TITLE

Fields of a thousand shimmers: canopy architecture determines high frequency light fluctuations.

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LENGTH

Total word count:	6897	No. of figures:	8 (all in colour)
Summary:	196	No. of Tables:	3
Introduction:	1138	No of Supporting Information files:	4 (3 figures, 1 data sheet)
Methods :	1440		
Results:	2020		
Discussion:	2299		
Acknowledgements:	48		

SUMMARY

- Wind-induced movement in the canopy produces rapid fluctuations in irradiance, called “windflecks”. They create a dynamic environment for photosynthesis that bears little resemblance to the stable controlled conditions under which plants are typically measured.
- We recorded time-series of irradiance to assess the diversity of windfleck properties (intensity, duration, frequency, clustering, spectral composition) in canopies of four crops and five tree species. We also measured traits associated with leaf morphology and canopy architecture, which could be associated with canopy-specific differences in windflecks.
- Distinct features of windfleck properties were identified both between and among crop and tree canopy. Windflecks in crops were generally more intense and longer, baseline irradiance was much higher than even the peak irradiance during a windfleck in a forest. The change of spectral composition during a windfleck was species-specific. Overall, irradiance fluctuations in denser canopies were less frequent and less intense; as found with increasing canopy depth and plant height.
- Our systematic exploration of how canopy structure dictates light dynamics, provides new insight into windfleck creation. Coupled with progress in elucidation of the mechanisms of photosynthetic induction, this knowledge should improve our capacity to model canopy ecophysiology and understand light use efficiency in shade.

KEY-WORDS

canopy architecture, crops, forests, light quality, solar radiation, shade, spectral composition, sunfleck

INTRODUCTION

Plants canopies are ever-changing environments where steady conditions are an exception rather than the norm (Kaiser *et al.*, 2018; Murchie & Ruban, 2020; Durand *et al.*, 2022). Even under a clear sky at the very top of a canopy, a light breeze will cause leaves to move and change the relative angle of incidence of sunlight, affecting the irradiance they receive and the leaf boundary-layer conductance. In such conditions, those plants that can respond faster to fluctuations in the environment, may have an advantage in terms of maximizing carbon gain (Kromdijk *et al.*, 2016; Hubbart *et al.*, 2018). Improving plant performance by accelerating the response of photosynthesis to light fluctuations has received increasing interest in recent years (Murchie *et al.*, 2009; Kaiser *et al.*, 2018; Slattery *et al.*, 2018; Long *et al.*, 2022). This is regarded as a way to, in principle, mitigate climate-related declines in agricultural plant productivity (Asseng *et al.*, 2014), and the rising worldwide demand for food (Ort *et al.*, 2015). Better models that account for the dynamic response of photosynthesis to fluctuating environments will also allow us to predict canopy net carbon assimilation more accurately and how it is impacted by global changes.

Multiple physiological processes, operating at different time scales, in plant canopies are affected by changes in irradiance (Way & Pearcy, 2012). Patterns of light fluctuations, in terms of frequency, duration, and intensity, determine the activation state of Rubisco (Taylor *et al.*, 2022), Ribulose 1,5-bisphosphate regeneration (Sassenrath-Cole & Pearcy, 1994), stomatal opening (Allen & Pearcy, 2000), and the rate of non-photochemical quenching (Murchie & Ruban, 2020). These limitations control the efficiency at which the subsequent period of high light can be used. Even brief light fluctuations will affects these relatively slow (15-45 min duration) processes, dictating the induction state of the photosynthetic machinery, and ultimately determining photosynthetic rates. For instance, rapid light fluctuations will maintain Rubisco activation (Tanaka *et al.*, 2019) and keep stomata open (Zeiger *et al.*, 1985), and the frequent intermittent brief occurrence of shade may prevent the accumulation of photoprotection. Over a shorter time-scale (< 1 min), the efficiency at which photosynthesis can use brief light fluctuations (its momentary induction state), such as those induced by wind, will depend on several processes. First, the build-up of Ribulose 1,5-bisphosphate reaches a non-limiting state 1-2 min after illumination (Sassenrath-Cole & Pearcy, 1992). Second, CO_2 assimilation is sustained for several seconds post-illumination due to residual photosynthetic metabolic pools (McAlister, 1939; Laisk *et al.*, 1984). Third, pools of photorespiratory metabolites can induce a CO_2 burst after illumination, which can offset the overall CO_2 assimilated (Vines *et al.*, 1983; Pearcy, 1990). These processes are often neglected in models, and yet the degree to which they affect long-term photosynthetic rates in fluctuating light environments will depend on the duration, frequency and intensity of light fluctuations (Pons & Pearcy, 1992; Roden & Pearcy, 1993b; Kaiser *et al.*, 2015). Only by characterizing the dynamics of light in natural environments, and associated changes in spectral composition, can we hope to understand how these photosynthetic processes alter plant productivity under realistic light fluctuations (Murchie *et al.*, 2018).

To date, exploration of the probable links between canopy structure and the properties of light fluctuations has received little attention (Way & Pearcy, 2012; Smith & Berry, 2013). Yet, we know that light distribution in the canopy is shaped by the morphological, architectural, and mechanical traits of the species that compose it, which interact with environmental factors such as the sun position, clouds and the wind. For example, a higher leaf area in the upper canopy will intercept more light, thus creating a darker lower canopy (Lang, 1986). Among others, canopy height, stand density and branching patterns, as well as leaf shape, size, and orientation (Falster & Westoby, 2003), create the 3D canopy architecture determining the penetration of light through the canopy and thus its interception by leaves (Burgess *et al.*, 2017). In recent years, there has been increasing recognition of the effect of wind on plant productivity, especially in crops, creating movement in the canopy that depends on the mechanical properties of stems and leaves (de Langre, 2008; Burgess *et al.*, 2016). In contrast, the lignified stems of trees present a stronger resistance to wind, meaning that wind-induced movements will be stronger around the petiole axis (Roden & Pearcy, 1993a). Forest canopies, being taller than crop canopies, also generate more penumbra (or partial shade; Smith *et al.*, 1989). Therefore, the arrangement of species that compose the canopy will likely affect the light fluctuations found therein, impacting the light environment in the understorey.

Historically, most research on light fluctuations, where brief periods of high irradiance are often called sunflecks, has been focused on solar-induced movements (e.g. helio- and photo-tropisms) in understorey species in forests (Atkins & Poole, 1937; Evans, 1956; Pearcy, 1990; Chazdon & Pearcy, 1991). Light fluctuations were much more rarely examined in crops (Pearcy *et al.*, 1990; Barradas *et al.*, 1998). More recently, light fluctuations induced by wind have been dubbed “windflecks” (Burgess *et al.*, 2021), as a sub-category of sunflecks, to distinguish them from those induced by sun and clouds (generally longer than 30 s). Sunflecks are notorious for being hard to define, and are often characterized as periods of irradiance above an arbitrary threshold contingent on the surrounding shade (e.g. 50 µmol m^{-2} s^{-1} in Miyashita *et al.*, 2012; 300 µmol m^{-2} s^{-1} in Roden & Pearcy, 1993, 70% of the irradiance at the top of the canopy in Barradas *et al.*, 1998). This makes comparison between studies and canopies difficult, as for example 50 µmol m^{-2} s^{-1} could correspond to a shade environment in one canopy but the peak of a sunfleck in another. We recently devised a method of tracking light fluctuations that provides a more generic and repeatable means to define sunflecks as brief periods of high irradiance relative to the background shade environment, based on motifs in time-series of irradiance (Durand *et al.*, 2021a). This allows us to describe key features of windflecks, consistently in any canopy.

We recorded time-series of irradiance at very high frequency to describe with appropriate resolution the rapid wind-induced light fluctuations in four crop and five tree canopies. To allow for best comparison, measurements were done in a short period of time, allowing similar environmental conditions (cloudless sky, similar solar angle), and phenological stages. Using our published method, we then characterized the properties of these light fluctuations, hereafter called windflecks. We also recorded longer light fluctuations (> 1 min.) using hemispherical pictures, hereafter defined as sunflecks. We then investigated their potential relationships with leaf morphological and canopy architectural traits. We aimed to: (1) characterize windfleck properties in both crop and tree canopies, (2) examine how the spectral composition is modified during a windfleck, and (3) identify the main canopy architectural traits that drive the patterns of light fluctuations.

MATERIALS & METHODS

Study site and plant material measured in 2021

We conducted this experiment at the University of Helsinki, Finland (60.227 N, 25.018 E, 10 m above sea level) at Viikki Experimental Farm and Viikki Field Plots for the crop species, and at Viikki Arboretum for the tree stands. We measured separate cultivated fields of oats (*Avena sativa*, L.), rapeseed (*Brassica napus*, L.), barley (*Hordeum vulgare*, L.), and broad bean (*Vicia faba*, L.), as well as pure stands of Norway maple (*Acer platanoides*, L.), silver birch (*Betula pendula*, Roth.), Norway spruce (*Picea abies*, L.), and grey alder (*Alnus incana*, L.). Information on the growing conditions of the crops can be found in Table 1. We also measured in an experimental European beech stand (*Fagus sylvatica*, L.) planted in 2010. The stand is composed of trees from four provenances: Blaviksliarna southern Sweden, Eichelberg and Rindelpholz in Germany, and Montejo de la Sierra, in Spain. The plot was thinned by removing half of the trees in May 2020 (for more information, see Durand *et al.*, 2022).

