ORIGINAL ARTICLE

The effect of canopy architecture on the patterning of "windflecks" within a wheat canopy

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Abstract

Under field conditions, plants are subject to wind-induced movement which creates fluctuations of light intensity and spectral quality reaching the leaves, defined here as windflecks. Within this study, irradiance within two contrasting wheat (*Triticum aestivum*) canopies during full sun conditions was measured using a spectroradiometer to determine the frequency, duration and magnitude of low- to high-light events plus the spectral composition during wind-induced movement. Similarly, a static canopy was modelled using three-dimensional reconstruction and ray tracing to determine fleck characteristics without the presence of wind. Corresponding architectural traits were measured manually and in silico including plant height, leaf area and angle plus biomechanical properties. Light intensity can differ up to 40% during a windfleck, with changes occurring on a sub-second scale compared to ~5 min in canopies not subject to wind. Features such as a shorter height, more erect leaf stature and having an open structure led to an increased frequency and reduced time interval of light flecks in the CMH79A canopy compared to Paragon. This finding illustrates the potential for architectural traits to be selected to improve the canopy light environment and provides the foundation to further explore the links between plant form and function in crop canopies.

KEYWORDS
light intensity, photosynthesis, spectral quality, wheat (*Triticum aestivum*), wind-induced movement

1 | INTRODUCTION

Light intensities can differ 20- to 50-fold between the top and bottom of a canopy, with lower leaf layers often experiencing low levels of light interspersed with brief periods of high light termed "sunflecks" (Evans, 1956; Stadt, Gendron, Lieffers, Messier, & Comeau, 1999; Townsend et al., 2018). Traditionally, these sunflecks have been

viewed as direct light penetrating often static canopy gaps, such as in an understorey environment, and thus are related to solar movement. However, sunflecks are also prevalent within crop canopies, largely as a result of wind-induced movement. Wind is a feature of all field environments, yet the impact of wind-induced movement on the characteristics of light reaching individual leaf elements has received little attention. A number of factors contribute to these light characteristics including canopy architectural traits, which develop with plant age, the biomechanical movement of the canopy, the optical properties

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and structure of leaf material, coupled with local weather conditions including sun elevation, cloud cover plus wind speed and direction (Burgess et al., 2016; de Langre, 2008; Grace, 1988).

Historically, research in plant and crop photosynthesis has focused on rates of CO_2 uptake under steady state light conditions. However, it is increasingly apparent that photosynthetic productivity is also determined by dynamic changes in environmental variables, and there is often a time lag before photosynthesis can respond (Murchie et al., 2018). The heterogeneity of the light environment influences how plants respond to and exploit available resources for photosynthesis and crop production. This has been recently demonstrated through changes in biomass production via altering capacity for photoprotection and the speed of recovery (Hubbart et al., 2018; Kromdijk et al., 2016). However, to quantify the impact of a particular photosynthetic process on potential productivity requires knowledge of the precise "signature" of light dynamics and the accompanying changes to spectral composition. For example, rapid fluctuations may lead to an overall increase in productivity due to maintenance of a higher induction state of photosynthesis (Acevedo-Siaca et al., 2020; Burgess et al., 2016; Retkute et al., 2015; Roden & Pearcy, 1993a; Wang, Burgess, de Becker, & Long, 2020). Longer periods of low light cause the de-activation of enzymes and stomatal closure and vice versa. Another benefit of wind-induced changes in the light environment could arise through homogenizing the light available such that photosynthesis will be increased if there is a narrower distribution for a given time-integrated photon flux density due to the non-linear response. Understanding the precise spatiotemporal light dynamics in different canopy structures is thus essential for predicting the impact of these different processes on whole-plant photosynthesis.

The majority of existing studies have characterized the effect of sunflecks within a forestry setting, where periods of high light can persist for minutes or even hours depending on the structure of tree crowns (Chazdon & Pearcy, 1991; Pallardy, 2008; Way & Pearcy, 2012). In such cases, the sunflecks, on a background diffuse irradiance (i.e., shade), can contribute a large percentage of incident irradiance for understorey plants (Barradas, Jones, & Clark, 1998; Pfitsch & Pearcy, 1989; Roden & Pearcy, 1993a; Tang, Washitani, Tsuchiya, & Iwaki, 1988). However, more interest has arisen recently on the effect of fluctuating light in the agricultural setting, where the structure of a crop stand leads to very different patterns of radiation over smaller spatial, and often temporal, scales, with direct consequences in terms of photosynthetic productivity (Kromdijk et al., 2016; Murchie et al., 2018; Murchie, Pinto, & Horton, 2009; Slattery, Walker, Weber, & Ort, 2018; Wang et al., 2020).

Wind affects both the plant canopy and its interactions with the environment, according to both the wind speed and the duration of gusts. In turn, and as a consequence, the structure of a plant is constrained and shaped by wind such as dwarfing characteristics (Gardiner, Berry, & Moulia, 2016). The resulting *in canopy* light environment will be altered in terms of frequency, duration and amplitude of high light events. It can be expected that the most drastic effects of wind-induced movement are felt in lower canopy layers, where the movement of overhanging leaf material can lead to increased light penetration. A period of high light intensity becomes more likely as the canopy starts to move, but the average duration of such periods may be lower than during still conditions (Tong & Hipps, 1996). The effect (and possibly biological function) of movement, especially in upper layers, therefore, becomes that of light scattering and distribution, facilitating photosynthesis in lower leaf layers. Previously, this has been compared to a disco "mirrorball" spinning at fast or slow speeds; with spin speed correlating with likelihood of a high light event (Burgess et al., 2016).

The response of an organ to wind will depend upon its length, surface area and mass. The range of motion or potential risk of breakage will also depend upon the strength of the supporting structure as well as the leaf blade, which is in turn related to dry matter accumulation combined with the strength of the vein and thus the water status (Derzaph & Hamilton, 2013; Gonzalez-Rodrigues, Cournède, & de Langre, 2016). In the case of cereal crops, the size, weight and surface area of the ear will also determine movement properties. However, cultivation in dense stands makes movement difficult to characterise due to collisions between neighbouring plants (Doaré, Moulia, & de Langre, 2004). Nevertheless, at low wind speeds, leaf movement is expected to dominate due to low mass and high surface area, whilst higher wind speeds induce greater movement in supporting structures (i.e., stems or branches). Few studies consider wind-induced movement under low wind speeds, with more work aimed at the biomechanical properties required to prevent stem or root failure under damaging wind speeds during lodging events (Berry, Spink, Foulkes, & Wade, 2003; Berry, Sylvester-Bradley, & Berry, 2007). One key structural trait to reduce lodging risk is plant height; with reduced heights leading to a reduction in the leverage that is imposed by the aerial organs on the supporting structure (Berry, Sterling, & Mooney, 2006). Consequently, plant height will be critical in determining overall biomechanics and light patterning within a crop stand as plant height is closely linked to natural frequency with taller plants generally having a higher natural frequency.

The spatial arrangement of leaf material combined with wind-induced movement leads to a complex pattern of both light intensity and spectral composition throughout canopies. As light enters the canopy, leaves will preferentially deplete the most useful wavelengths for photosynthesis, predominantly red and blue, and scatter those absorbed less effectively by chlorophyll such as ultraviolet, green and far red (Evans & Anderson, 1987; Smith, McAusland, & Murchie, 2017). This leads to alterations in the proportion of wavelengths reaching lower canopy layers with a steep decrease in the red: far red (R:FR) ratio (R = λ600-700, FR = λ700–800 nm) and a concurrent increase in UV-A:PAR ratio (UV-A = λ315-400, PAR = λ400–700) followed by a more shallow decline in the blue: green (B:G- where B = λ400–500 nm, G = λ500–600 nm) light gradient (Smith et al., 2017). However, as leaf material alters position, we can expect both the quantity and spectral composition of light to change.

