reported when the data was not measured during the experiment.

Canopy trait	*Avena sativa*	*Hordeum vulgare*	*Vicia faba*
Varieties	Meeri	Harbinger	Kontu
Planting density (seed m^{-2})	500	500	70
Row spacing (cm)	12.5	12.5	12.5
Seed spacing (cm)	1.6	1.6	11.4
Canopy height (cm)	85	65	55
Above-ground biomass per plant (g)	3.45 ± 0.50[*]	1.83 ± 0.45[†]	
LAI ($m^2 m^{-2}$)	4.1 ± 0.8[*]	3.7 ± 1.8[†]	4.35 ± 0.6[‡]
Mean tilt angle (°)	57.8 ± 4.6[‡]	45.8 ± 4.8[‡]	27.1 ± 3.8[‡]
Natural frequency (Hz)	1.32 ± 0.17[§]	1.37 ± 0.13[§]	
Leaf width (cm)	1.8[#]	1.1 ± 0.1[**]	3.6 ± 0.3[¶]
Leaf length (cm)	27.3[#]	33.9 ± 5.8[**]	8.0 ± 0.5[¶]

[*] Mäkelä et al. (2004): oat grown in the field at the same location and planting density.

[†] Mäkelä and Muurinen (2012): barley grown in the field at the same location and planting density.

[‡] Zou et al. (2014); Zou et al. (2018): oat, barley and beans grown in the field at the same location and planting density.

[§] Susko et al. (2019): oat and barley grown in the field in Minnesota, USA at lower planting density (row spacing was 30 cm).

[#] Finnan et al. (2019): oat grown in the field in Ireland at the same planting density.

[**] Wyka et al. (2019): barley grown in large pots in Poland.

[¶] Peksen (2007): beans grown in the field in Turkey.

resolution one.

2.2. Light measurements

Measurements were taken from July 8th to July 17th 2020, before the stalks and heads of the barley, and the panicle and grains of the oats turned yellow. Spectral photon flux density (μmol $m^{-2} s^{-1}$) was measured using a CCD array spectroradiometer Maya 2000 Pro (Ocean Optics, Dunedin, FL, USA) attached to a cosine diffuser (D7-H-SMA, Bentham Instruments Ltd., Reading, UK) with a fiber-optic cable (FC-UV400–2 400 μm, Avantes, Leatherhead, UK). The spectral range of the instrument is from 200 to 1100 nm, and it was calibrated by the Finnish Radiation and Nuclear Safety Authority (STUK; Ylianttila et al., 2007) in April of 2019. Spectral photon flux density was recorded for 1377 wavelengths in the range 280–898 nm with the diffuser in the horizontal position. In each crop canopy, a set of 10,000, 5000, 3334, 2500, 2000, 1667 and 1250 spectroradiometer measurements were carried out with an integration time of 10, 20, 30, 40, 50, 60 or 80 ms, respectively, to construct 100s-long time-series. Those measurements were used to investigate the effect of integration time on sunfleck properties. To identify and compare sunfleck properties in different crop canopies, sets of 10,000 consecutive measurements ($n = 7$, 3 and 5 for oat, barley and bean, respectively) with a 10 ms integration time were used. To assess differences in sunfleck properties with height in the oat field, three randomly chosen locations in the field were used as replicates. The sensor was small enough that we were able to place it at different locations in the canopy, but always equidistant from all stems, without noticeably changing the canopy structure. Time-series were recorded at 30, 50, 65, and 85 cm from top of the canopy. We used a small tripod for heights above the ground. For each set of measurements, a place in the field was randomly chosen, and two additional recordings were carried out to provide further correction of the photon flux density. The first was done by placing a darkening cap over the diffuser blocking all UV and visible radiation and recording the noise that was later subtracted from

the actual measurement. The second correction was applied by placing a polycarbonate cap (blocking 280–400 nm radiation) over the diffuser, and using the recording to correct for stray light following Ylianttila et al. (2007). Spectral photon flux density above the canopy was recorded by mounting the diffuser on a tripod between one and three times for each day and canopy, depending on the duration of the measurement period. All data were recorded within three hours of solar noon (at about 13:30) from 10:30 to 15:30, local time in the absence of clouds. The data were processed using the R packages "*ooacquire*" and "*photobiology*" (R Core Team, 2020).

2.3. Sunfleck detection

The photosynthetically active radiation waveband (PAR, 400–700 nm) was used to detect sunflecks because of its relevance for plant functions (Fig. A2, Appendix B). Sunfleck detection was based on an algorithm using the property of first order derivatives with respect to time, which represents the rate of change of PPFD (Δ_{PAR}), and crosses zero when PPFD switches from increasing to decreasing, and *vice versa*. The time step of the PPFD time series was artificially increased by ten times, using the same value of photon flux density measured for each set of ten points. This helped the algorithm pinpoint which measurement was the actual starting point, thus correcting observed artefacts during the development of the algorithm. Δ_{PAR} was calculated for each point n at time t in the time series and its following measurement $n + 1$ as:

$$\Delta_{PAR} = \frac{PPFD_{n+1} - PPFD_n}{t_{n+1} - t_n}$$

Then, each point in the Δ_{PAR} time-series was assessed and flagged when the sign (+/-) at point n differed from $n + 1$, signalling that Δ_{PAR} crossed zero between the two data points. A potential sunfleck shows Δ_{PAR} crossing zero three times, which corresponds to the starting point, peak, and endpoint of the sunfleck. For each of these three time points, the corresponding PPFD represents the baseline level of PPFD before the sunfleck (BBF), the peak level of PPFD during the sunfleck (PK), and the baseline level of PPFD after the sunfleck (BAF, Fig. 1a). For each potential sunfleck, if PK - BBF < 0.2 (PK - BAF) or if PK - BAF < 0.2 (PK - BBF), the algorithm will look for earlier or later time points (up to three), respectively, that don't satisfy these inequalities. If these are found, the PPFD of this time point will be used to define a new baseline, if not, the chosen representative background PPFD level for this sunfleck is the one that produces the maximum difference in PPFD between the peak and either the starting or endpoint. This operation was performed for cases when sunflecks had multiple peaks, in order to classify as a single sunfleck those fluctuations that produced multiple peaks without a significant decrease in PPFD (Fig. 1b), and to classify as separate sunflecks those that produced multiple peaks with a significant decrease in PPFD between them (Fig. 1c). Additionally, the baselines were trimmed (*i.e.* displaced to the time point after the starting point and/or before the endpoint of the sunfleck, respectively) until the percent difference between the starting point and the next time point (likewise for the endpoint and previous time point) was higher than 5% (Fig. 1d). Potential sunflecks were discarded if the difference in PPFD between the PK and either BBF or BAF was less than 5 μmol $m^{-2} s^{-1}$, or represented a less than 5% increase in PPFD. When overlapping sunflecks were found, the smaller one was discarded to associate each light fluctuation with a single sunfleck (Fig. 1e).