Light measurements

We measured spectral irradiance with a CCD array spectroradiometer Maya 2000 Pro (Ocean insights, Dunedin, FL, USA) using a cosine diffuser (D7-H-SMA, Bentham Instruments Ltd., Reading, UK) attached to a fiber-optic cable (FC-UV400-2 400µm, Avantes, Leatherhead, UK). The Finnish Radiation and Nuclear Safety Authority calibrated the spectrometer in April 2021 (STUK; Ylianttila *et al.*, 2007). With the diffuser in the horizontal position, we recorded sets of contiguous 10,000 scans, each scan comprised of 1,377 wavelengths in the range 280-898 nm measured simultaneously, with an integration time of 10 ms. Each set thus made up a 100s-long time-series. We used the “high-speed acquisition” routine of the SpectraSuite software (Ocean insights, v2.0.162), that captures raw data without processing it, to prevent delays between detection by the sensor and communication between the software and the operating system. All times-series were recorded from June 30th to July 14th 2021 (n = 8-16), before the panicle and grains of the oats, and the stalks and heads of the barley turned yellow. Rapeseed was measured first and beans last, both during their early flowering stages. Measurements were recorded at mid-canopy depth in the crops, and at 50-cm above the ground in forest stands. In the beech stand, we also recorded at every meter from 0 to 4 m in canopy height (the top of the canopy being at 6 m). The diffuser is a small flat cylinder (4.2 x 1.8 cm) which can be placed inside dense canopies, equidistant from stems, on a small tripod without affecting the canopy structure. After each time-series was recorded, we took two additional control recordings to correct for stray light and dark signal. The first recorded the baseline noise, which was subtracted from the measurements, by placing a darkening cap over the diffuser to block all UV and visible radiation. The second record was to correct for stray light in the UV region, made by placing a polycarbonate cap (blocking 280-400 nm radiation) over the diffuser (Aphalo & Ylianttila, 2022). We recorded all data within three hours of solar noon (at about 13:30) from 10:30 to 15:30, local time in the absence of clouds. Above-canopy measurements were recorded between one and three times per day, above the crop fields, or in the open outside of the forest stand. We used the "*ooacquire*" and "*photobiology*" R packages (Aphalo, 2015; Aphalo & Ylianttila, 2022) to process the raw spectrometer counts into irradiance values, and perform the corrections mentioned above.

Windfleck detection and properties

The method used to detect and measure windfleck properties is detailed in Durand *et al.* (2021a). Briefly, we calculated the rate of change between two time points along the measured time-series of PAR irradiance (400-700 nm, Δ_{PAR}), for each point n at time t in the time series and its following measurement $n+1$ as:

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

Δ_{PAR} has the property of crossing 0 when PAR irradiance switches from decreasing to increasing, and likewise in reverse. This allowed us to pinpoint the start, peak and end of a windfleck and associated PAR irradiances. Potential windflecks corresponded with an increase in PAR irradiance larger than 5 µmol m^{-2} s^{-1}, or represented an increase in PAR irradiance between peak and baseline more than 5%. This was done to remove natural noisy oscillations in the irradiance.

We calculated windfleck duration as the time between the start and end of a windfleck, and its intensity as the difference in PAR irradiance between the peak and the baseline, taken as the lowest PAR irradiance at either the start or end of the windfleck. This approach avoids potential inaccuracies caused by asymmetry. We calculated a median time between windflecks (T) as the time between the end of a windfleck and the start of the next windfleck, and the overall frequency (F) as the total number of windflecks recorded divided by the combined duration of all time-series. We also calculated an index of windfleck clustering as (F^{-1} – T) / F^{-1}, which varies between 0 (least clustered) and 1 (most clustered). The integrated increase in PAR irradiance caused by the windfleck was calculated as the total integrated PAR irradiance during the windfleck, from which the residual PAR irradiance (the linearly interpolated PAR irradiance between the start and end of a windfleck) was subtracted. To assess windfleck spectral composition, UV-A:PAR, blue:red (B:R), blue:green (B:G), and red:far-red (R:FR) spectral photon ratios were calculated (UV-A: 315-400nm; PAR: 400-700nm; blue: 420-490nm; green: 500-570nm; red: 620-680nm; far-red: 700-750nm).

Canopy architecture

We took hemispherical photographs at 10 measurement points for crops species, and 5 for forest stands, using a Canon Eos 800D (Canon Inc., Japan) camera with a CMOS 24 MP image sensor combined with a circular fisheye lens (Sigma 4.5 mm f2.8 EX DC HSM, Sigma Corporation of America, USA). All photographs were taken in RAW format, at 10 cm above the ground using a tripod under overcast sky. ISO was fixed at 100 and aperture at F22, varying only shutter speed to adjust exposure. We produced a sharpened gamma-corrected and contrast-stretched blue channel 8-bit jpeg from the RAW files following Macfarlane *et al.* (2014). Photographs were analyzed with the Hemisfer software (Schleppi *et al.*, 2007) following the weighted ellipsoidal method from Thimonier *et al.* (2010) and using the non-linearity and canopy clumping corrections (Chen & Cihlar, 1995; Schleppi *et al.*, 2007). This allowed us to estimate mean tilt angle of the leaves, plant area index (PAI, *i.e.* leaf area index without correction to remove stems), and canopy light transmission. Hereafter, we designate as sunflecks the period for which the sensor experienced direct sunlight, by contrast to the spectrometer method described above to record windflecks. The distribution of sunfleck duration can be calculated by plotting a time course of the sun using the same hemispherical photographs with the Gap Light Analyser software (Simon Fraser University, BC, Canada). We considered the period June 30th to July 14th, the same as for the light measurements, and used an automatic thresholding according to Nobis & Hunziker (2005). Finally, we also measured plant height (n = 10), as well as leaf width, and length (n = 50) in all canopies sample at mid-canopy height (crops) or green freshly fallen (trees).

Statistical analysis

We used Type II ANOVA to test for significant differences between canopy species in light fluctuations and canopy architectural traits. Normality and homoscedasticity were checked graphically. We performed *post-hoc* pairwise contrast analyses to test for differences among factor levels, and adjusted p values to control the false discovery rate. Significant differences were considered at $p < 0.05$ for all tests. These tests were made using R 4.2.1 (R Core Team, 2022) with the packages "*car*" (Fox & Weisberg, 2019), "*emmeans*" (Searle *et al.*, 1980) and "*multcomp*" (Hothorn *et al.*, 2008). Windfleck properties cannot be directly paired with canopy architecture at the individual measurement level, thus to test for a correlation we had to use species means. This had the effect of reducing our statistical power, as each species is considered as a single replicate even though it is informed by a large number of observations. To address this problem, we randomly paired windfleck properties and canopy architecture at the species level 100,000 times (similar to a bootstrap with replacement), and calculated a value "*b*" representing the percentage of random pairings that gave a p value < 0.05, following Durand *et al.* (2020). If two variables are uncorrelated, it would be expected that 5% of the random pairings would result in a correlation with a p value < 0.05, thus only b values higher than 5% would provide evidence of a possible correlation between the two variables.

RESULTS

Variability of canopy architecture at the species level

There were generally large difference between the canopy architecture of trees and crops (Fig. 1), although a single genotype per species was examined. PAI was 1.75 times higher in the tree species than in the crops, with an average canopy light transmission of 63% in the crops but only 8.2% in the tree stands. Leaves were generally erectophile in the crops (72.2 ± 1.9°) but more planophile in the tree stands (32.4 ± 2.6°, Fig. 1**e**). Among the crop species, only the rapeseed canopy showed a PAI significantly lower (by 39%) than the other three canopies (Fig. 1**a**). This was despite rapeseed being the tallest crop canopy (75.3 ± 3.9 cm, Fig. 1**b**). The bean canopy had the most planophile leaves (57.1 ± 1.7°) and barley the most erectophile ones (85.6 ± 1.8°), which resulted in beans having the lowest (39.7 ± 2.2%) and barley highest (85.6 ± 5.7%) canopy light transmission among crops (Fig. 1**d**). Barley had very long leaves (Fig. 1**c**), 1.25, 4.6 and 4.0 times longer than oat, bean and rapeseed respectively, which had wider leaves (Fig. 1**f**).

Among the trees, PAI was much more similar across stands, with only the spruce stand having a PAI 16% higher than the maple, birch and beech stand ($p < 0.007$, Fig. 1**a**). We could not detect significant differences in canopy light transmission ($p = 0.08$), but spruce leaves were the most erectophile (48.6 ± 2.1°) and beech leaves the most planophile (19.8 ± 8.2°). The beech stand being the youngest, it was also the shortest (5.6 ± 1.4 m), followed by the maple, spruce, alder, and birch as the tallest stand (20.6 ± 6.0 m, Fig. 1**b**). The maple leaves were the widest (more than 2.7 times wider than the other trees), the longest, and the only ones that were wider than long (Fig. 1**c-f**). On the contrary, the spruce leaves were the smallest, both in length and width, but had the higher length to width ratio (11.7).