Here we will use "windfleck" to refer to the more rapid changes in light intensity brought about by canopy movement, which are our primary focus, compared to high-light events induced by solar movement penetrating [static] canopy gaps (the traditional "sunfleck"). "Fleck" is used as a term to describe an overall change in irradiance

(with or without wind). These periods of high light are often defined as irradiances differing by a certain threshold value or from a certain percentage of the baseline irradiance (Barradas et al., 1998; Miyashita et al., 2012; Roden & Pearcy, 1993b). They can be distinguished based on whether their divergence is positive or negative, with a "sunfleck" referring to an increase in irradiance from a baseline, and a "shadefleck" a decrease, in irradiance from a baseline of direct sun. Until recently, very little research has been aimed at uncovering the optimal protocol to detect and measure the properties of light fluctuations taking place within canopies. This includes among others, analytical approaches to circumvent arbitrary thresholds described above, and quantifying the impact of measurement frequency and integration time of the measurement of light. Previous work has used diverse measurement frequencies ranging from every 50 ms to 5 s (Pfitsch & Pearcy, 1989; Roden, 2003). This can lead to significant loss of information when measuring frequency, peak intensity and duration of any changes in irradiance (Chazdon, 1988). A new method and an associated algorithm is available to characterize key features of light fluctuations including duration, amplitude and average time between high-light events (Durand, Matule, Burgess, & Robson, 2021).

Whilst studies are beginning to arise that assess light interception within canopies of different crops subject to wind-induced movement (Durand et al., 2021), there is very little information on how specific architectural traits influence light patterning at the high-resolution required to assess windflecks. Due to the wide range of architectural differences seen between different crops, it is therefore difficult to attribute a specific trait to the characteristics of windflecks that are observed. Thus, there is a need for comparative studies with diverse varieties of the same crop type. Within this study, we aim to determine how wind-induced movement alters the pattern of light quantity and quality reaching different layers within a wheat canopy. Two architecturally contrasting varieties will be used determine how features such as plant height and leaf stature alter both biomechanics and the resulting light environment. By measuring the canopies subject to wind, and modelling the canopies using ray tracing techniques in a static formation, we aim to characterize the key features of light reaching leaves under field conditions.

2 | MATERIALS AND METHODS

2.1 | Plant material and growth

Two wheat (*T. aestivum*) lines with contrasting canopy architectures were selected from an ongoing field trial at the University of Nottingham farm (Sutton Bonington Campus) in Leicestershire, UK (52.834 N, 1.243 W), on a sandy loam soil type (Dunnington Heath Series) in 2019. The spring bread wheat cultivar Paragon, a representative high yielding variety from the United Kingdom, was contrasted against variety CMH79A.955/4/AGA/3/4*SN64/CNO67//INIA66/5/NAC/6 /RIALTO; hereby referred to as CMH79A taken from the CIMMYT Mexico Core Germplasm Panel (CIMCOG; Piñera-Chavez, Berry, Foulkes, Jesson, & Reynolds, 2016). The experiment used a completely randomized block design with three replicate blocks. The

plot size was 6×1.65 m^2, and the sowing date was 1st March 2019. Previous cropping was winter oats (*Avena sativa*). The field was ploughed, power harrowed and rolled after drilling. The seed rate was adjusted by genotype according to 1,000 grain weight to achieve a target seed rate of 350 seeds m^{-2}; rows were 0.125 m apart. A total of 120 kg/ha N fertilizer as ammonium nitrate was applied in a two-split program. P and K fertilizers were applied to ensure that these nutrients were not limiting. Plant growth regulator was applied at GS31 (stem elongation) to reduce the risk of lodging. Herbicides, fungicides and pesticides were applied as required to minimize the effects of weeds, diseases and pests. One growth stage was analysed: post-anthesis ($\sim$GS70; Zadoks, Chang, & Konzak, 1974).

A weather station was situated in close proximity (approx. 30 m) to the field site. Photosynthetically active radiation (PAR) above the canopy, wind speed, wind direction, temperature, humidity, soil moisture and rainfall were monitored throughout growth using the following sensors: SQ-110 Quantum sensor (Apogee, Utar, USA), WindSonic1 ultrasonic wind sensor (GillInstruments, Lymington, UK), CS215 temperature and humidity probe (Sensirion, Switzerland), 107 thermistor probe (BetaTherm, Galway, Ireland) and the Kalyx-RG aerodynamic rain gauge. The wind sensor was mounted approximately 1.5 m above the ground. Measurements were recorded at every second using the CRX1000X data logger (Campbell Scientific, Leicestershire, UK) from 45 days after sowing (DAS) until harvest.

2.2 | Structural, biomechanical and leaf optical measurements

Ten plants of each variety across the three replicate plots were removed for biomechanical and physical analysis using the lodging protocol described in Berry et al. (2000). This included measurements such as plant height, height at the centre of gravity, root and ear number per plant, ear area, internode length and wall width and breaking strength. A validated model for lodging in winter wheat (Berry et al., 2003) was used to calculate biomechanical features of the two contrasting genotypes including natural frequency.

Absorbance by epidermal flavones, anthocyanins and leaf chlorophyll content was measured non-invasively with optical leaf clip Dualex Scientific + (henceforth Dualex) at two canopy positions (at 25 and 50 cm height) at the leaf tip, centre and base of both adaxial and abaxial sides of leaves. The measurements were performed around solar noon (approximately ±2 hr) to exclude potential diurnal variation in UV absorbance by flavones and chloroplast movement (Barnes et al., 2016; Williams, Gorton, & Witiak, 2003).

2.3 | 3D canopy reconstruction for architectural analysis

3D analysis of plants was made according to the protocol of Pound, French, Murchie, and Pridmore (2014) with further details given in Burgess et al. (2015). Two wheat plants per plot (i.e., six per line) were selected and carefully removed for imaging. Water was supplied to the

roots to prevent wilting. At least 40 images per plant were taken and reconstructions made as described in Burgess et al. (2015). Reconstructed canopies were formed by duplicating and randomly rotating the four best reconstructed plants in a 5 by 3 grid, with 13 cm between rows and 5 cm between plants, in accordance with the planting pattern. Each reconstructed canopy is formed of a set of triangles.

Total light per unit leaf area was predicted using a forward ray-tracing algorithm implemented in fastTracer (version 3; PICB, Shanghai, China; Song et al. (2013). Latitude was set at 53 (for Sutton Bonington, UK), atmospheric transmittance 0.5, light reflectance 7.5%, light transmittance 7.5%, day 184 (3rd July). FastTracer3 calculates light as direct, diffused and transmitted components separately; these were combined together to give a single irradiance level for all canopy positions. Irradiance values were recorded for the 3 hr around solar noon (1130–1430 hr) at 1 min time intervals; the highest resolution possible via this method. This allowed the analysis of fleck patterns in a static canopy (i.e., they do not move with a simulated wind) during full sun. The ray tracing boundaries were positioned so that they bisect the outer plants (e.g., Retkute, Townsend, Murchie, Jensen, & Preston, 2017) to reduce boundary effects.

All modelling was carried out in Mathematica (Wolfram Research Inc., IL). Cumulative leaf area index (cLAI; leaf area per unit ground area as a function of depth) and cumulative fractional interception (cF; fractional interception as a function of depth) was calculated from each of the canopy reconstructions as in Burgess et al. (2015) for the solar noon time point.

Fleck analysis was performed as described in Section 2.5 using 1,586 time series of triangles (i.e., canopy locations) at 25 and 50 cm (±2.5 cm) per each variety reconstructed canopy.