2.4. Sunfleck properties

Various properties of each identified sunfleck were estimated to characterise their patterns and importance within a PPFD time series. Sunfleck duration (SFD) was calculated as the time between the starting and endpoint of the sunfleck. In order to avoid potential inaccuracies caused by asymmetry (*e.g.* Fig. 1c), the amplitude (SFA) was estimated as the difference in PPFD between PK and the baseline with the lowest
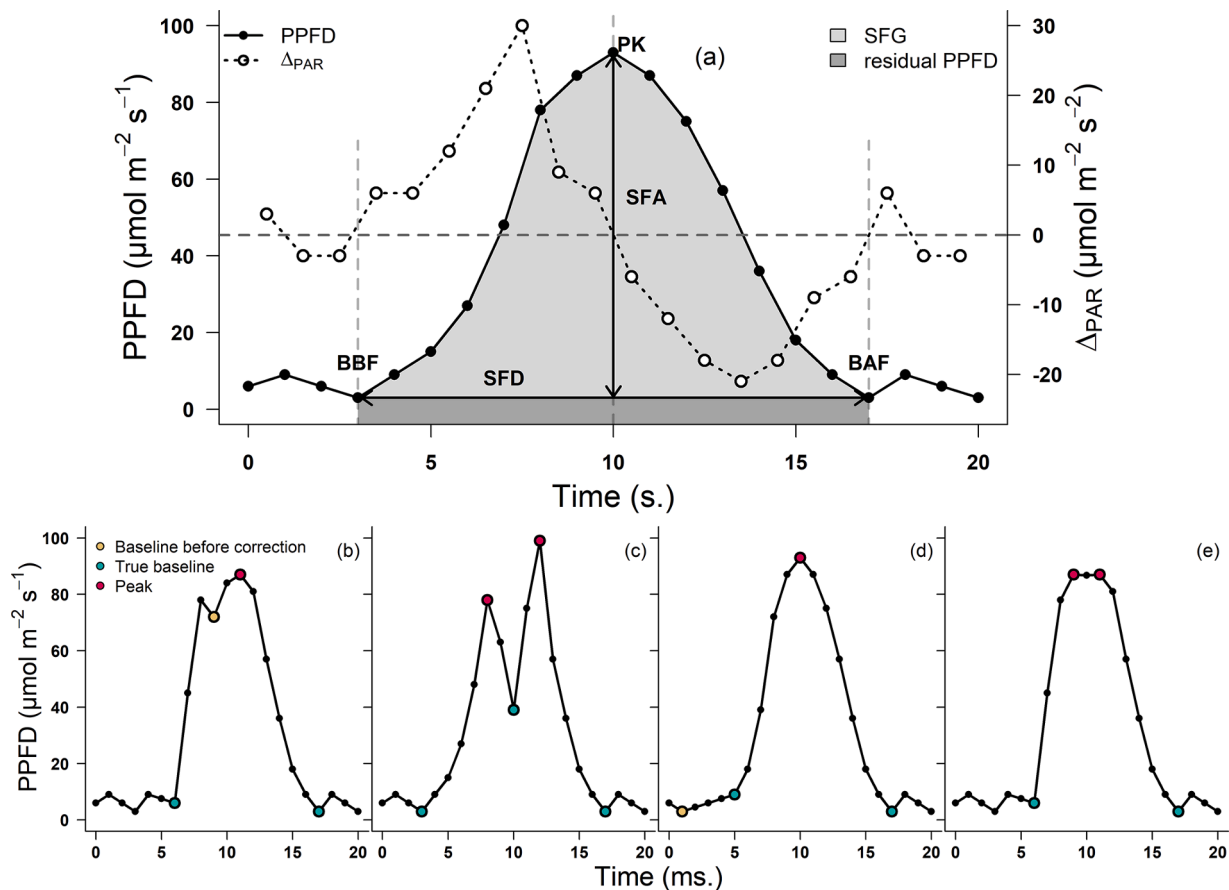
Fig. 1. (a) Example of a PPFD time-series. a) PPFD during a sunfleck with its rate of change (Δ_{PAR}). SFA, SFD, and SFG are the sunfleck amplitude, sunfleck duration, and the increase in PPFD caused by the sunfleck, respectively. The dark and light gray area are the residual PPFD and SFG, respectively. The horizontal grey dashed line shows when $\Delta_{PAR} = 0$. BBF, PK and BAF are the starting, peak and endpoint of the sunfleck represented by vertical grey dashed lines. b) A single sunfleck with a local minimum. c) Two separate sunflecks. d) A sunfleck starting with a long left shoulder (slow initial increase in PPFD). e) Two overlapping sunflecks merged into one by the algorithm. Red, brown and blue filled circles are the peak, the baseline estimated before correction, and the true baseline after correction, respectively.

PPFD, instead of the average of PPFD at BBF and BAF. The PPFD between the starting and endpoint was linearly interpolated to simulate the PPFD in the absence of the sunfleck. This value of residual integrated PPFD was subtracted from the total integrated PPFD, to obtain the increase in PPFD caused by the sunfleck (SFG). We used the summed total of all the increases in PPFD due to sunflecks to examine which sunfleck properties contribute the most to the PPFD attributable to sunflecks. Finally, each time-period between the end of one sunfleck and the start of another was calculated and averaged to estimate the mean time between sunflecks (SFI). SFA and SFG were normalized by dividing them by the PPFD above the canopy. For every time-series, the spectrum at the highest and lowest PPFD was used to investigate differences between spectral composition during a sunfleck and the surrounding shade. We used the following wavebands: 315–400 nm (UV-A), 450–500 nm (blue), 620–680 nm (red), 700–750 nm (far red). UV-A/PAR, red to far red (R/FR), and blue to red (B/R) ratios were normalized by dividing them by their above-canopy value.

2.5. Data treatment and statistics

We used those times-series recorded with the shortest integration times (10 ms) to reconstruct time-series as if measured with longer integration times. For example, by adding the first and second data point in our time series, we could calculate the first data point in a simulated time-series at 20 ms integration time. This operation was repeated for the entirety of each time-series to simulate times-series of 20, 30, 50 and 100 ms integration time.