Species-specific windfleck properties

Overall, the baseline and peak irradiance was 7.0 and 6.4 times higher in the crops than in the tree stands (respectively, Table 2). This resulted in windflecks being much more intense, by 5.3 times, in the crop (on average 266.4 ± 3.2 µmol m^{-2} s^{-1}) than in the tree canopies (60.6 ± 1.0 µmol m^{-2} $s^{-}1$, $p < 0.001$). Windfleck duration was on average longer in the crop (206.4 ± 0.2 ms) than in the tree stands (132.3 ± 0.1 ms, $p < 0.001$), although this was species dependent. This led to an integrated PAR increase of 34.6 ± 0.7 µmol m^{-2} per windfleck on average in the crops, compared to only 5.6 ± 0.2 µmol m^{-2} per windfleck in the tree stands. Differences of time interval between windfleck, windfleck frequency and clustering was strongly species-specific, rather than being arranged according to the crop/tree distinction (Table 2). As for longer sunflecks, we found them between June 30th to July 14th to be 3.9 times more numerous in the crop canopies than in the tree stands for those lasting less than 10 min, and 7.4 times as numerous when considering those lasting more than 10 min.

Among crop canopies, barley had the highest baseline irradiance, twice as high as in the bean canopy, and 47%, and 9% higher than the oat and rapeseed canopies, respectively (Fig. 2). There was a similar trend for the peak irradiance of the windflecks. This led to windflecks being 2.3, 1.7 and 1.5 times more intense in the barley canopy compared to bean, oat and rapeseed, respectively (Fig. 2**a**). Due to a smaller difference in windfleck duration than intensity between canopies, the average integrated PAR increase per windfleck followed a similar pattern (Table 2). Windfleck duration was shortest in the rapeseed canopy, by 28%, 18%, and 50% compared to the barley, bean, and oat. Along with a lowest average time between windflecks, this resulted in a windfleck frequency in rapeseed that was 1.5, 2.5 and 2.4 times lower than in the barley, bean, and oat canopy respectively (Fig. 2**c**). Overall, windflecks in the bean and oat canopies tended to be more clustered together than in the other canopies (Table 2). For longer sunflecks, we found that those lasting less than 10 min occurred most often in the rapeseed canopy, but those lasting more than 10 min were more frequent in the barley.

The ranking among tree species was the same for both baseline and peak irradiance during windflecks, with the highest irradiance in beech followed by birch, spruce, maple and alder stands (Fig. 3). Yet, irradiance increased by 82.2% during a windfleck in the alder stand, but only by 37.2% in the spruce stand, resulting in a similar windfleck intensity in the maple, alder and spruce stand, but still on average 2.3 times lower than that of birch or beech stands (Fig. 3**a**). Maple had one of the least intense windflecks, but they were also the longest, 2.6 times as long as the shortest windflecks of the alder stand. This led to maple and beech stands having the highest average integrated PAR increase per windfleck, the former due to longer windflecks, and the latter due to more intense ones (Table 2). The maple stand also had the least frequent windflecks, with an average time between windflecks being at least 2.6 times as long as in the other stands. This pattern was in part due to a higher degree of windfleck clustering in the maple stand, while the least clustering was found in the birch stand where windflecks were shortest and most frequent. Some long sunflecks were present in the forest stands, unlike the crops canopies. The maple stand had the most sunflecks shorter than 10 min, and the spruce stand the least (Fig S2). For sunflecks longer than 10 min, the intra-group variability was too high to detect significant differences between tree stands.

Changes of spectral composition during a windfleck

The ratio of UV-A to PAR generally decreased from the baseline to the peak of the windfleck, by as much as 22% in the barley canopy, whereas in the beech and spruce canopy, UV-A:PAR was lowest, and increased by 6% and 30% during windflecks. The lowest baseline B:G ratio was also in the beech stand, where it increased by 14% on average during a windfleck, while other canopies had either a similar or lower B:G ratio during a windfleck. For all canopies, the average B:R ratio decreased by 10% and the R:FR ratio increased by 31% during a windfleck. In general, a smaller baseline ratio was correlated with a larger increase (or a smaller decrease) during the windfleck ($p < 0.002$; Fig. S1).

In barley, UV-A radiation and blue light did not increase as much as green or red light, and there was a modest increase of R:FR in a windfleck (Table 3, Fig. 4). The other crops showed a similar trend, with rapeseed having the smallest proportional change of spectral composition overall. In maple, while the shortwave part of the spectrum showed small changes of spectral composition, there was a large increase in red light, leading to a large reduction in B:R and increase in R:FR in a windfleck. In alder and birch, this increase extended to the green light as well, cause a reduced B:G during the windfleck, unlike in maple (Table 3). We recorded the largest relative increase of both blue and red, compared to green, in the beech canopy, while in the spruce there was a relative increase in UV-A radiation but minor changes in the blue, green and red regions.

A gradient of windfleck properties with canopy height

We recorded a large number of windflecks at each canopy height, allowing high statistical power, even when correlations are relatively weak. For example, there was a minor reduction in windfleck duration compared to their distribution, from 0.89 ± 0.01 s at the ground level to 0.64 ± 0.02 s at 4 m (Fig. 5**a**). Yet, the range of windfleck durations was large, with 50% of windflecks either longer than 1.2 s or shorter than 0.5 s at ground level. While at 4 m, 50% of windflecks were either longer than 0.8 s or shorter than 0.4 s. The correlation was also weak, although statistically significant, for the average time interval between windflecks, which had a Pearson's coefficient of correlation (R) of -0.06. Still, a stronger correlation was found with windfleck intensity (R = 0.42, Fig. 5**c**), which increased from 102.3 ± 4.4 µmol m^{-2} s^{-1} at ground level to 480.0 ± 17.6 µmol m^{-2} s^{-1} at 4 m. This led to a similar, albeit weaker, positive correlation between the integrated PAR increase per windfleck and canopy height (R = 0.25). In general, with height in the beech canopy, windflecks tended to be shorter, more frequent, and much more intense (Fig 5).

Relationships between canopy architecture and the properties of light fluctuations therein

The architecture of the canopy was generally well correlated with the properties of windflecks, even though our statistical power was reduced by using species means. We found PAI to be negatively correlated with the number of sunflecks longer than 10 min (R = -0.77, *p* = 0.02, Fig. 6**a**), the intensity of windflecks (R = -0.83, *p* = 0.005, Fig. 6**b**), and the integrated increase in PAR per windfleck (R = -0.78, *p* = 0.013, Fig. 6**d**). Both canopy light transmission and the average PAR irradiance were positively correlated with the number of sunflecks longer than 10 min (R > 0.88; p < 0.002, Fig. 6**e-i**), windfleck intensity (R > 0.98, *p* < 0.001, Fig. 6**g-k**), and the integrated increase in PAR per windfleck (R > 0.93, *p* < 0.001, Fig. 6**h-l**). Windfleck duration was neither correlated with PAI, canopy light transmission, nor the average PAR irradiance (*p* > 0.46, Fig. 6**b-f-j**) or sunfleck frequency (data not shown). In general, denser canopies produce fewer long sunflecks than sparser canopies, and less intense windflecks, but of similar duration and frequency to sparser canopies. Some correlations could only be detected in either the crops or the tree canopies but not both. For example, average leaf angle was positively correlated with windfleck intensity in the crops (R = 0.96, *p* = 0.04, Fig. 7**a**), but only a relatively weak negative tendency was found in the forest stands (R = -0.82, *p* = 0.09, Fig. 7**b**). Sunfleck clustering produced a negative trend with leaf angle (R = -0.8, *p* = 0.21) and canopy light transmission (R = -0.91, *p* = 0.09) in the crops, but not among the tree species (*p* > 0.37, Fig. 7**c**-**f**).

We found correlations between windfleck properties and architecture in the crop fields. Among the crop canopies, plant height was negatively correlated with windfleck duration (R = -0.93, *p* = 0.07, Fig. 8**a**). The significance of this correlation (*p* value) was marginally above the threshold of 0.05. Yet, more than 21% of random pairings between plant height and windfleck duration had a *p* < 0.05, providing more evidence of a possible link between the two variables. This pattern was repeated but with a weaker trend for plant height and the integrated increase in PAR per windfleck (Fig. 8**c**). Windfleck intensity was neither correlated with plant height, leaf length nor width (*p* > 0.25), but leaf length was positively related to the integrated increase in PAR per windfleck (R = 0.96, *p* = 0.044, Fig. 8**f**), due to similar positive trends with windfleck duration and intensity (Fig. 8**d**-**e**). By contrast, there was a negative trend between leaf width and both windfleck duration (R = -0.89,

Fig. 8**g**) and the integrated increase in PAR per windfleck (R = -0.82, Fig. 8**i**). Overall, both the increase in plant height and wider leaves were associated with shorter windflecks.