2.4 | In canopy light measurements

Solar spectral irradiance within the wheat canopies was measured with portable CCD array spectroradiometer; the Maya 2000 pro (Ocean Optics, Dunedin, FL, USA) with D7-H-SMA cosine diffuser (Bentham Instruments Ltd., Reading, UK) with spectral range of 200–1100 nm. The spectrometer had been calibrated within the last 6 months by Finnish Radiation and Nuclear Safety Authority (Aphalo, 2017; Aphalo, Robson, & Piiparinen, 2016; Ylianttila, Visuri, Huurto, & Jokela, 2005) for accurate outdoor solar radiation measurement from UV-B to near-infrared radiation (290–900 nm). A detailed measurement and post-processing protocol used is described in Hartikainen, Jach, Grané, and Robson (2018). Integration time for measurements was set to 2-to-4 Hz to capture at high signal-to-noise ratio rapid changes in irradiance and spectral quality brought about by wind-induced movement. Measurements were taken over three consecutive days during full sun conditions but with similar average wind speeds of approximately 3 m/s.

All irradiance measurements were made within 3 hr of peak solar irradiance at solar noon. Measurements were taken in either the top or bottom half of the canopy, using the midpoint at 35 cm height as a cut-off; hereby referred to as top and bottom. At least four time-series of 20–100 spectra, were recorded at the two heights × two

measurement points × two genotypes. Each time series captured the range of variation in the canopy, recording the dynamics flecks over a period of up to ∼30 s according to the integration time selected. To achieve measurements which encompassed the range of variation in under-canopy irradiance, sets of measurements were made at different measuring points that consisted of, either (a) predominantly direct radiation (sunfleck; Smith & Berry, 2013), or (b) predominantly diffuse radiation (shade), with the wind creating patterns of light fluctuations during the course of the measurement hereafter.

2.5 | Windfleck analysis

The windfleck analysis was performed on a subset of the dataset for increased repeatability of the results. Only measurements recorded with an integration time of 300 ms or lower were used. Each time-series was reviewed manually to decide whether to identify brief increases (sunfleck) or decreases (shadefleck) of irradiance depending on which dominated the time-series. Because integration time will influence the description of sun- or shadefleck properties, a simple linear model was created to take the integration time into account (Durand et al., 2021), whilst a second model was applied to the residuals of the original model to determine the fleck characteristics. Briefly, time-series of photosynthetically active radiation (PAR, 400–700 nm) were used to detect windflecks using an algorithm based on the properties of first order derivatives. The start and endpoint of fleck can be identified when the numerical derivative crosses zero (i.e., when PAR switches from increasing to decreasing, and vice versa). The algorithm corrects for cases where flecks have multiple peaks; in order to classify as a single fleck those fluctuations that produced multiple peaks without a significant change of PAR (Durand et al., 2021). The duration (i.e., time difference between the start and end of the fleck), the difference in PAR between the peak and baseline irradiance, and frequency (average time between two flecks) were measured for each windfleck.

2.6 | Statistical analysis

Analysis of Variance (ANOVA) was carried out using Genstat for windows (19th Edition; VSN International Ltd., UK). Data was checked to see if it met the assumption of constant variance and normal distribution of residuals. For optically measured leaf pigments, modelled and measured fleck characteristics, the post hoc Tukey's test was used at a probability level of $p < .05$.

3 | RESULTS

3.1 | Plant structural and biomechanical features

Two contrasting wheat genotypes were chosen to assess the effect of wind-induced movement on the duration, magnitude and frequency of high light events in a field grown canopy (Figure S1). These

differences were reflected in the key structural and biomechanical traits of each genotype given in Table 1. Paragon was significantly taller than CMH79A (~34%), with a correspondingly higher centre of gravity (~32%). Similarly, Paragon had, on average, more ears per plant (~13%), but a much-reduced ear surface area (~51%). These features did not lead to a significant difference in natural frequency between the two varieties.

To further explore the architectural properties of the two genotypes, plants were reconstructed in silico. Figure 1 indicates the final reconstructed plant canopies for each line post anthesis. Visual differences can be seen between the two genotypes; namely the increased plant height and curled leaf stature in paragon compared to a sparser canopy in CMH79A. Leaf angle distributions were calculated for each canopy and averaged at each canopy depth (Figure 2; Burgess et al., 2015, 2017), where a leaf inclination angle towards 0 indicates a more horizontal leaf and an inclination angle of 90 indicates a more vertical leaf. When viewed as a distribution as a function of the percentage of the canopy, Paragon orientated a larger amount of leaf material approaching horizontal angles whilst CMH79A had a greater percentage of the canopy with more erect leaf angles. This confirms the visual observation of more horizontal and straighter flag- and lower-leaves in CMH79A.

Leaf area index (LAI) was calculated as the area of mesh (reconstructed plant material) relative to ground area and was 7.10 and 3.69 in Paragon and CMH79A, respectively (Table 1). Whilst these values are highly disparate, they are in line with previous studies on UK- and Mexican-varieties (Rivera-Amado, Molero, Trujillo-Negrellos, Reynolds, & Foulkes, 2020; Townsend et al., 2018). This can be viewed as a function of depth (cumulative LAI; cLAI) to indicate how plant material was distributed throughout the canopy. Figure 3a indicates a greater amount of leaf material is found in the lower half of the Paragon canopy, whereas leaf material appeared to be relatively consistent throughout the CMH79A canopy; determined by the steepness of the curve. Differences in the distribution of leaf material has consequences for light attenuation through canopies calculated as cumulative fractional interception (cF). A slightly greater proportion of light was intercepted by Paragon, with full saturation of the cF curve by approximately ~85 cm from the top of the canopy (Figure 3b). Within CMH79A, leaf material between 15 and 35 cm from the top of the canopy intercepts the majority of light however not all radiation is intercepted by the canopy, and some was able to reach the ground (i.e., cF does not reach 1.0). The more "open" characteristics of the CMH79A canopy led to an overall increase in the mean light intensity experienced by the majority of leaf area, which is seen by the existence of two distinct positions for peaks in surface area fractions in the top halves of the canopy: as seen in Figure 3c. These are positioned remarkably far apart with Paragon peaking at around 50 μmol m^{-2} s^{-1} and CMH79A at 200 and again at 1000 μmol m^{-2} s^{-1}. Similar results are seen for the time averaged light intensity over the 3-hour period around solar noon (Figure S2). This indicates striking differences in light distribution for two canopies of spring wheat cultivars with comparable productivity and yield potential.

3.2 | Patterns in optically measured leaf pigments

Non-destructive optical measurements of leaf pigments were made at the top of the canopy and in the lower canopy at equivalent heights to the spectral irradiance measurements (Figure 4). Leaf chlorophyll content was up to 50% higher in CMH79A than in Paragon at the base and mid leaf positions in both the top and bottom halves of
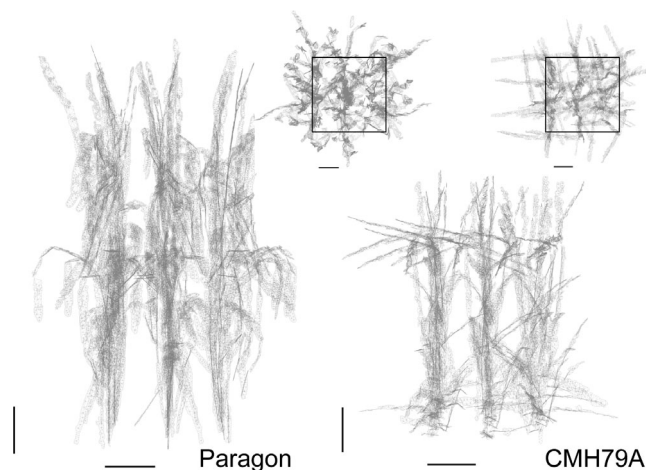