Statistical analyses were made using R 4.0.2 (R Core Team, 2020) with the packages "car", "emmeans" and "multcomp". A Type I ANCOVA was used to detect significant differences in sunfleck properties between crop species. The wind speed was used as a regressor in the analysis, and we deliberately choose a Type I (or sequential) sum of squares in order to take into account the variability attributed to wind speed. To test for significant differences between integration times, or category of light condition (i.e. sunfleck or shade), Type II ANOVAs were used. The effect of wind speed could not be tested in these cases, because all the data for each analysis were recorded at the same time, with similar wind conditions. Normality and homoscedasticity were checked graphically. Post-hoc contrast analyses were performed to test for differences between modalities of each factor. Significant differences were considered at $p < 0.05$ for all tests.

3. Results

3.1. Sunfleck properties are affected by the integration time at which they are recorded

Over seven 100s-long measured time-series per species with integration times of 10, 20, 30, 40, 50 60 and 80 ms (one time-series of each), 1294 sunflecks were identified in oat, 1945 in barley, and 334 in beans. At 10 ms integration time, no sunflecks were detected in the Vicia faba time-series. No trend was found between the integration time and the number of sunflecks identified. Similarly, while significant differences were found between integration times for SFA, SFG and SFI (data

not shown), partly because of the high statistical power provided by the large number of sunflecks identified, they did not show a consistent or meaningful trend. Only the SFD tended to increase for longer integration times in all three crop canopies ($p < 0.001$, Fig. 2). Sunflecks were also up to twice as long in the dicot broad bean than in the two monocot crops for integration times higher than 30 ms. Moreover, SFD was higher in the oats than in the barley for integration times higher than 60 ms.

By reconstructing times-series as if they had longer integration times from one measured with a 10 ms integration time, to allow the effects of integration time on apparent sunfleck properties to be directly tested, we were able to eliminate the variability in sunfleck occurrence and properties due to changes in wind intensity or canopy movement from our comparisons (Fig. 3). The results of these comparisons were consistent among all three crop canopies but with differing magnitude. SFA decreased slightly with longer integration times, but this trend was only significant in beans (Fig. 3a). Apparent SFD increased significantly by nearly 30 ms for each 10 ms increase in integration time (Fig. 3b). Longer integration times tended to produce sunflecks with a larger SFG (Fig. 3c); a trend which differed among species: oat (non-significant), barley, and even more strongly in beans where the effect of each increase in integration time was a significantly larger SFG. Finally, the SFI tended to increase with increasing integration times (Fig. 3d). Overall, sunflecks measured with a longer integration time had a longer duration and a lower amplitude (representing a smaller PPFD increase), as well as being less frequent, than when measured at a shorter integration time. More generally, our assessment of sunflecks will depend strongly on the integration time used.

3.2. Distinct sunfleck properties in three crop canopies

For the rest of this study, we consistently used an integration time of 10 ms to identify and measure short sunflecks as accurately as possible, and to allow direct comparison between our measurements. The wind speed had a significant effect on all sunfleck properties ($p < 0.002$ in every case), but accounted for a very small part of the explained variance (partial R^2 of 1.4%, 0.2% and 0.3% for SFA, SFG and SFI), except for SFD (partial $R^2 = 8.8\%$). Periods of higher wind speed, recorded as local hourly averages above the canopy, caused shorter sunflecks. Results were similar whether we included wind speed or not in the statistical analysis (including post-hoc tests). The species of crop that made up the canopy had a significant impact on all four sunfleck properties

tested (in every case $p < 0.001$). SFA normalized to above-canopy PPFD in the dicot beans canopy was about twice as large as in the two monocot canopies, and it was marginally but significantly higher in barley than in oats (Fig. 4a). The frequency distribution of SFD was similar for each species with very few sunflecks longer than 200 ms (Fig. A3). The longest sunfleck recorded in each canopy was 340, 450 and 360 ms in oat, barley and bean, respectively. Slight but significant differences in SFD were found among all three crop canopies, with the longest mean SFD (100 ± 2 ms) in the canopy of dicot beans and the shortest (85 ± 2 ms, Fig. 4b) in the barley canopy. Consequently, the mean SFG due to sunflecks, normalized to above-canopy PPFD, was twice as large in beans as in the two monocots (Fig. 4c). Furthermore, SFI was at least 30% longer in oats than in the other two canopies; being $0.32\,s \pm 0.03$, $0.20\,s \pm 0.02$ and $0.17\,s \pm 0.01$ for oat, barley and bean, respectively (Fig. 4d). Interestingly, on average, 2.3, 2.5 and 3.5 sunflecks per second were recorded in the oat, barley and bean canopies, which suggests a higher degree of sunfleck clumping (*i.e.* their propensity to occur in clusters) in barley than in oats. Overall, sunflecks in beans were more frequent, longer and had a larger amplitude than those in either of the two monocot canopies. Consequently, the SFG in beans was 4.2 and 3.7 times larger than that of oats and barley, respectively.

Fig. 5 illustrates the average and sum SFG as a function of SFD. Results were similar for all three species, with a sharp decline in the total contribution of sunflecks longer than 0.2 s, so we did not differentiate between species in this figure. Sunflecks of longer duration tended to make the largest individual contribution to the total increase in PPFD. On the other hand, since sunflecks of shorter duration were much more frequent, they were responsible for most of the increase in PPFD due to sunflecks.

3.3. Impact of canopy height on sunfleck properties

In oats, several times-series recorded at different canopy depths allowed us to identify significant differences in sunfleck properties with depth (in every cases $p < 0.001$, Fig. 6). The trend in SFA normalized to above-canopy PPFD was surprising, with sunflecks recorded at 50 cm above the ground having the smallest amplitude, and those recorded at 30 cm the largest (Fig. 6a). SFD decreased by more than 30% with canopy depth from 30 to 85 cm, although no significant difference in duration was found between sunflecks recorded at 30 and 50 cm below the top of the canopy ($p = 0.22$, Fig. 6b). Similar to SFA, the SFG
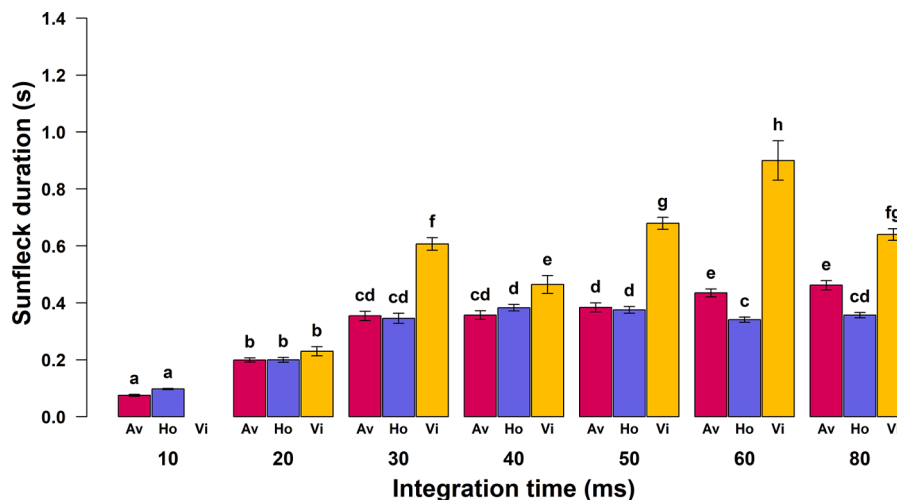