Those relationships across the tree stands were weaker than in field crops, and often driven by a single species (*e.g.* the much shorter tree height of the beeches, or the much larger leaf width of the maples), which we decided not to consider in detail (see Fig. S2 for a corresponding Fig. 8 in the tree species).

DISCUSSION

Considerable disparity between light fluctuations in crops and forests

One of the striking differences we found regarding windflecks, was that their intensity in forests was considerably lower than that in crops. The windfleck peak was often lower in tree canopies than the baseline irradiance in the crops (Fig. 2**b**, Fig. 3**b**). Penumbral effects amplify as the distance between a gap in the canopy and ground increase, therefore they are much more prevalent in tall forests canopies than in crops (Smith *et al.*, 1989; Pearcy, 1990). Indeed, the least intense windflecks were recorded in the spruce canopy which is highly clumped, and less susceptible to wind, with its more rigid needle-shaped leaves (Table 2). While this result has been predicted, from measurements in a soybean (*Glycine max*, L.) canopy (Pearcy *et al.*, 1990), to our knowledge our study is the first systematic examination and quantification of this pattern. It should be noted that our measurements in crops were performed within the canopy, but further below in the trees. We could expect higher windfleck intensity when measuring within the tree canopy (Fig. 6). Pearcy *et al.* (1990) also found windflecks in soybean canopies to be shorter and more frequent than those in forest understories. Here, we showed that this pattern is not consistent among field crops, rather windfleck duration and frequency seem to be species-specific (Table 2), although an assessment of genotypic variation is needed before a definitive conclusion can be reached. This finding is somewhat unexpected, as the woody stems of trees makes them more resistant to wind. Instead, the biomechanics of the petioles in trees seem to play as much of a role as the stems of crops, in determining duration and frequency of light fluctuations.

There is a dearth of studies investigating the diversity of light fluctuation patterns in plant canopies. Kaiser *et al.* (2018) found ten times more sunflecks in Durum wheat (*Triticum durum*, Desf.) than in white mustard (*Sinapis alba*, L.) during the same time period: these sunflecks were also longer and more intense. A comparison of sunflower (*Helianthus annuus*, L.), wheat (*Triticum aestivum*, L.), and maize (*Zea mays*, L.) canopies detected only marginal differences (Peressotti *et al.*, 2001). There are some differences between those windfleck properties among oat, barley and broad bean canopies reported here, and in a previous study (Durand *et al.*, 2021a), yet we used the same method to detect windflecks in both studies. In summer 2020, we found windflecks in the barley canopy to be more intense, shorter, and less frequent than in the oat canopy, which is similar to our current results. However, while in 2020 the broad bean canopy generated windflecks with the highest intensity, duration and frequency, measurements from 2021 found broad beans to have the lowest intensity, duration, and frequency (Table 2, Durand *et al.*, 2021a). Differences in the stage of canopy development at the time of measurement may be partially responsible for the inconsistency between the measurements in the two consecutive years, as the barley and oats canopies were planted six and eight days later, respectively, but the beans were planted 15 days earlier, in 2021 than in 2020. This meant that at the time of measurement the bean canopy was nearly 20 cm taller, switching from the shortest crop in 2020, to the tallest crop in 2021. A time course of measurements in a common bean (*Phaseolus vulgaris*, L.) canopy found windflecks to become shorter as the canopy grew taller (Barradas *et al.*, 1998). Across a vertical gradient mimicking an increase in canopy height, we found a similar pattern of windflecks becoming less intense, and less frequent further away from the top of the canopy (see Fig. 5). Windfleck duration also decreased with height within the canopy, but decreased with plant height in crops (Fig. 6**a**) suggesting that each imply the specific patterns of light fluctuations. These considerations may also explain why the relatively young and short beech canopy produced windflecks of high intensity and duration compared to the other tree canopies measured (Fig. 1**b**). A better understanding of the impact of plant height, and depth in the canopy would be gained if future studies focus their attention on genotypic variability in plant height, and developmental stages.

Canopy-dependent changes in spectral irradiance of windflecks

Since a full record of spectral irradiance can be accessed for each time-point of the time-series we used to detect windflecks, we could specifically examine the change in spectral composition during a windfleck. Comparison of regions of the spectrum allowed for smaller, but more precise, differences between the baseline and the peak of the windfleck to be identified, than was possible from comparing only the spectral integral, i.e. PAR (e.g. as in Durand *et al.*, 2021a).

Spectral composition of solar radiation in the canopy can be highly variable (Hartikainen *et al.*, 2018; Hovi & Rautiainen, 2020). In part, this depends on the structural and biochemical composition of the leaves affecting their optical properties (Gates, 1965), but also on canopy properties such as leaf area and angle (Asner, 1998). These features partly explain the diversity of spectral composition we found between canopies. The B:R and R:FR spectral photon ratios we recorded were higher than those reported in Hertel *et al.* (2011), although in both studies the ratios were higher in the spruce than in the beech canopy. While generally windflecks provide disproportionately more blue and red light within canopies as shade is depleted in these wavelengths, we found that changes in spectral composition during a windfleck were characteristic to each canopy type. This means that differences in spectral composition, resulting from overstorey structure and species with different leaf optical properties, could be detected during a windfleck. This could differentially affect those understorey species that are thought to exploit the brief fluctuating irradiances provided by windflecks for photosynthesis, with the efficiency of this process depending on spectral composition (Brodersen & Vogelmann, 2010; Smith *et al.*, 2017).

Our results show that light fluctuations in natural environments should be considered along with variations in spectral composition. While the potential physiological effects these changes have on photosynthesis remain to be determined, penetration and absorption of light is wavelength dependent (Brodersen & Vogelmann, 2010). Green light penetrates deeper in the mesophyll (Terashima *et al.*, 2009; Smith *et al.*, 2017) than blue or red because it is less efficiently absorbed by chlorophylls, but is it still the case when light is predominantly green, as is the case in shade? To our knowledge, no study investigated whether diffuse light that is enriched in green and far-red light penetrates as deeply or deeper in the mesophyll than direct solar radiation. The pertinence of this question is also dependent on the location of chloroplasts which will condition the potential to use light at various depth in the mesophyll. These differences in spectral composition may also more generally affect their phenology and development (Wang *et al.*, 2020; Brelsford *et al.*, 2022); factors which ultimately limit species' spatial distribution. Combinations of species in agroforestry systems, where one plant grows under the shade of another, may also benefit from a specific coupling of overstorey/ canopy species that, through their leaf traits and canopy architecture, creates a better light environment that provides favourable conditions for particular under-canopy species.

Generally, UV-A:PAR was lower during the peak of a windfleck than at the baseline, except in the beech and spruce canopies. This general decline is in agreement with evidence of lower UV-B to PAR ratio in sunflecks compared to shade (Flint & Caldwell, 2002; Hartikainen *et al.*, 2018; Burgess *et al.*, 2021; Durand *et al.*, 2021a). Moreover, the ratio of UV over PAR commonly increases with height in the canopy (Yang *et al.*, 1993; Grant, 1997; Deckmyn *et al.*, 2001; Burgess *et al.*, 2021). This could be partly attributable to a higher relative absorption of UV radiation than PAR by leaves, leading to a larger increase of UV than PAR with height in the canopy (Day *et al.*, 1994; Grant *et al.*, 2003). This would mean that the effect of a sunfleck on UV:PAR would be different at the top and bottom of a canopy. A higher scattering probability of shortwave radiation (*e.g.* UV-B, UV-A and blue light) in the atmosphere (Durand *et al.*, 2021b), results in diffuse light that is enriched in UV radiation compared to direct light (Flint & Caldwell, 2002). At the top of the canopy, the direct and diffuse radiation incident on leaves is mainly scattered by the atmosphere, and coming from all directions of the sky. This results in relatively high UV:PAR. By contrast, the light incident on leaves during a windfleck at the bottom of a canopy mainly originates from a direction close to the solar disc, where UV radiation is comparatively depleted. In all the canopies we measured, B:R always decreased during a windfleck (Table 3), but increase with height (Hertel *et al.*, 2011), suggesting a similar impact of differential scattering. This can have meaningful consequences for the functional traits, survival, and thus community composition of understorey and overstorey vegetation. A large array of leaf traits are regulated by UV and blue light (Siipola *et al.*, 2015; Wang *et al.*, 2020), *via* photoreceptors like phototropins, cryptochomes and UVR8, among others (Rai *et al.*, 2019).They may impact cross-tolerance to stress (Jansen *et al.*, 2019), and even affect flowers and fruit visibility to animals (Endler, 1993).