FIGURE 1 Structural differences between the two contrasting wheat lines; Paragon and CMH79A Plants were imaged and reconstructed as a single plant according to the protocol of Pound et al. (2014). These were then duplicated and rotated and arranged on a 3 × 5 canopy grid with 12.5 cm between rows and 5 cm between plants within a row, reflective of cultivation practice. The scale bar indicates 10 cm whilst the top right insert shows the top-down view of each canopy with the ray tracing boundaries (see Materials and Methods) depicted by the outline

TABLE 1 Select plant structural and biomechanical characteristics for each genotype at growth stage (GS) 71–73 (Zadoks et al., 1974)

Genotype	Height to ear tip (cm)	Height at centre of gravity (cm)	Ear number	Ear area (cm^2)	Natural frequency (Hz)	Reconstructed LAI
Paragon	80.36 ± 20.15*	42.71 ± 13.61*	1.7 ± 0.21	8.937 ± 0.32*	1.298 ± 0.10	7.10*
CMH79A	60.17 ± 19.92*	32.35 ± 15.06*	1.5 ± 0.17	17.556 ± 1.30*	1.146 ± 0.08	3.69*

Note: Measurements were taken according to the lodging protocol of Berry et al. (2003). Results are the average of 10 plants ± *SEM*. Reconstructed LAI was calculated as the area of the mesh (triangles) of the reconstructed plants within the designated ray tracing boundaries (see Section 2), statistically measured based on the LAI of the individual plants forming the canopy.

*Indicates a significant difference between genotypes calculated using an ANOVA ($p < .01$).

FIGURE 2 Leaf angle distributions as a percentage of total canopy area where an angle towards 90° indicates a more horizontal leaf and towards 0° indicates a more vertical leaf. (a) Frequency distributions as a function of area, (b) Average leaf inclination angle as a function of height above ground
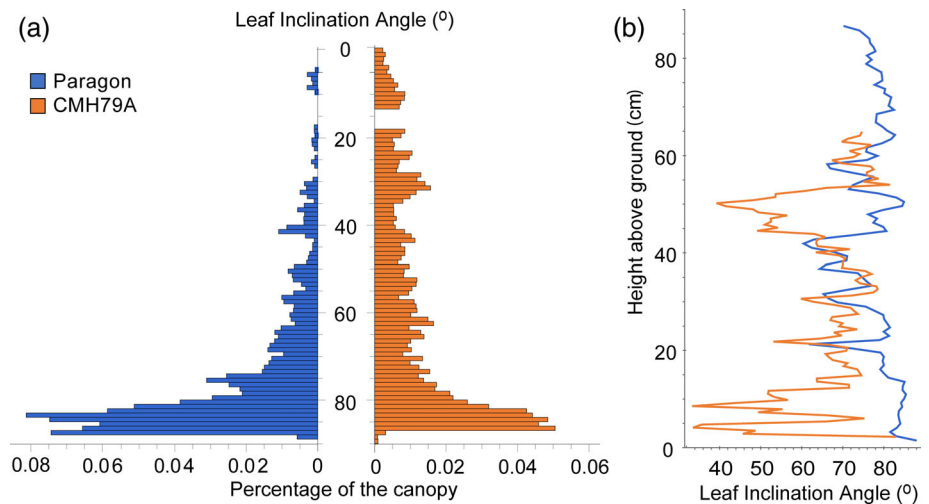
the canopy. The decline in chlorophyll content from leaf base to leaf tip was also more pronounced in CMH79A at both positions; with up to 30% at both the top and bottom halves of the canopy compared to up to 20% for the top half of Paragon, only. Paragon leaves were visibly starting to discolour in the lower canopy, also evident from their lower chlorophyll content. The base-to-tip increase in epidermal flavones on the abaxial side was less pronounced in Paragon, which has a curl in its upper leaves, than in CMH79A which does not exhibit a curl, with a high flavone index in the mid-leaf section which is most-prominently exposed to sunlight. Anthocyanins followed a similar general pattern to flavones between varieties but were higher at the tips of the adaxial side of the leaf in Paragon in the bottom of the canopy.

3.3 | Fleck characteristics in architecturally contrasting wheat canopies

Within this paper, sunflecks generally refer to an increase in irradiance from the background value whilst a shadefleck refers to a decrease in irradiance from the background value. This can occur in either static canopies (not subject to wind) or in mechanically moving canopies (subject to wind). This latter example can be grouped into the term "windflecks." The first derivative of a time series in irradiance values, measured either manually or simulated through ray tracing, was analysed to determine key features of the flecks (Figure 5).

3.3.1 | Flecks in static canopies

Under [modelled] static conditions, irradiance was lower in paragon than CHM79A at equivalent canopy positions (Figure 6a). Baseline PAR values in the top half of the canopy in CMH79A were approximately three times that of Paragon, whilst the bottom half of the canopy experienced PAR values approximately twice as high as Paragon. However, during both a sunfleck and a shadefleck, the percentage change in irradiance was greater in Paragon, up to 50% (Figure 6a inset), despite an overall similar absolute change in irradiance

(Figure S3a). For both varieties, the duration of—and time between—sunflecks was greater in the bottom half of the canopy compared to the top half (Figure 6b,c); with each fleck lasting between 3 and 4 min, with 4–5 min between flecks. The duration of—and time between—flecks is consistently lower in CHM79A indicating an overall faster frequency of changes in irradiance of a reduced magnitude in a canopy with upright leaves, compared to Paragon (Figure 6).

3.3.2 | Flecks in mechanically moving canopies: Windflecks

In general, the irradiance was lower at equivalent heights in Paragon than in CMH79A, especially in the lower canopy (Figure 7a).