Fig. 2. Average sunfleck duration (SFD) in crop canopies of *Avena sativa* (*Av*, in red), *Hordeum vulgare* (*Ho*, in blue), and *Vicia faba* (*Vi*, in orange) from 100 s time-series of PPFD recorded using different integration times ($n = 1$). Each bar represents the mean $\pm$ 1 standard error of sunfleck duration from one time-series. Different letters indicate statistically significant differences ($p < 0.05$) between groups tested by *post-hoc* pairwise comparisons.
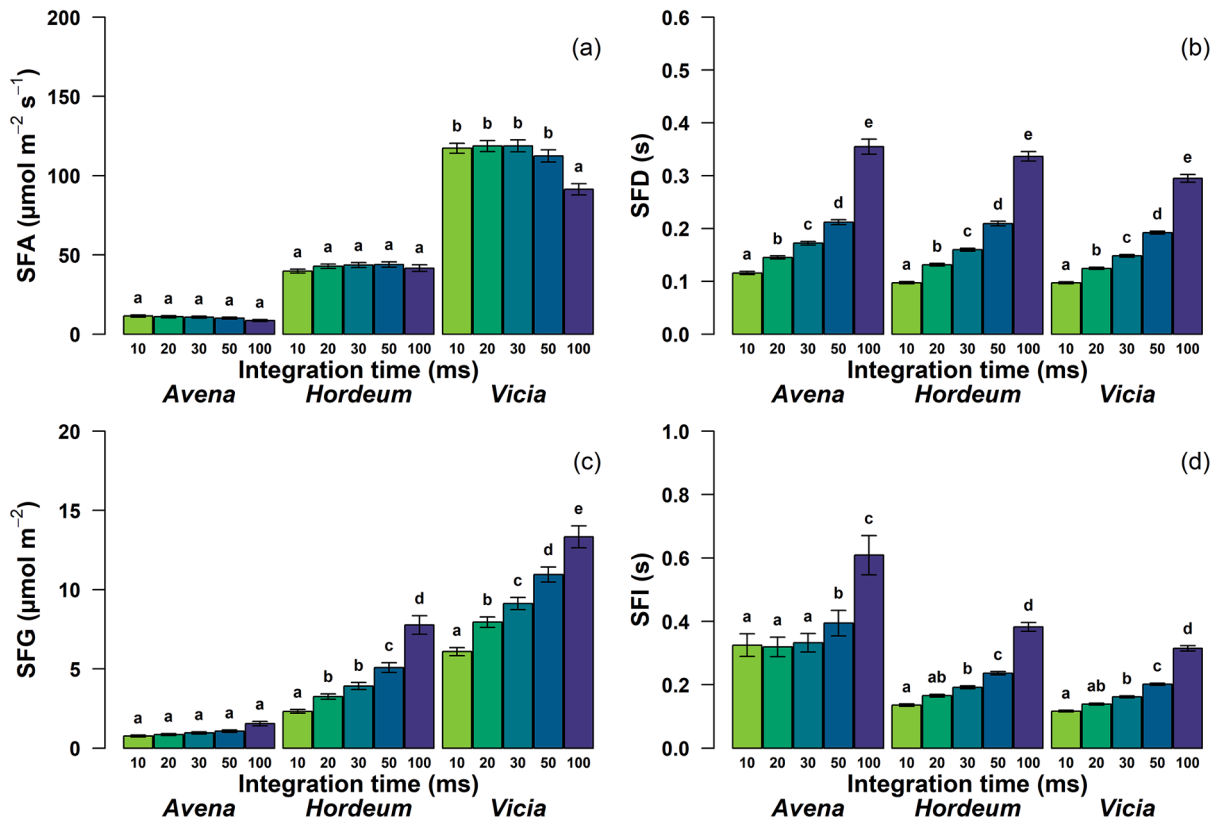
Fig. 3. Sunfleck properties in *Avena sativa, Hordeum vulgare* and *Vicia faba* from reconstructed times-series at longer integration times from one measured with a 10 ms integration time. (**a**) Sunfleck amplitude normalized to above-canopy PPFD (SFA), (**b**) sunfleck duration (SFD), (**c**) integrated increase in PPFD during the sunfleck normalized to above-canopy PPFD (SFG), and (**d**) mean time between sunflecks (SFI). Color gradient from green to blue indicates increasing integration time of the time-series (10, 20, 30, 50 and 100 ms). Bars show means ± 1 standard error. Within each crop species canopy, different letters represent statistically significant differences between groups tested by *post-hoc* pairwise comparisons ($p < 0.05$).
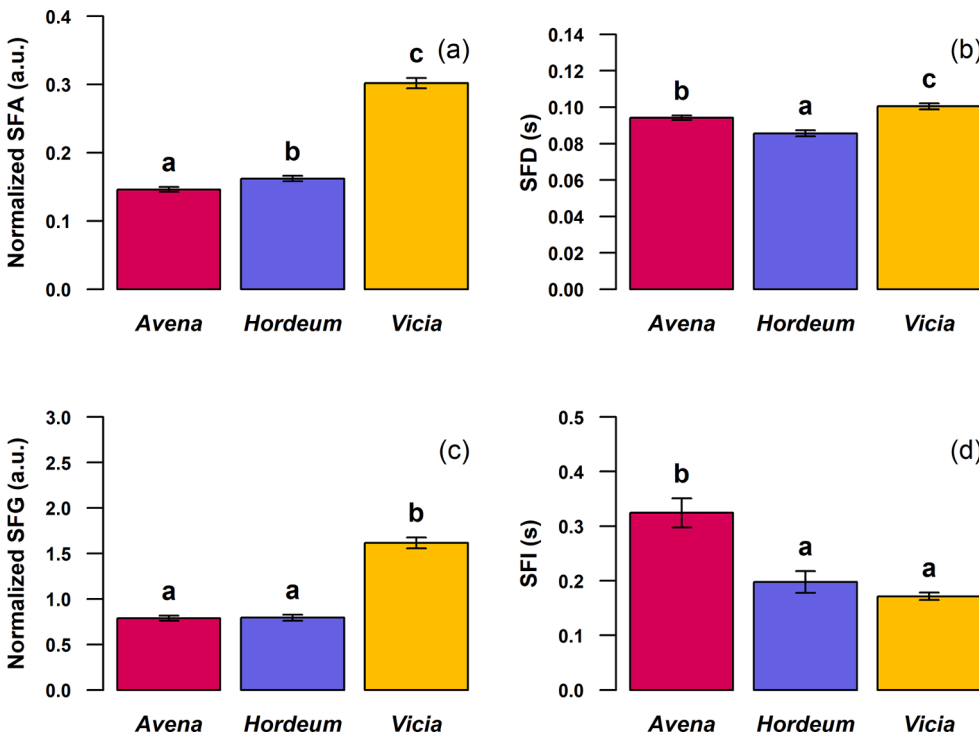