How canopy architecture shapes the light fluctuations within

As a canopy gets denser and darker, sunflecks become less frequent, and windflecks intensity fades (Fig. 1). This diminishes the potential photosynthetic gains from light fluctuations, because a higher proportion of the total available light will come in the form of shade, rather than transient patches of high light. This is especially the case at the bottom of a canopy, where windfleck intensity is reduced compared to the upper layers (Fig. 5). Because they are acclimated to shade, leaves in the lower canopy also tend to get light saturated more quickly under high light (Boardman, 1977; Earles *et al.*, 2017). The low light of a tree canopy induces physiological acclimation that make them slower to react to a change of light conditions (Durand *et al.*, 2022). These factors reduce their capacity to use flecks of light efficiently. Yet, shade light is of lower spectral quality as well as lower irradiance level, because it is enriched in green and far red wavelengths that are absorbed less efficiently by chlorophylls (Terashima *et al.*, 2009), and it is more diffuse, which penetrates the mesophyll less deeply than direct light (Cui *et al.*, 1991; Gorton *et al.*, 2010). As an example, blue gum (*Eucalyptus tereticornis*, Sm.) trees often have a sparse canopy, which allows lower leaves to maintain photosynthetic induction and benefit from sunflecks (Campany *et al.*, 2016), whereas the lower leaves of beech trees, acclimated to deep shade, have a reduced photosynthetic capacity and are slower to respond to an increase of irradiance compared to sun leaves (Durand *et al.*, 2022). Whether leaves prioritize temporary bursts of high light, or the more reliable but lower quality shade light will likely depend on the species' physiology contingent on its functional strategy, and its canopy architecture which creates the spatial light fluctuations in the first place.

A greater leaf width in the crops was related to shorter windflecks. We know that greater leverage is gained when a force is exerted at a longer distance from a fulcrum (the support about which a lever turns, see the law of levers; Davidovits, 2008). Therefore, it is possible that wider leaves flutter more rapidly around the midrib, creating faster fluctuations of irradiance. In crops, canopies with a larger leaf angle were associated with more intense windflecks, but in contrast this trait in tree canopies led to windflecks of reduced intensity. The larger leaf angles of crop canopies would lead to larger gaps in the canopy, increasing the penetration of direct light (Falster & Westoby, 2003). Such an effect may not occur in canopies with a more planophile leaf orientation (such as our tree canopies), and where an increase of leaf angle may tilt the leaves in the direction of the sun, actually reducing canopy gaps (van Zanten *et al.*, 2010).

Conclusion

Most studies of photosynthesis are done under steady light conditions, especially those in controlled environments. This means that we lack knowledge of natural patterns of light fluctuations, how canopy architecture affects them, and related plant responses. This research is needed if we want to better apply laboratory findings to the field, and find ways to improve canopy photosynthesis. In this study, we described the diversity of light fluctuation occurring in plant canopies, and outlined major differences between crops and forest windflecks. While this study considered only one genotype per species, there is some evidence of intra-specific variability (Burgess *et al.*, 2021), but further research is needed to assess its extend. We found that the change in spectral composition during a windfleck is dependent on the species that forms the canopy, and that canopy density and architecture affect the properties of light fluctuations. Leaf morphology seemed to play an important role in creating different types of light fluctuations.

Although this study found that short fluctuations are omnipresent in all types of canopies, one should not consider inconsequential longer changes in light (> 1 min), that involves other processes such as stomatal movements. Light has a certain fractal quality where rapid fluctuations symphonize with longer changes, each involving different processes that affect the overall photosynthetic dynamic. Still, the ubiquitous nature of windflecks provides a strong incentive to better understand the biomechanics of wind-induced leaf movements, and their consequence for photosynthesis. This will require a combined approach, to disentangle the complex interaction between wind patterns, the biomechanics of plant movements, and the resulting the light fluctuations in plant canopies, to grasp the benefits of them dancing in the wind.

FUNDING

This research was funded by Academy of Finland decision #351008 and #324555.

ACKNOWLEDGMENTS

The authors would like to acknowledge the Viikki Experimental Farm, and Viikki Greenhouse and Field Trials for providing planting and maintaining the fields for this experiment. We would like to thank Baiba Matule for their technical help, and Anna Lintunen for reviewing a previous version of this manuscript.

CONFLICT OF INTEREST

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

AUTHOR CONTRIBUTION

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

DATA AVAILABILITY

The data that supports the findings of this study are available in the supplementary material of this article. More information is available upon request.

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Legend for Supplementary Information

Table S1: Dataset used for statistical analysis (see separate Excel file).

Fig. S1: Correlations between the baseline spectral ratios before a windfleck and the percent change in the spectral ratio between the peak and the baseline of a windfleck.

Fig. S2: Tree-specific correlations between architectural traits and windfleck properties

Fig. S3: Distribution of sunfleck durations per species.

TABLES

Table 1: Information on growing conditions for field crops: barley (*Hordeum vulgare*), broad bean (*Vicia faba*), oats (*Avena sativa*), and rapeseed (*Brassica napus*). Values are means ± standard deviation.

Crop species	**Variety**	**Day of planting**	**Row spacing (cm)**	**Plant spacing (cm)**	**Density (plants m^{-2})**	**Soil type**	**Fertiliser**	**Fertiliser application**
Avena sativa	Meeri	June 2nd	12.5	1.6	500	Clay loam	Belor Premium N27	300 kg ha^{-1}
Brassica napus	Synneva	May 16th	12.5	2.6	300	Clay loam	Belor Premium N27	350 kg ha^{-1}
Hordeum vulgare	Alvari	May 14th	12.5	1.6	500	Silt loam	Belor Premium N27 + manure (May 4th)	280 kg ha^{-1} + 25 m^{3} ha^{-1}
Vicia faba	Louhi	May 12th	12.5	1.6	70	Clay loam	YaraMila Y1	100 kg ha^{-1}

Table 2: Summary of windfleck properties in crop fields (*Hordeum vulgare*, *Vicia faba*, *Avena sativa*, *Brassica napus*) and tree stands (*Acer platanoides*, *Alnus incana*, *Betula pendula*, *Fagus sylvatica*, *Picea abies*) in Helsinki. Windfleck frequency and clustering were calculated over the whole measurement period, as such they couldn't be included in statistical analyses, all other properties differed significantly among stands. Values are means ± standard error of sets of 10,000 measurements at different locations within each stand/field (n = 8-16). Distribution of durations given in Fig. S3. Letters represent statistically significant differences between groups tested by *post-hoc* pairwise comparisons ($p < 0.05$).

Species	**Baseline irradiance (μmol m^{-2} s^{-1})**	**Peak irradiance (μmol m^{-2} s^{-1})**	**Windfleck intensity (μmol m^{-2} s^{-1})**	**Windfleck duration (ms)**	**Windfleck time interval (s)**	**Windfleck frequency (s^{-1})**	**Windfleck clustering (a.u.)**	**Integrated PAR increase (μmol m^{-2})**	**No. sunfleck < 10 min**	**No. sunfleck > 10 min**
Hordeum vulgare	708.5 ± 9.7 g	1088.3 ± 10.5 h	379.8 ± 8.5 f	227.1 ± 3.3 d	0.61 ± 0.04 c	1.61	0.4	51.3 ± 1.7 g	437.8 ± 41.1 d	52.8 ± 9.2 c
Vicia faba	350.9 ± 5.9 d	514.2 ± 9.4 e	163.3 ± 7.0 c	208.3 ± 4.0 c	1.04 ± 0.09 d	0.77	0.65	22.2 ± 1.4 d	383.4 ± 23.3 cd	41.5 ± 6.1 c
Avena sativa	481.8 ± 8.1 e	711.6 ± 10.6 f	229.8 ± 6.8 d	265.1 ± 6.0 e	1.00 ± 0.07 d	0.92	0.65	38.7 ± 1.9 f	634.5 ± 43.5 e	17.7 ± 5 ab
Brassica napus	646.3 ± 4.2 f	902.2 ± 6.4 g	255.8 ± 3.8 e	176.3 ± 2.3 b	0.41 ± 0.01 b	2.23	0.49	29.4 ± 0.7 e	1413.0 ± 35.0 f	35.2 ± 7.4 bc
Acer platanoides	57.5 ± 7.6 ab	90.1 ± 8.8 ab	32.6 ± 4.1 a	296.4 ± 23.8 f	4.29 ± 0.79 f	0.15	0.87	10.1 ± 3.3 bc	269.8 ± 71.1 bc	2.4 ± 1.2 a
Alnus incana	41.1 ± 1.7 a	74.9 ± 2.3 a	33.8 ± 1.3 a	114.4 ± 2.1 a	0.55 ± 0.06 c	1.68	0.72	2.2 ± 0.1 a	123.2 ± 16.4 ab	1.2 ± 0.9 a
Betula pendula	100.8 ± 1.3 c	170.5 ± 2.3 c	69.7 ± 1.4 b	115.0 ± 1.1 a	0.30 ± 0.02 a	3.24	0.51	5.3 ± 0.2 b	260.4 ± 11.5 bc	9.4 ± 6.1 a
Fagus sylvatica	113.0 ± 5.3 c	190.7 ± 7.7 d	77.7 ± 4.1 b	205.6 ± 5.8 c	1.14 ± 0.14 d	0.53	0.81	12.8 ± 1.5 c	141.8 ± 47.4 ab	0.2 ± 0.2 a
Picea abies	76.0 ± 3.7 b	104.3 ± 4.8 b	28.4 ± 2.3 a	177.3 ± 7.3 b	1.67 ± 0.13 e	0.46	0.69	5.1 ± 1.0 ab	101.0 ± 15.4 a	10.0 ± 6.3 a

Table 3: Summary of windfleck spectral composition in crop fields (*Hordeum vulgare*, *Vicia faba*, *Avena sativa*, *Brassica napus*) and tree stands (*Acer platanoides*, *Alnus incana*, *Betula pendula*, *Fagus sylvatica*, *Picea abies*) in Helsinki. Values for windfleck peaks and baselines are given (means ± standard deviation), as the statistical significance of changes in spectral composition between the baseline and the peak of the windfleck for each species (*p*). Letters represent statistically significant differences between species tested by *post-hoc* pairwise comparisons ($p < 0.05$).