The duration of sunflecks was longer in Paragon than in CMH79A (1 and 0.5 s, respectively) in the bottom half canopy, with comparatively similar durations for the top of the canopy in both varieties (Figure 7b). Similarly, the mean time between sunflecks was greater in Paragon in the bottom half of canopy (2 and 0.75 s in Paragon and CMH79A, respectively), with a similar, though non-significant, trend visible in the top half of the canopy (Figure 7c). Whilst CMH79A produced sunflecks of a reduced length with a reduced time between them, the difference in PAR during the windfleck was much greater, both as a percentage change and absolute (Figure 7a, inset; Figure S3b) indicating a more intense sunfleck (up to 35% increase in irradiance) during movement. To determine how the properties of the windflecks influenced the intensity and spectral composition of light reaching the leaves, ratios of different spectral regions were compared. The UVA:PAR, B:R and B:G ratios remained relatively consistent with baseline shade levels during sunflecks in Paragon (Figure 8a–c). However, within CMH79A higher values for all three ratios were experienced in the top half of the canopy compared to that of Paragon, with greater percentage reductions than Paragon during sunflecks. As expected, the R:FR ratio was lower in the bottom half of the canopy for both genotypes but was lower in Paragon than CMH79A at each canopy position (Figure 8d). Whilst the relative difference in the R:FR ratio was not significant with depth in Paragon, both the top and bottom halves of the CMH79A canopy showed
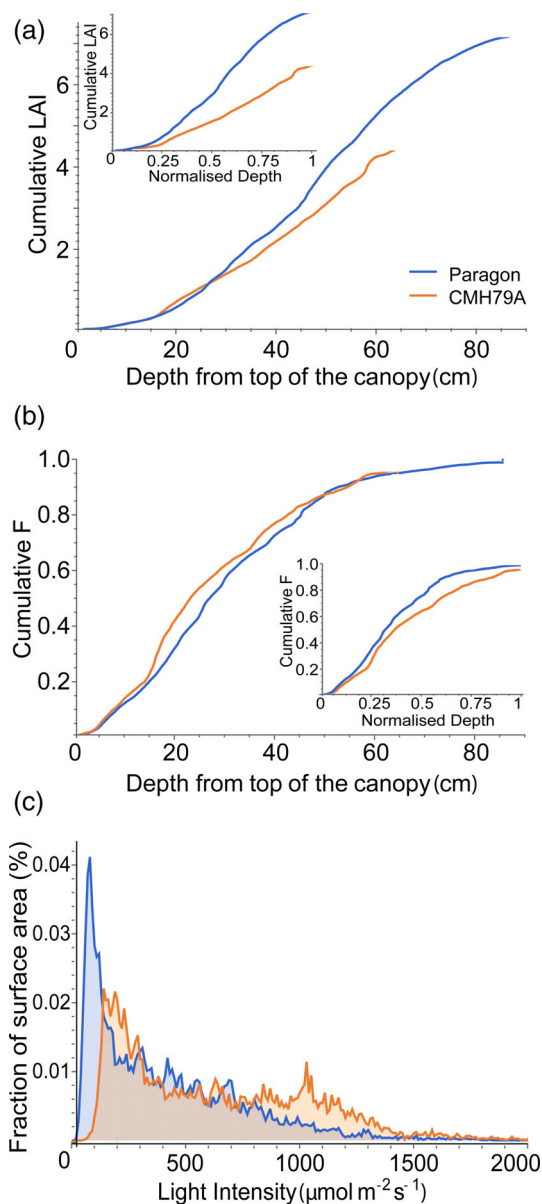
FIGURE 3 Canopy leaf area and light interception for Paragon and CMH79A. (a) Modelled cumulative leaf area index (cLAI), the area of leaf material (or mesh area) per unit ground as a function of depth through the canopy (i.e., distance from the top). (b) Modelled cumulative fractional interception (cF), the fractional interception of light per unit ground area as a function of depth through the canopy where $F = 1.0$ when all light is intercepted (i.e., no light reaches the ground). The inset graphs show cLAI and cF as a function of normalised depth in the canopy. (c) Light intensity as a fraction of the total area of the canopy calculated using ray tracing (Song et al., 2013) at 1300 hr under a full-sun simulation in the top half of each canopy [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 4 Content of optically measured leaf pigments in Paragon and CMH79A canopies. (a) Chlorophyll content, (b) anthocyanin content, (c) flavone content. Different letters indicate significant differences following ANOVA and post hoc Tukey's test at the $p < .05$ level [Colour figure can be viewed at wileyonlinelibrary.com]

significant (up to 12%) differences in the ratio or R:FR during a sunfleck compared to the baseline values. Together, this indicates that during a sunfleck, the spectral composition of light reaching leaf material in Paragon is relatively consistent compared to the irradiance in the background shade, whereas in CMH79A leaves experience a shift in the
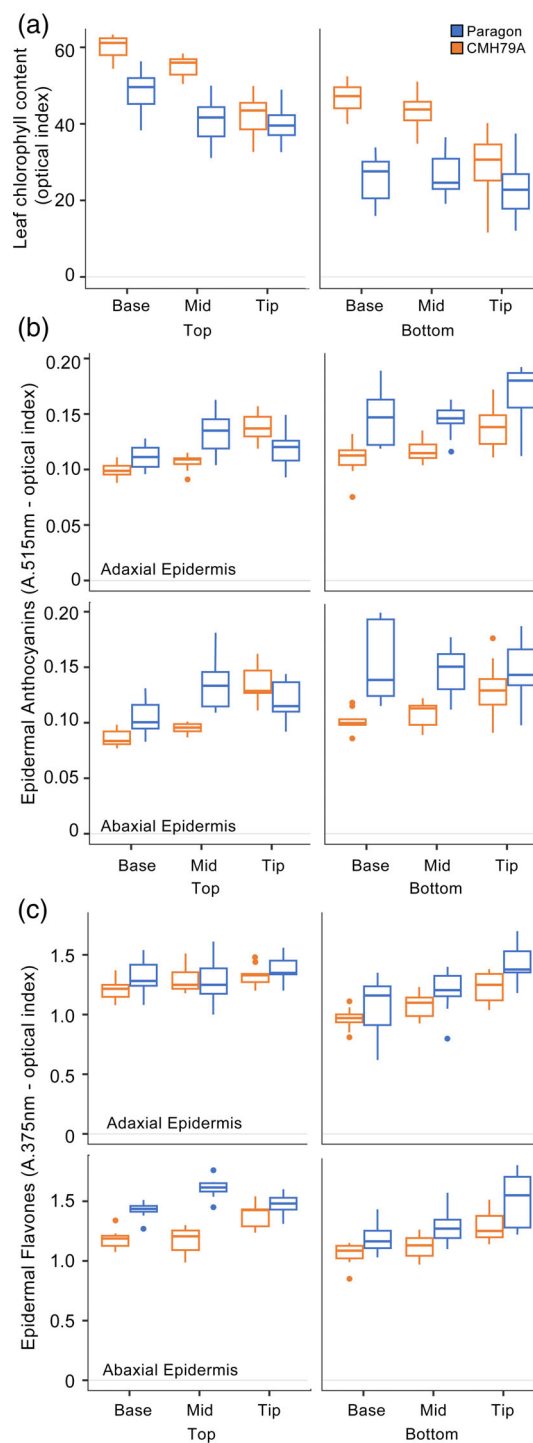
quality of light available in both canopy positions for the UVA:PAR and R:FR ratios as well as in the bottom of the canopy for the B:R ratio. It may be expected that R:FR and B:G change in a coordinated way and that is generally what is observed here.
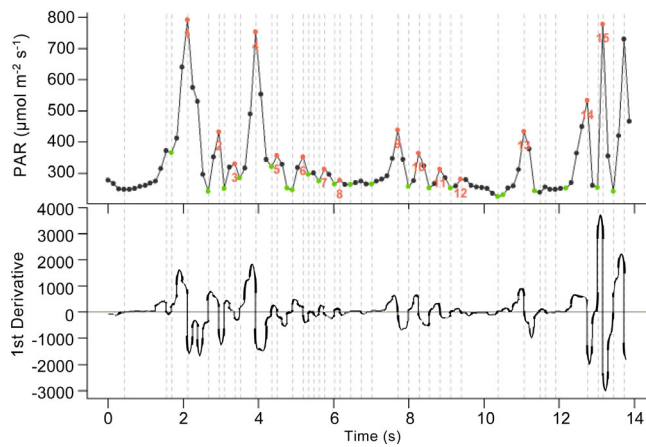
FIGURE 5 Example time series of a sunfleck from the top of an CMH79A wheat canopy. Upper panel indicates the fluctuation in light intensity with green dots showing the base level of each sunfleck and red, numbered dots indicating the peak of each fleck in order during the time course. The lower panel indicates the first derivative of the same time series where the base and peak coincide with the point where the line crosses the x-axis, as shown with the dotted lines. See Durand et al. (2021) for further details [Colour figure can be viewed at wileyonlinelibrary.com]

The PAR level experienced at the baseline during shadeflecks were much greater than those during sunflecks (Figure 7a). Whilst both Paragon and CMH79A receive similar PAR irradiance ($\sim$1200 µmol m^{-2} s^{-1}) within the top half of the canopy, CMH79A receives approximately three times the PAR of Paragon in the bottom of the canopy as a result of its open structure (Figures 1–3). During a shadefleck, PAR irradiance was significantly reduced (up to 15%) in CMH79A in the lower canopy, whilst Paragon did not experience a significant change in PAR irradiance. The duration of—and time between—shadeflecks was relatively consistent in both varieties (Figure 7b,c). The UVA:PAR, B:R and B:G ratios were significantly higher in CMH79A compared to Paragon in the top half of the canopy only, but these ratios did not differ significantly during shadeflecks relative to the background sun values (Figure 8a–c). Similarly, the R:FR ratio was higher in CMH79A relative to Paragon throughout the whole canopy, with a significant decrease in the ratio in the lower portion of CMH79A during a shadefleck (Figure 8d).