Fig. 4. Sunfleck properties in *Avena sativa* (in red), *Hordeum vulgare* (in blue) and *Vicia faba* (in orange) canopies. (**a**) Sunfleck amplitude normalized to above-canopy PPFD (SFA), (**b**) sunfleck duration (SFD), (**c**) integrated increase in PPFD during the sunfleck normalized to above-canopy PPFD (SFG), and (**d**) mean time between sunflecks (SFI). Bars show means ± 1 standard error. Different letters represent statistically significant differences between groups tested by *post-hoc* pairwise comparisons ($p < 0.05$).
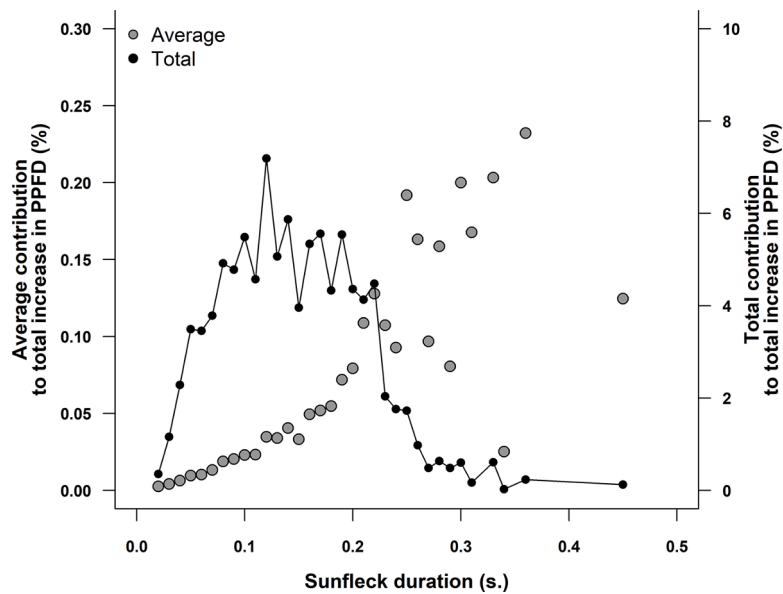
Fig. 5. Average (gray dots – left *y*-axis) and total (black dots and line - right *y*-axis) contribution to the total increase in PPFD (*i.e.* the proportion of the sum total increase in PPFD) due to a sunfleck in relation to the sunfleck duration in *Avena sativa*, *Hordeum vulgare* and *Vicia faba* canopies.

Fig. 6. Sunfleck properties in an *Avena sativa* canopy at a depth of 30, 50, 65 and 85 cm (on the ground since the canopy was 85 cm high). (**a**) Sunfleck amplitude normalized to above-canopy PPFD (SFA), (**b**) sunfleck duration (SFD), (**c**) integrated increase in PPFD during the sunfleck normalized to above-canopy PPFD (SFG), and (**d**) mean time between sunflecks (SFI). Darker colored bars indicate measurement was taken deeper in the canopy. Bars show means $\pm$ 1 standard error. Different letters represent statistically significant differences between groups tested by *post-hoc* pairwise comparisons ($p < 0.05$).
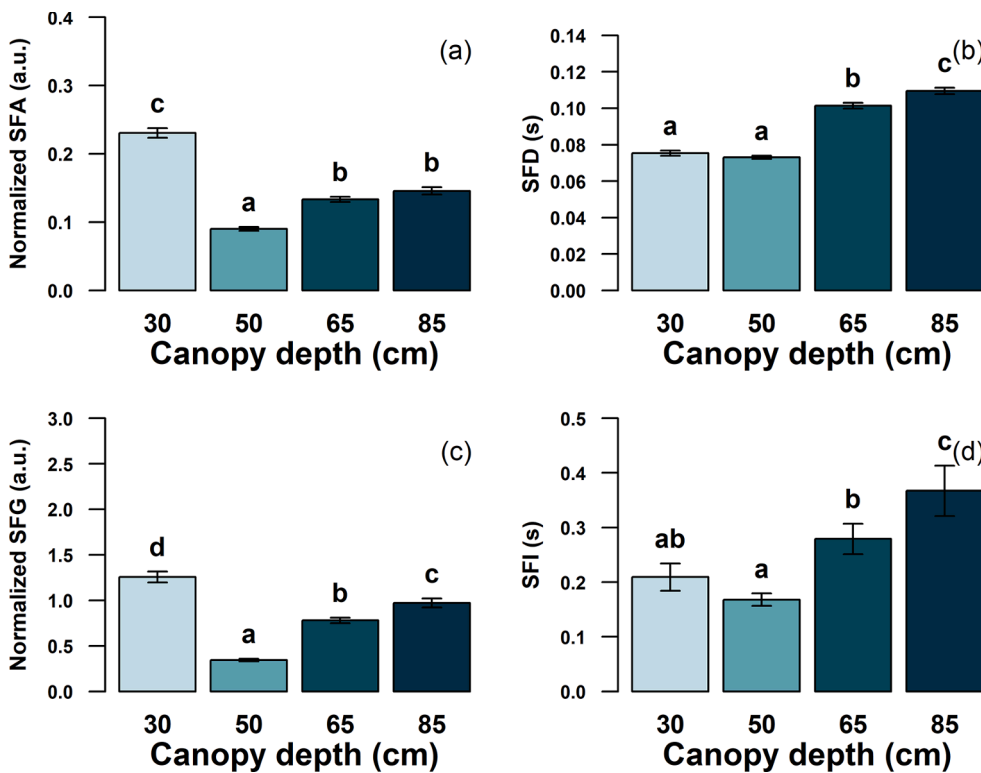
normalized to above-canopy PPFD decreased from the top of the canopy until 50-cm depth: it was highest at 30 cm below the canopy top, however also increased significantly at every depth beneath 50 cm ($p <$ 0.001, Fig. 6c). On average, 2.6, 3.6, 5.8 and 4.7 sunflecks occurred per second for recordings 85, 65, 50 and 30 cm beneath the top of the canopy. The SFI decreased with canopy depth until 50 cm ($0.37\ s \pm 0.05$, $0.28\ s \pm 0.03$, $0.17\ s \pm 0.01$ and $0.21\ s \pm 0.03$ for 85, 65, 50 and 30 cm, Fig. 6d). No significant difference in SFI was found between time-series recorded at 50 and 30 cm above the ground. Overall, sunflecks higher in the oat canopy tend to be shorter and more frequent.