Species	***UV-A : PAR***			***Blue : Green***			***Blue : Red***			***Red : Far-red***		
	Baseline	**Peak**	***p***	**Baseline**	**Peak**	***p***	**Baseline**	**Peak**	***p***	**Baseline**	**Peak**	***p***
Hordeum vulgare	0.158 ± 0.001 f	0.123 ± 0.001 d	**< 0.001**	0.996 ± 0.002 h	0.940 ± 0.001 h	**< 0.001**	1.559 ± 0.009 e	1.309 ± 0.005 d	**< 0.001**	1.037 ± 0.005 f	1.208 ± 0.003 h	**< 0.001**
Vicia faba	0.138 ± 0.001 e	0.123 ± 0.001 d	**< 0.001**	0.909 ± 0.001 e	0.897 ± 0.001 e	**< 0.001**	1.451 ± 0.005 d	1.325 ± 0.004 d	**< 0.001**	0.757 ± 0.005 d	0.907 ± 0.005 d	**< 0.001**
Avena sativa	0.130 ± 0.001 d	0.109 ± 0.001 b	**< 0.001**	0.917 ± 0.001 f	0.892 ± 0.001 de	**< 0.001**	1.384 ± 0.008 c	1.237 ± 0.006 bc	**< 0.001**	0.907 ± 0.009 e	1.075 ± 0.007 f	**< 0.001**
Brassica napus	0.123 ± 0.000 c	0.112 ± 0.000 c	**< 0.001**	0.875 ± 0.000 c	0.877 ± 0.000 c	0.058	1.285 ± 0.002 b	1.233 ± 0.001 b	**< 0.001**	0.895 ± 0.003 e	1.020 ± 0.003 e	**< 0.001**
Acer platanoides	0.127 ± 0.003 cd	0.117 ± 0.002 c	**0.012**	0.832 ± 0.003 b	0.846 ± 0.002 b	**0.021**	1.468 ± 0.023 d	1.247 ± 0.012 bc	**< 0.001**	0.918 ± 0.136 e	1.287 ± 0.173 i	**< 0.001**
Alnus incana	0.160 ± 0.001 f	0.138 ± 0.001 e	**< 0.001**	0.900 ± 0.001 d	0.888 ± 0.001 d	**< 0.001**	1.732 ± 0.010 g	1.399 ± 0.006 e	**< 0.001**	0.283 ± 0.005 a	0.478 ± 0.006 a	**< 0.001**
Betula pendula	0.174 ± 0.001 g	0.149 ± 0.001 f	**< 0.001**	0.937 ± 0.001 g	0.921 ± 0.001 g	**< 0.001**	1.660 ± 0.005 f	1.440 ± 0.004 f	**< 0.001**	0.468 ± 0.003 b	0.652 ± 0.004 b	**< 0.001**
Fagus sylvatica	0.067 ± 0.001 a	0.087 ± 0.001 a	**< 0.001**	0.715 ± 0.006 a	0.816 ± 0.003 a	**< 0.001**	1.181 ± 0.008 a	1.138 ± 0.004 a	**< 0.001**	0.491 ± 0.014 c	0.759 ± 0.013 c	**< 0.001**
Picea abies	0.085 ± 0.001 b	0.090 ± 0.001 a	**0.022**	0.915 ± 0.002 f	0.905 ± 0.002 f	**0.002**	1.289 ± 0.009 b	1.258 ± 0.015 c	**0.033**	1.031 ± 0.011 f	1.130 ± 0.010 g	**< 0.001**

UV-A: 315-400nm ; PAR: 400-700nm; blue: 420-490nm ; green: 500-570nm ; red: 620-680nm ; far-red: 700-750nm

FIGURES

Figure 1: Canopy architectural traits measured in crop fields (Ba: barley, *Hordeum vulgare*; Bn: bean, *Vicia faba;* Ot: oat, *Avena sativa;* Rp: rapeseed, *Brassica napus*) and tree stands (Ac: *Acer platanoides*, Al: *Alnus incana*, Be: *Betula pendula*, Fa: *Fagus sylvatica*, Pi: *Picea abies*) in Helsinki. Traits measured included plant area index (**a**), plant height (**b**), leaf length (**c**), canopy light transmission (**d**), leaf angle (**e**), and width (**f**). Note the different scales of plant height for crops and trees. Values are means ± standard error (*n* = 10-50). The asterisk on the top left shows for each trait when there was a significant difference between crop and tree species. Letters represent statistically significant differences between groups (crops and trees were tested separately) tested by *post-hoc* pairwise comparisons ($p < 0.05$).

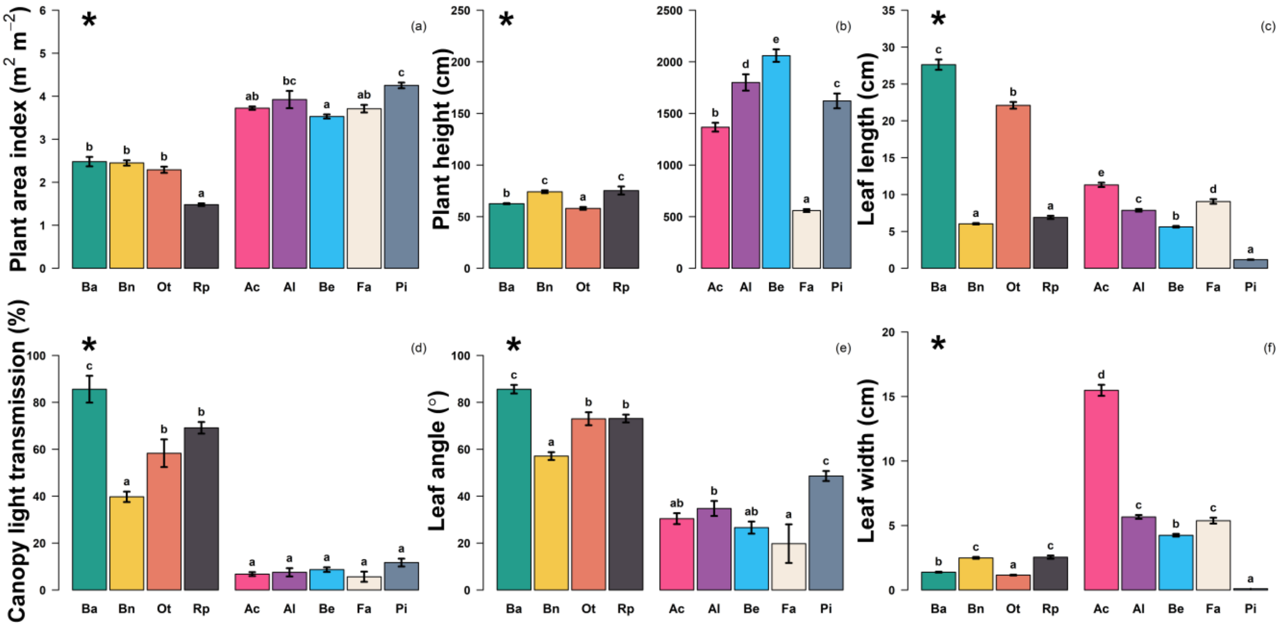

Figure 2: Typical windfleck properties recorded in the four crop fields (Ba: barley in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba;* Ot: oat in orange, *Avena sativa;* Rp: rapeseed in black, *Brassica napus*) in Helsinki. (a) Typical windfleck calculated using average windfleck duration and intensity for each species (*n* = 828 - 2675). The shape of the windfleck followed a normal density distribution. (b) Average windfleck intensity relative to the irradiance at the top of the canopy. Crossed areas show the relative baseline irradiance. (c) Reconstructed time-series of typical windflecks accounting for sunfleck duration and average time interval between windfleck. Windfleck intensities were normalized to the most intense windfleck (in barley).