In short, while sunflecks were longer and less frequent in the Paragon canopy, CMH79A experienced more intense light fluctuations as both sunflecks and shadeflecks in the mechanically moving canopies.

4 | DISCUSSION

4.1 | Canopy architecture affects the dynamics of light in a canopy

Architectural features such as plant height, LAI and leaf area density (LAD), leaf shape and leaf-, stem- or tiller-angle combined with the biomechanical properties of plant material all determine the potential
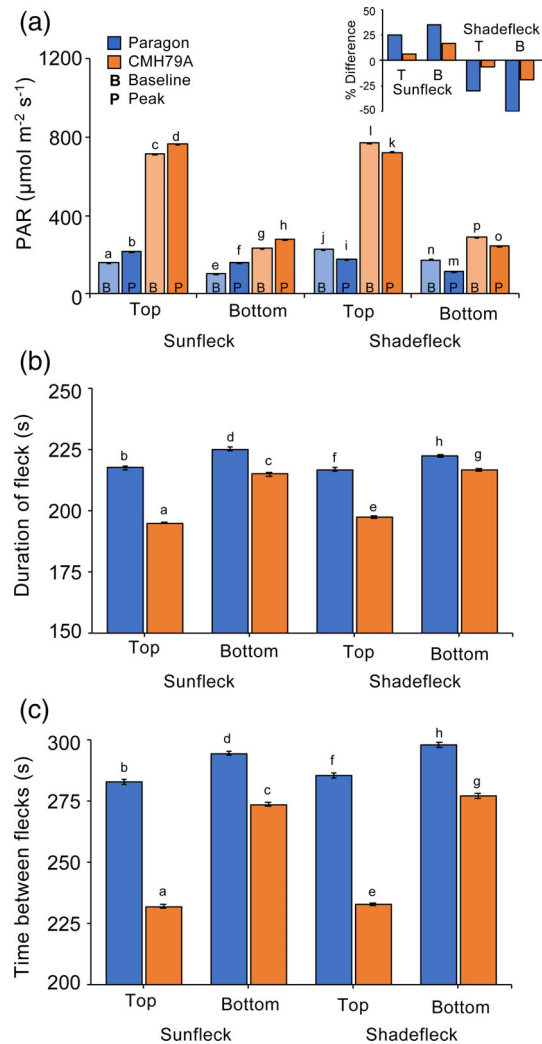

FIGURE 6 Modelled characteristics of sun- and shadeflecks throughout two architecturally diverse wheat canopies in a static formation calculated using three-dimensional reconstruction and ray tracing. (a) Average light intensity during the peak and base of the fleck where the inset indicates the percentage difference in PAR between the baseline and peak of each fleck, (b) average sunfleck duration, (c) mean time between sunflecks; calculated from ray tracing data. The data is grouped based on the nature of the variation of light: either sunfleck (temporary increase of irradiance) or shadefleck (temporary decrease of irradiance) and the height at which the measurement was taken: in the top or bottom half of the canopy. $M \pm SEM$ where different letters indicate significant differences following ANOVA and post hoc Tukey's test at the $p < .05$ level [Colour figure can be viewed at wileyonlinelibrary.com]

conformations and movement of a canopy in response to the environment. Whilst usually given as a measure to predict the failure wind speed of cereal crops during lodging events (Berry et al., 2007), natural frequency describes the shape and speed at which plant elements, such as wheat stems, will sway when subject to wind. Natural frequency is determined by a number of structural traits and will influence the dynamics of light reaching lower canopy layers, thus linking the form and function of a plant. In general, it has been seen that the lower the natural frequency, the lower the failure wind speed
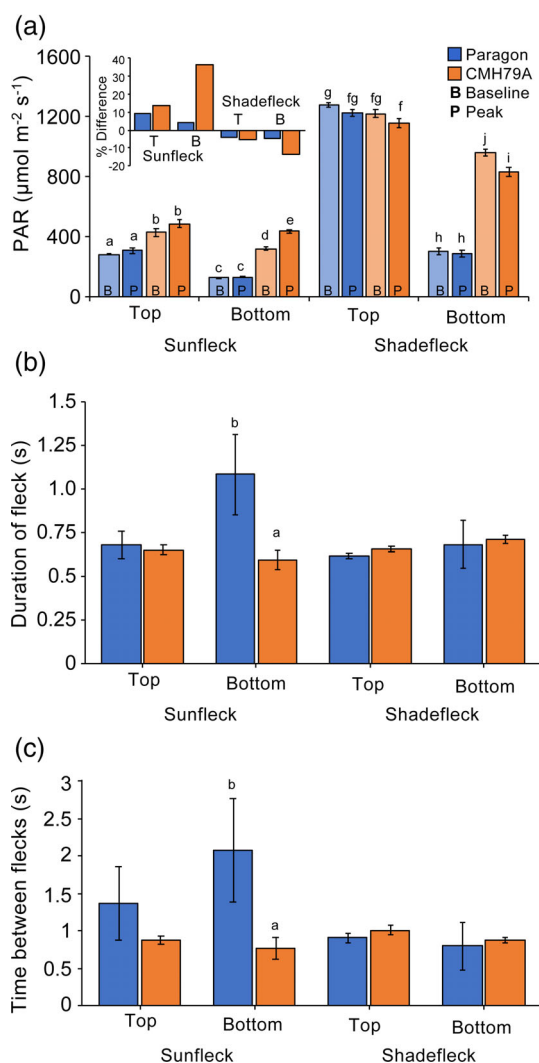
FIGURE 7 Measured characteristics of sun- and shadeflecks throughout two architecturally diverse wheat canopies during mechanical movement in the wind captured using a spectroradiometer. (a) Average light intensity during the peak and base of the fleck where the inset indicates the percentage difference in PAR between the baseline and peak of each fleck, (b) average sunfleck duration, (c) mean time between sunflecks. The data is grouped based on the nature of the variation of light: either sunfleck (temporary increase of irradiance) or shadefleck (temporary decrease of irradiance) and the height at which the measurement was taken: in the top or bottom half of the canopy. $M \pm SEM$ where different letters indicate significant differences following ANOVA and post hoc Tukey's test at the $p < .05$ level [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 8 Changes in the spectral composition of light during a sun- and shadefleck in two architecturally contrasting varieties of wheat. (a) UVA to PAR ratio (b) blue to red ratio (c) blue to green ratio and (d) red to far red ratio. Each inset indicates the percentage difference in the given ratio between the baseline and peak of each fleck. $M \pm SEM$ where different letters indicate significant differences following ANOVA and post hoc Tukey's test at the $p < .05$ level [Colour figure can be viewed at wileyonlinelibrary.com]