3.4. Distinct spectral composition of sunfleck and shade photon flux density

The spectral composition of incident radiation during a sunfleck was very different from that of the surrounding shade (Fig. 7). The normalized UV-A/PAR ratio was 1.9, 1.5, and 1.5 times higher in the shade than during a sunfleck for oats ($p < 0.001$), barley ($p = 0.003$) and beans ($p = 0.003$), respectively (Fig. 7a). Moreover, in the shade the UV-A/PAR ratio was 1.2 times higher in oats than in beans ($p = 0.027$). On the other hand, R/FR was up to 3.3 times higher during a sunfleck than in
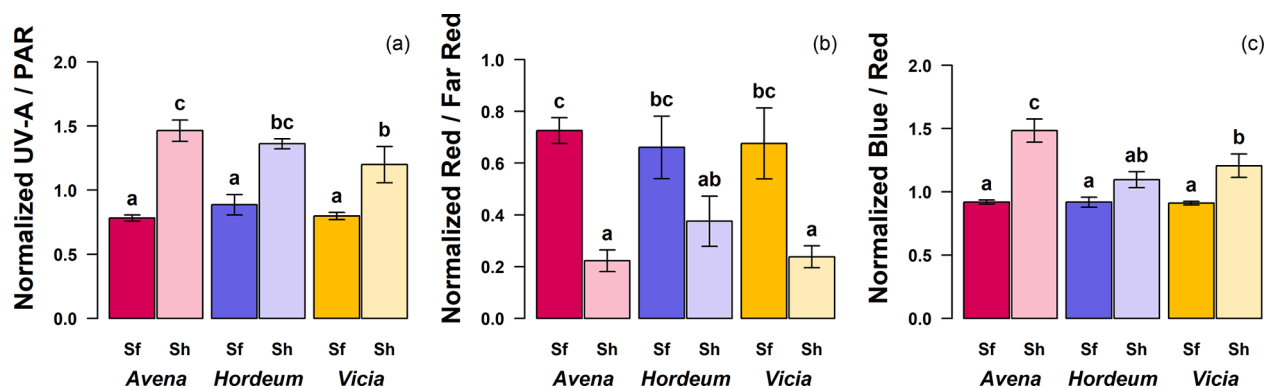
Fig. 7. Spectral composition of photon flux density during a sunfleck (Sf) or under shade (Sh) in *Avena sativa* (in red), *Hordeum vulgare* (in blue) and *Vicia faba* (in orange) canopies. (**a**) UV-A/PAR, (**b**) Red/Far Red and (**c**) Blue/Red were normalized to above-canopy PPFD. UV-A: 315–400 nm, Blue: 450–500 nm, Red: 620–680 nm, Far red: 700–750 nm. Bars show means ± 1 standard error. Different letters represent statistically significant differences between groups tested by *post-hoc* pairwise comparisons ($p < 0.05$).

the surrounding shade, although the difference was not significant in barley ($p = 0.1$, Fig. 7b) only in oats and beans ($p < 0.004$). As for the B/R ratio, only oats and beans exhibited a respective 38% and 25% decrease in the ratio during a sunfleck as compared to the shade ($p < 0.001$), despite a similar trend in barley (Fig. 7c).

4. Discussion

4.1. Sunfleck properties are affected by the measurement integration time

Most studies investigating sunfleck properties have measured irradiance every 1 to 5 s (Tang et al., 1988; Vierling and Wessman, 2000), only occasionally as often as every 50 ms (Roden and Pearcy, 1993), and rarely report the integration time, because of technical limitations or a focus on sunflecks of longer duration. While our comparison of times-series made with different integration times showed strong variabilities dues to wind patterns (*e.g.* no sunfleck were detected in the beans at 10 ms, Fig. 2), reconstructed time-series showed that using a shorter integration time allowed us to better discriminate between sunflecks (Fig. A4) and resulted in the identification of shorter and more frequent sunflecks with a higher amplitude (Fig. 3). This effect of decreasing the integration period is consistent irrespective of the time steps compared, as illustrated by Chazdon (1988) who compared two time-series with 2 or 10 s intervals. This is due to smoothing of fluctuations in photon flux density over longer integration times (see Fig. A4), whereby the peaks of the sunflecks are averaged with neighbouring data points of lower PPFD. Using a shorter integration time leads to a substantial gain of information about the interval of time between sunflecks, their duration and amplitude. The decrease in integration time actually reduces the PPFD increase attributable to sunflecks, as the significant reduction in their duration is greater than the concurrent marginal increase in their amplitude (Fig. 3). This pattern is again due to the averaging of photon flux density over longer integration times producing longer sunflecks but with simpler shapes and a higher baseline of PPFD in shade (Fig. A4). Every threshold value in the algorithm mentioned above was found to correctly detect all features that were expected to be sunflecks; as verified by visually inspecting every time-series. Although, we cannot exclude the possibility that different threshold values may work better for time-series from other canopies under different conditions (see R code in appendix B).

With these considerations in mind, the integration time chosen when measuring sunflecks should be adapted to the goal of the study. In general, an integration time at most a third the duration of the sunflecks of interest is recommended, in order to describe each sunflecks with a minimum of four time points. Significant measurement errors, and misinterpretations could be produced when analysing shorter sunflecks,

e.g. from wind flutter. Our results also suggest that it would be complicated to accurately compare sunfleck properties from studies using different sampling rates or integration times.