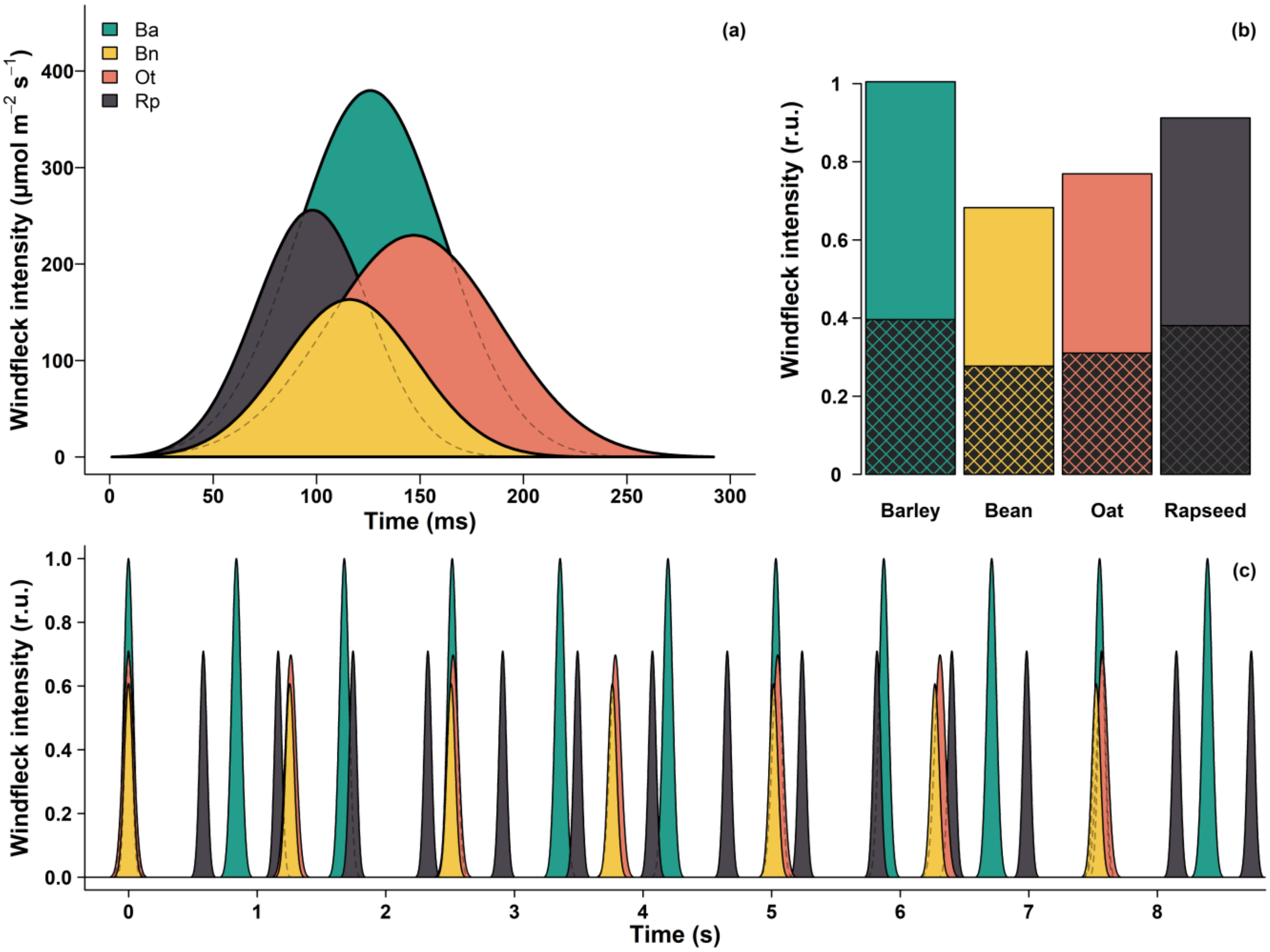

Figure 3: Typical windfleck properties recorded in the five forest stands (Ac: *Acer platanoides* in pink, Al: *Alnus incana* in purple, Be: *Betula pendula* in blue, Fa: *Fagus sylvatica* in white, Pi: *Picea abies* in grey) in Helsinki. (a) Typical windfleck calculated using average windfleck duration and intensity for each species (n = 149 - 4858). The shape of the windfleck followed a normal density distribution. (b) Average windfleck intensity relative to the irradiance at the top of the canopy. Crossed areas show the relative baseline irradiance. (c) Reconstructed time-series of typical windflecks accounting for sunfleck duration and average time interval between windfleck. Windfleck intensities were normalized to the most intense windfleck (in *F. sylvatica*).

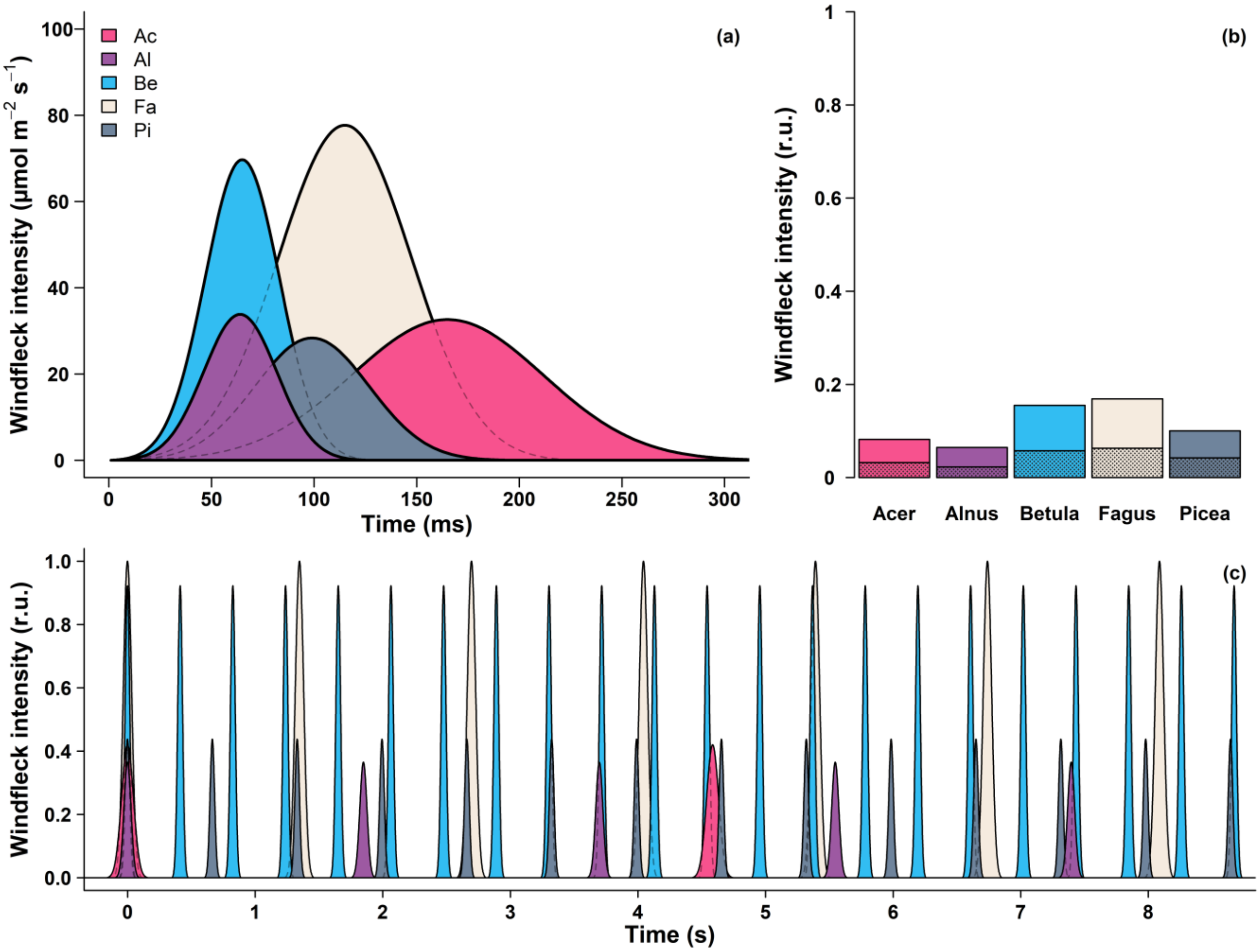

Figure 4: Relative change in spectral composition during a windfleck in four crop fields (a, Ba: barley in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba;* Ot: oat in orange, *Avena sativa;* Rp: rapeseed in black, *Brassica napus*) and five forest stands (b, Ac: *Acer platanoides* in pink, Al: *Alnus incana* in purple, Be: *Betula pendula* in blue, Fa: *Fagus sylvatica* in brown, Pi: *Picea abies* in grey) measured in Helsinki. Peak and baseline spectral irradiance were normalized to 450 nm, where irradiance was highest, to highlight difference in composition rather than amount of radiation. The curve shown here is the difference between the peak and baseline normalized spectral irradiance. Positive values reflect an increase of this wavelength during a windfleck, whereas negative values reflect a decrease. We applied a smoothing spline (in color) to each curve (in grey) to emphasize general trends. The wavebands used to calculate spectral ratios in the main text are shown at the top of the figure.