(Baker, 1997). Within this study, there was no significant differences between the natural frequency of the two varieties. Whilst the values are within the range of those seen in other studies of natural frequency with measured values between 0.9 and 2.5 Hz and theoretical values up to 5.3 Hz (Piñera-Chavez, Berry, Foulkes, Molero, & Reynolds, 2016; Susko, Marchetto, Heuschele, & Smith, 2019), a greater difference in the natural frequency value may have led to stronger differences in the characteristics of flecks seen.
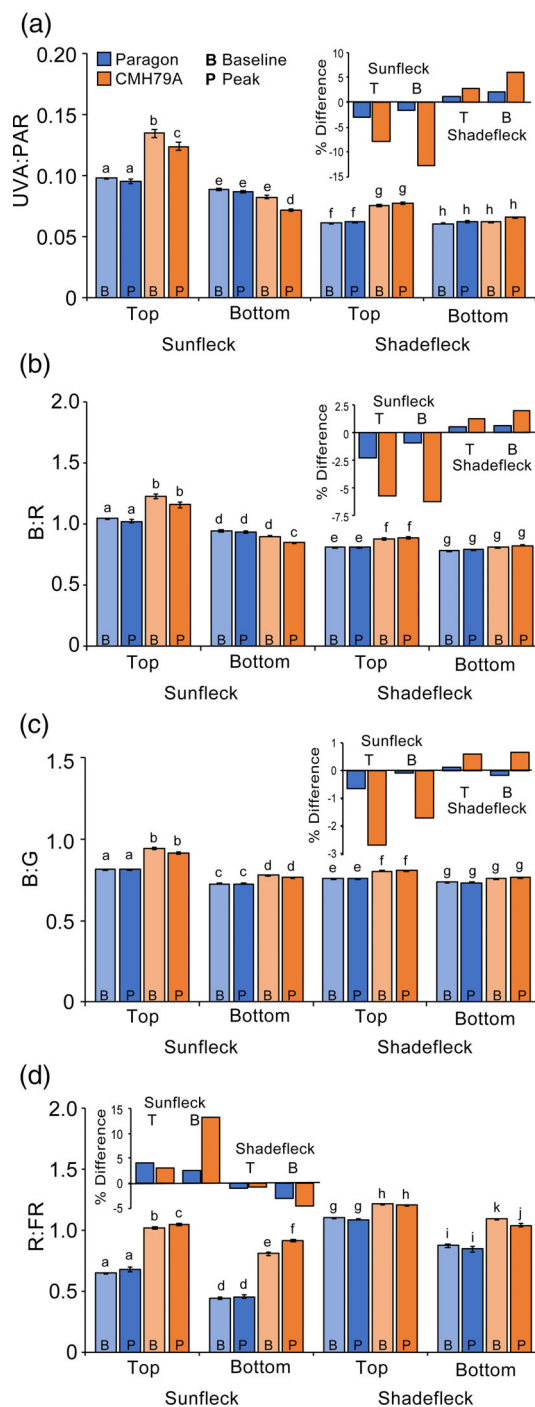
Changes in the frequency and duration of low to high light transitions has consequences for photosynthetic processes. It has previously been shown that there is an inverse relationship between

optimal maximum photosynthetic capacity and the frequency of transitions (Retkute et al., 2015; Yin & Johnson, 2000). However, the average background light intensities (baseline/shade) and those during the sunfleck (peak) are higher in CMH79A relative to Paragon for both the top and bottom parts of the canopy, with up to a 40% increase in intensity over the background values. However, the overall value of PAR is reduced during the measured data (i.e., during wind) compared to the simulated day (i.e., using ray tracing) indicating that whilst the percentage difference was greater, the actual difference between the two varieties during win-induced movement is reduced. Thus, although the frequency of light intensity changes is increased, more photons are received in total. In other words, the integrated and peak photon dose is higher overall (Niinemets & Anten, 2009) and likely to result in a higher induction state overall. This overall increase of light within the CMH79A canopy is partly a result of differences in height and architectural features such as leaf angle, whereby the open and erect stature of the canopy leads to an increased penetration of light to lower layers seen as an increased solar irradiance in the bottom of the canopy for both sunflecks and shadeflecks. This contrasts with the taller canopy of Paragon whereby the diffusor positioned at the top of the canopy received shading from the overhead curled flag leaves and, to some extent, the ears. The difference in light distribution expressed as % of surface area between the two varieties is remarkable with the upright canopy clearly receiving a greater photon dose and maintaining leaves at a point close to light saturation (Figure 3c) (Burgess et al., 2016).

Upon exposure to a sunfleck following a period in shade, a leaf will undergo photosynthetic induction involving several processes which are not instantaneous including activation of the Rubisco enzyme and stomatal opening. Conversely, once the fleck has passed, an induction phase will occur in reverse with enzyme deactivation and stomatal closure. Typically, the reverse induction phase will be slower than the induction, increasing the probability that photosynthesis will be able to respond rapidly to any subsequent sunflecks (Porcar-Castell & Palmroth, 2012). This will also depend on the characteristics of the fleck that are experienced; with the magnitude of change and time spent under each intensity influencing the rate, and potential, of response. However, a trade-off with this potential gain is the response of photoprotective processes including non-photochemical quenching (NPQ). As light intensity increases, excitation energy in photosystem II (PSII) can be dissipated as heat through NPQ (Li, Wakao, Fischer, & Niyogi, 2009) which helps to prevent over-reduction of PSII and electron transport. Similarly to photosynthetic induction, NPQ induction and relaxation are not instantaneous and there will be a lag period between the change in irradiance and response. The rate of NPQ relaxation is slower than that of NPQ induction, intensified by prolonged exposure to high light intensities (Pérez-Bueno, Johnson, Zia, Ruban, & Horton, 2008). Thus, following a decrease in irradiance, CO_2 fixation will be transiently depressed by the slow rate of recovery of NPQ (Kromdijk et al., 2016). The balance between competing photosynthetic processes will therefore be important in determining the exact response to fluctuations in light intensity. This has potential implications for the two opposing canopies studied here.

Windflecks are of a much higher frequency and shorter duration than sunflecks considered previously (e.g., Matthews, Vialet-Chabrand, & Lawson, 2018; Morales et al., 2018; Retkute et al., 2017). It is pertinent therefore to consider time constants for each photosynthesis component and compare this to the frequency of the light fluctuations. Previous papers considering sunflecks have accommodated sufficient time for induction and relaxation of photosynthesis, taking into account the typical rates for the slowest elements (Acevedo-Siaca et al., 2020; Kromdijk et al., 2016; Pearcy, 1990; Taylor & Long, 2017). Maximum photosynthesis rates can take up to 20 min to be reached and has been observed to correlate with induction state (Soleh et al., 2017; Taylor & Long, 2017). The actual time required will be dependent on local environmental conditions and the Rubisco activation state, driven in part by the enzyme Rubisco activase. Stomata are also an important rate limiting component: numbers vary according to species and conditions, but it is not uncommon for stomata to take 10–30 min to fully open following a period of darkness. They also require several minutes to respond to light fluctuations during the day (Lawson & Blatt, 2014). Factors limiting photosynthesis on high to low light transfer can include NPQ relaxation, with the faster qE component taking several minutes to recover (Kromdijk et al., 2016). Clearly the frequency of windflecks do not, individually, permit time for induction and relaxation of such processes. Light pulses of 20, 50 and 100 Hz have been shown capable of maintaining high photosynthesis rates (Gaudillere, 1977). Although this is slower than time constants for light harvesting and electron transport this might be considered akin to continuous light presumably because during the dark intervals, metabolite pool sizes and enzyme activation states are retained and sufficient electron transport pathways are present, maintaining homeostasis. Windflecks should be highly efficient at allowing leaves to reach and maintain induction. The question then arises of the frequency and duration of "bursts" or "trains" of windflecks in canopies, and this is unknown. The current study provides estimates of sunflecks and shadeflecks which can be combined with the mathematical model of non-instantaneous leaf response to light patterns (Retkute et al., 2015) to investigate how light fluctuations of less than a second could further increase the assimilation lost due to induction limitations.