4.2. Sunfleck properties are affected by canopy structure

Although there is a strong presumption that canopy structure alters sunfleck properties (Pearcy et al., 1990), methodical examinations of the impact of specific canopy traits on sunfleck properties are strikingly rare (Kaiser et al., 2018). When comparing *Triticum aestivum, Zea mays* and *Helianthus annuus*, Peressotti et al. (2001) only found marginal differences between the three canopies. In another study examining the effect of canopy structure on light fluctuations, sunflecks in *Sinapis alba* were shorter, had a lower amplitude and were 12 times less frequent than in *Triticum durum* (Kaiser et al., 2018), but neither of these studies discussed potential canopy traits responsible for these differences. We found that beans had longer, more frequent sunflecks with a much larger amplitude than in the two monocots species. In oats and barley, sunflecks were more similar, with the same SFG, although they were shorter, less frequent, but with a higher amplitude in barley (Fig. 4).

Usually, leaf orientation in oats is found to be more erectophile than in barley, whereas beans have by far the most planophile leaf orientation distribution of the three (Table 1; Ross, 1981; Zou et al., 2014). Penetration of radiation into the canopy, and thus potentially sunfleck properties, is moderated by leaf orientation and biomechanical properties of the individual organs (Burgess et al., 2017). Using a modelling approach, Song et al. (2013) found that a more planophile leaf orientation distribution increases photosynthesis when plant area index (*i.e.* the one-sided area of canopy elements per unit ground surface area, PAI) is low because of a reduction in radiation incident on the ground, but decreases photosynthesis when PAI is high because of greater self-shading. The higher canopy and greater leaf area together with a more erectophile leaf distribution may have created a more open canopy that is also more sensitive to the wind, contributing to the higher frequency and duration of sunflecks found in oats compared with barley (Table 1, Fig. 4d). In forests, as tree height and leaf area increase, SFA and SFD are considered to decline in the understorey (Chazdon and Pearcy, 1991). In a study of *Phaseolus vulgaris* canopy development, the number of sunflecks shorter than 1.2 s increased while that of sunflecks longer than 1.2 s decreased with growing stages (Barradas et al., 1998). In our experiment, the canopy heights for oats, barley and beans were 85 cm, 65 cm and 55 cm, respectively. Although large differences in leaf area between canopy species depending on planting density are common in the literature (Zou et al., 2014; Baez-Gonzalez et al., 2020), the lower canopy height and planting density in beans (Table 1), and associated increased gap sizes, may have contributed to the higher SFA

and lower SFI we found in this canopy. While our study lays the groundwork, in showing clear differences in sunfleck patterns between crop species, the large species-specific differences in canopy structure make the task of attributing particular sunfleck properties to leaf or canopy traits difficult. More targeted research examining specific canopy traits, such as the differences in leaf shapes, will help to address this question.

With depth in the canopy, we found that sunflecks were longer and less frequent. This is consistent with Barradas et al. (1998) who found in *P. vulgaris* both a higher overall number, and a higher proportion of shorter sunflecks when the sensor was placed 20-cm above, rather than directly on, the ground (canopy height was 38.6 cm). Similar results were also obtained in a *Glycine max* canopy (Pearcy et al., 1990), and a Congolese rainforest canopy where sunflecks were measured at three heights (Vierling and Wessman, 2000). When considering the physics of branch architecture and a stem anchored to the ground at it base, it makes sense that the top of the canopy will be displaced further by wind-induced movement than lower parts of the canopy. In other words, there is more movement at the top than at the bottom of the canopy, thus SFD should decrease and sunfleck frequency increase with height in the canopy. The patterns of SFA with depth that we found; decreasing dramatically from the top until 50 cm in depth but then increasing again at 65 and 85 cm (Fig. 6a), are however not so easily explained. In forests, a decrease in SFA with depth due to a rise of penumbral effects is expected because of the reduction of the distance between the gap in the canopy and the sunfleck location (Smith et al., 1989; Vierling and Wessman, 2000). In crop canopies, where the canopy is compressed into a much smaller height, penumbral effects are less pronounced, thus are less likely to impact sunfleck properties. This is because their area on the incident surface is inversely correlated to the distance from the opening on the canopy to the incident surface. However, the decreasing background PPFD with depth in shade (from 540 to 137 $\mu mol\ m^{-2}\ s^{-1}$ between 30 and 85 cm in canopy depth) may play a role in increasing the SFA lower in the canopy. The sensor is relatively close to the top of the canopy, at 30 cm depth, where sunflecks are mainly created by the flag leaf and ears of oats. Under such circumstances, the peak PPFD of the sunfleck would be similar to the above-canopy PPFD, and the baseline PPFD would occur in the fully shaded inner region of a shadow cast by the flag leaf and ears (umbra), which would be darker than the surrounding light environment.

Most of the sunflecks we recorded in this study were generated by movements of the canopy prompted by light gusts of wind. Wind typically induces shorter sunflecks at a higher frequency than those created by the sun trajectory in the sky (Pearcy, 1990). A precise measure of the wind experienced by the plant, recorded in the canopy simultaneously with time-series of PPFD would better allow us to examine how wind speed and direction affect sunfleck properties. Moreover, canopy biomechanical properties will impact how wind creates movement in the canopy, and thus affect the patterns of light distribution. Although the natural frequency (ratio of stiffness to mass per unit length of the stem) of oat and barley is similar (Table 1), it may differ in beans due to their distinct morphology. Planting density can restrict these movements by providing mutual support by physical contact among plants (Burgess et al., 2019). Traits such as petiole and sheath flexibility, leaf and stem length, width, mass, and tensile strength will affect the canopy light environment differently depending on the 3D arrangement of stems and leaves in canopies (Burgess et al., 2016).

The differences in spectral composition during sunflecks compared with the shade were overall similar in the three canopies. The main exceptions being in oats shade where the UV-A/PAR ratio was higher than in beans, and the B/R ratio was higher than in barley (Fig. 7). Different leaf optical properties might potentially impact how radiation is scattered in the canopy (Endler, 1993; Grant, 1997), including species-specific differences of chlorophyll, anthocyanins, or flavonoid pigments in the leaves (Sims and Gamon, 2002). The higher B/R, and lower R/FR under shade than sunflecks is in agreement with established