Within and between species there is variation in the speed of response of the photosynthetic machinery (photoprotective and photochemical) to changes in light intensity. This is partly genetic but there is also a component related to the environmental conditions to which a plant is exposed (Acevedo-Siaca et al., 2020; Hubbart et al., 2018; Kromdijk et al., 2016; McAusland et al., 2020; Roden & Pearcy, 1993a; Salter, Merchant, Richards, Trethowan, & Buckley, 2019; Taniyoshi, Tanaka, & Shiraiwa, 2020). This creates a complex picture whereby the fleck characteristics and speed of response of photosynthesis both varies according to genotype and may be different according to environment. Solving this problem requires both physical and biological experimentation with mathematical modelling. Characteristics of sunflecks and shadeflecks estimated in this study takes the first step and will help to advance mathematical models of light dynamics in canopies (Retkute et al., 2017),

photoinhibition (Burgess et al., 2015) and photoacclimation (Retkute et al., 2015; Townsend et al., 2018). Such work will allow us to examine the potential of selecting varieties for a more efficient use of sunflecks.

4.2 | Canopy architecture determines the spectral composition of light reaching lower canopy layers

Light within lower canopy layers is often considered to be predominately made up of diffuse light interspersed with sunflecks mostly consisting of direct light. As the different wavelengths of light are absorbed by chlorophylls with varying efficiency, the spectral quality within the canopy also dictates the rate of photosynthesis (Hogewoning et al., 2010; Smith et al., 2017; Zhu, Long, & Ort, 2008). During a fleck, the change between direct- or diffuse-light leads to corresponding changes in the spectral quality of light available to leaves. Chlorophyll absorbs relatively weakly in the green, absorbing mostly in the red and blue regions of the spectrum (Evans & Anderson, 1987; Terashima, Fujita, Inoue, Chow, & Oguchi, 2009). Coupled with the highly refractive properties of leaf tissue, this leads to a larger portion of green photons in deep mesophyll layers and in the diffuse radiation reaching deeper canopy layers (Smith et al., 2017; Sun, Nishio, & Vogelmann, 1998). This has previously been postulated to contribute to increasing radiation use efficiency with depth in the canopy (Smith et al., 2017).

The light environment in which a plant develops will also affect the accumulation of pigments, which will in turn effect spectral composition available to the photosynthetic machinery. Here, the two varieties differ in the amount and distribution of epidermal flavones and anthocyanins (Figure 4). This pattern reflects the expected primary function of flavones as UV-screening compounds and antioxidants whose accumulation is induced by shortwave solar radiation (blue light, UV-A and UV-B radiation; Righini et al., 2019). Given this, it is interesting that Paragon, in which the extinction of sunlight through the canopy profile is steeper than in CMH79A, generally retained the greater flavone content throughout the canopy for both the abaxial and adaxial epidermis. One possible explanation would be that CMH79A is adapted to higher irradiances in its original environment in Mexico, so might have effective alternative mechanisms to cope with high levels of light requiring less photoprotection from flavones at the moderate irradiances found in the United Kingdom. The higher concentration of anthocyanins at the tips of leaves in Paragon in the bottom half of the canopy may possibly be a result of their induction early during leaf production, where they are typically synthesized in response to cold temperature stress.

In this study, there were differences in how the two varieties of wheat affected the spectrum of light in different canopy layers, and differences in the relative change in spectral ratios during sunflecks and shadeflecks. This includes an increase in the ratios of UVA:PAR, B:R, B:G and R:FR in CMH79A in the top of the canopy compared to Paragon. Under a relatively dense canopy such as Paragon, changes in the ratios of different spectral components are much reduced compared to that of the open and sparse canopy of CMH79A, with up to 5 times reduction in the ratio during flecks. Whilst there is increasing interest in understanding how diffuse radiation influences photosynthesis (Li et al., 2016; Li & Yang, 2015), future work is required to understand how the rapid changes in different spectral ratios of light that we recorded affect photosynthetic processes.

4.3 | Light characteristics can be optimized through changes in canopy architecture

To our knowledge, this is the first study aimed at linking architectural and biomechanical traits to the characteristics of light experienced within the canopy. This indicates a number of important features that could be targeted to enhance whole level canopy photosynthesis through optimisation of the light environment. Firstly, the frequency and duration of windflecks may be related to architectural characteristics such as ear area, plant height, height at the centre of gravity plus stem and root strength, as well as environmental conditions including the wetness of the soil (Baker et al., 1998). Whilst this study found no significant difference in the natural frequency values between varieties, a stronger link between natural frequency and fleck characteristics may be determined using varieties containing a greater variation (Piñera-Chavez, Berry, Foulkes, Molero, & Reynolds, 2016; Susko et al., 2019). It is expected that the lower the natural frequency, the shorter the expected duration of windflecks. This also correlates to the risk of lodging with a reduction in natural frequency associated with an increase in lodging risk (Baker et al., 1998; Piñera-Chavez, Berry, Foulkes, Jesson, & Reynolds, 2016). Therefore, selecting for an increased natural frequency could confer the potential to both reduce the risk of lodging and alter the duration of time spent under different light intensities. However, for photosynthesis to be fully maximized, further work is required to determine how the time period spent under different light conditions experienced in the field will influence photosynthesis. Whilst previous modelling studies indicate that optimal maximal photosynthesis is related to the frequency of switches, the duration spent under each intensity is also of importance and thus it must be determined whether there are differential effects of lengthening of the time period spent under high- versus low-intensities (Retkute et al., 2015).

A second architectural feature which can be manipulated to optimize the light environment is the sparseness of the canopy; determined by leaf stature, LAI and planting density. Within this study, the open canopy of CMH79A resulted in higher light intensities at both canopy positions for both the static [modelled] scenario and measured in the field (Figures 6 and 7). This can be related to light attenuation, with an increased probability of light penetration to lower leaf layers. Erect leaf stature has often been proposed to improve whole canopy photosynthesis in canopies with a larger LAI such as cereals and, as such, is often targeted during breeding as a trait for representative of the idealized plant type; or ideotype. This feature is associated with uniformity of light across the canopy, enhancement of light interception at low solar angles and a reduction in the susceptibility to photo-inhibition and heat load when the sun is directly overhead (Burgess

et al., 2015; Falster & Westoby, 2003; King, 1997; Peng, Khush, Virk, Tang, & Zou, 2008; Werner, Ryel, Correia, & Beyschlag, 2001). In comparison, the denser canopy of Paragon resulted in a non-significant change in light intensity and spectral quality during wind-flecks, but not in the static [modelled] configuration, thus suggesting that above a certain density (or LAI, etc.), the potential for a windfleck to allow the light to penetrate to lower canopy levels, thus homogenizing the light distribution is more limited.

Future work is required for a full understanding of the specific architectural traits which determine the light dynamics within crop canopies. Using large, genetically tractable breeding panels would enable a more detailed analysis and correlation between features of the canopy and of the corresponding fleck patterns. The methodology proposed here and in Durand et al. (2021) would provide the platform to characterize these sunflecks and will aid to guide breeding efforts under natural light fluctuations experienced in the field.

5 | CONCLUSION

In conclusion, combining time-series measurements of solar irradiance at different canopy positions with architectural analysis of contrasting wheat lines reveals the how interdependent traits such as plant height, leaf angle and LAI affect the characteristics of light reaching leaves through the canopy. This indicates that wind-induced movement can alter light intensity on a sub-second scale, compared to up to 5 min in a static canopy and that both plant height and canopy openness can determine the duration and intensity of windflecks in a canopy. This timescale is of a much higher resolution than considered by many current studies assessing photosynthetic performance. This necessitates the need for further studies to analyse the links between architecture and light characteristics under different weather conditions. Describing natural patterns in the dynamics of canopy light as well as the corresponding response of photosynthetic processes to rapid fluctuations in light will enhance our capacity to improve crop performance and yield through the manipulation of these processes.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and materials supporting the results or analyses presented in this paper are available upon reasonable request.

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