patterns of spectral composition from comparisons of spectral irradiance above and within canopies (Navrátil et al., 2007; Hertel et al., 2011; Hartikainen et al., 2018). These patterns are probably due to preferential leaf absorption in the red waveband compared to far red, and preferential scattering of blue wavelengths in the atmosphere, plus a stronger decrease in PPFD compared to UV in canopy shade led to a higher UV-A/PAR in the shade (Grant, 1997). Since small differences in the strength of blue light can have a large influence on stomatal conductance (Shimazaki et al., 2007; Košvancová-Zitová et al., 2009; Matthews et al., 2020), a higher proportion of blue light may lessen stomatal closing under shade. In general, low stomatal conductance in the shade can lead to diffusion limitations for photosynthesis, thus limiting carbon gain during a sunfleck (Tinoco-Ojanguren and Pearcy, 1993; Way and Pearcy, 2012). Moreover, while the B/R ratio is lower during a sunfleck than in the surrounding shade, more blue light is incident on the leaves during a sunfleck than in the shade, which often leads to increased stomatal conductance that can be sustained by frequent sunfleck occurrences (Kirschbaum et al., 1988). The blue light response is mediated by phototropins independent of photosynthesis, and considered to lead to faster stomatal opening than the red light response (Shimazaki et al., 2007; Matthews et al., 2020; Wang et al., 2020). With regards to the higher R/FR ratio in sunfleck than in the surrounding shade, this cue is perceived by phytochromes and is involved in the shade avoidance response, albeit at longer time scales than sunflecks (Ballaré, 1999). Furthermore, changes in the UV-A/PAR ratio received by barley has been found to affect their photosynthetic response. In an experimental manipulation, treatments creating distinct ratios of UV-A/PAR affected leaf morphology, photosynthetic capacity, and increased the abundance of specific photoprotective compounds in barley plants (Klem et al., 2012, 2015). Altogether these responses show that during development, the canopy structure influences sunfleck properties, but the sunflecks themselves can also affect canopy structure and processes in return.

4.3. Sunfleck properties and their potential to affect photosynthesis

We found that shorter sunflecks contributed more to the total PPFD than longer sunflecks, because they occur at much higher frequency, regardless of canopy species (Fig. 5). This finding differs from what is commonly reported in the literature for both forests and crops (Way and Pearcy, 2012), where shorter sunflecks, while being numerous, are not considered as important for canopy photosynthesis (Pearcy, 1990; Kaiser et al., 2018). Our results may reflect the higher resolution at which we recorded sunflecks compared with previous studies. In a soybean canopy, sunflecks shorter than 1.6 s contributed less than 7% to the total irradiance available for photosynthesis, but longer sunflecks (up to 10 s) contributed 33% (Pearcy et al., 1990). Similarly, sunflecks longer than 60 s, while representing only 2% of all sunflecks, contributed by more than 80% of the daily total irradiance in a Queensland rainforest understorey (Pearcy et al., 1994). In forests, sunflecks longer than a minute (non-existent in most crop canopies) due to the movement of the sun may contribute more to the irradiance attributable to sunflecks. Latent photosynthetic metabolic pools allow sustained post-illumination CO_2 fixation, extending the total period of photosynthesis attributable to a sunfleck beyond its duration, and representing a larger proportion of the total CO_2 assimilated as sunflecks get shorter (Pons and Pearcy, 1992). Moreover, in longer sunflecks (> 10 s), pools of residual photorespiratory metabolites lead to a temporary reduction in net CO_2 assimilation, thus longer sunflecks are considered to be less efficiently used by the photosynthetic machinery (Chazdon and Pearcy, 1991). Consequently, short but more frequent sunflecks would lead to better sunfleck use efficiency (calculated by comparing actual CO_2 assimilation to the modelled steady-state rates of CO_2 assimilation) than long but less frequent sunflecks summing to the same total integrated irradiance. However, frequent sunflecks are likely to have a cumulative effect on leaf temperature which can enhance photorespiration (possibly mediated by the temperature response of photosynthesis) partially offsetting

the dividend from increased photosynthetic CO_2 assimilation (Leakey et al., 2003). Similarly, repeated sunflecks can impede the slow relaxation of non-photochemical quenching, and thus could lead to further reductions of CO_2 assimilation in between sunflecks (Kromdijk et al., 2016; Murchie and Ruban, 2020). Considering the short time-scale of the sunflecks we measured (down to 20 ms), one may wonder about the degree to which increasingly shorter sunflecks can contribute to photosynthesis, and the lower limit of what can be considered a biologically relevant sunfleck? Gorton et al. (2003) estimated a resistance to CO_2 diffusion of about 5 s cm^{-1}, which for a path length of CO_2 of 100–500 µm would lead to 50–250 ms for a molecule of CO_2 to diffuse from the stomata to the chloroplasts. This could limit the efficient use of short sunflecks when CO_2 diffusion is limiting, for example when stomatal conductance is low. Although photosynthetic processes operate at different time-scales, if we consider the case when photosynthesis is light-limited, even a single additional photon would contribute to increasing NADPH and ATP pools that can be used in the Calvin cycle, thus increasing CO_2 assimilation. To our knowledge, this question has not yet been answered, partly because of instrument limitations dictating the minimum time steps feasible for photosynthesis measurements. While chlorophyll fluorescence can be used to measure electron transport at very short time scales (typically up to 400,000 records s^{-1}), devices measuring gas exchange struggle to record data faster than 1 record s^{-1}, because of diffusion limitations and a low signal to noise ratio. Moreover, models of photosynthesis predominantly use a steady-state framework (Way and Pearcy, 2012). This can lead to large errors in the estimation of photosynthesis (Naumburg and Ellsworth, 2002). Further research and technical development are required before we understand the impact of these high-frequency light fluctuations on photosynthesis, which may also affect modelling of photosynthesis.

4.4. Conclusion

Contrary to previous studies, we found that sunflecks shorter than 0.2 s contributed substantially more than longer ones to the total PPFD attributable to sunflecks because of their greater frequency (Fig. 5). While the effects this can have on photosynthesis still need to be determined, this knowledge will help researchers define relevant fluctuating light conditions for studying plant growth in controlled environments (Kaiser et al., 2018), when considering that the dynamics of photosynthesis differs depending on growth conditions (Kursar and Coley, 1993; Durand et al., 2020).

Our results show that measurement frequency directly impacts the perceived properties of sunflecks recorded, whereby shorter integration times allow the dynamics of the canopy light environment to be described more precisely. We also characterized differences in sunfleck properties and their frequency with canopy depth and between crop species differing in canopy structure. The physiological effect of very short sunflecks on the ecophysiology of photosynthesis has received little attention, thus more research and technological improvements such as faster direct measurement of CO_2 assimilation, are needed to understand how they are used in photosynthesis and how they affect plant productivity. This knowledge should help agricultural scientists better optimize crop selection for effective light use. In the future, researchers may consider improving canopy photosynthesis models by modelling sunfleck patterns, which would require the identification of specific canopy traits linked with sunfleck properties and would thereafter open the possibility to model sunfleck patterns from canopy structure.

Author contribution

M.D., B.M. and T.M.R. contributed to the data collection and experimental design. M.D., T.M.R., and A.J.B. contributed to the data analysis and interpretation and all authors contributed to the writing of the manuscript.

Data availability

The data that supports the findings of this study are available upon request.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108554.

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