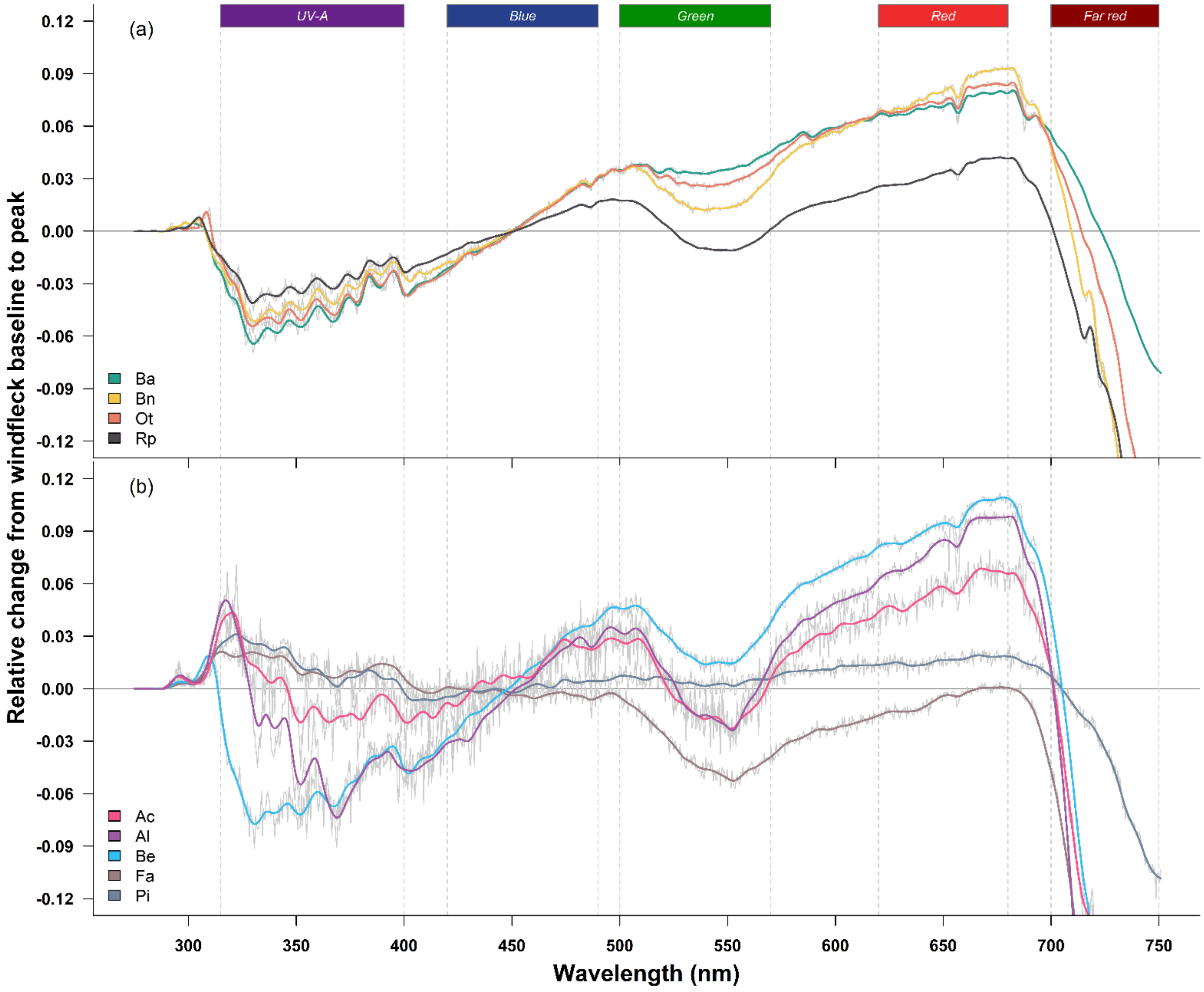

Figure 5: Windfleck properties along a vertical gradient recorded in a *Fagus sylvatica* stand in Helsinki. Windfleck duration (a) average time interval (b), intensity (c), and integrated increase in PAR irradiance due to the windfleck (d) were recorded at every meter from the ground to 4 m high. Values are means ± standard error of measurements at 7 locations in the stand. Pearson correlation coefficient and *p* values are reported.

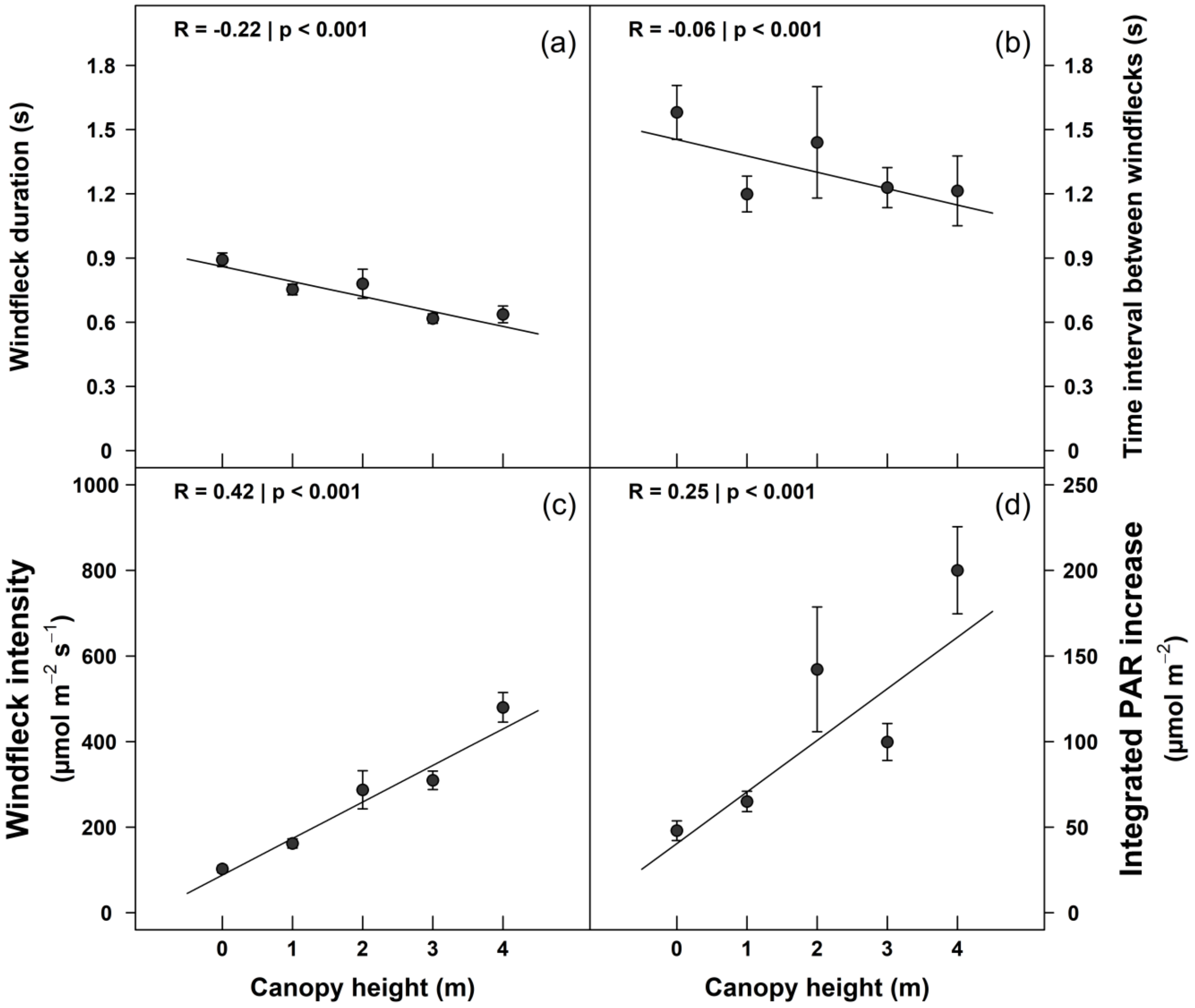

Figure 6: Correlations between canopy architectural traits and windfleck properties in four crop fields (Ba: barley in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba;* Ot: oat in orange, *Avena sativa;* Rp: rapeseed in black, *Brassica napus*) and five forest stands (Ac: *Acer platanoides* in pink, Al: *Alnus incana* in purple, Be: *Betula pendula* in blue, Fa: *Fagus sylvatica* in white, Pi: *Picea abies* in grey) measured in Helsinki. Plant area index (a-d), canopy light transmission (e-h) and median PAR irradiance (i-l) were correlated with the number of sunfleck longer than 10 min (a, e, i), windfleck duration (b, f, j), intensity (c, g, k) and integrated increase in PAR irradiance due to the windfleck (d, h, l). Values are means ± standard error. Pearson correlation coefficient, *p* values, and the percent of *p* values < 0.05 in the bootstrap analysis (*b* value) are reported.

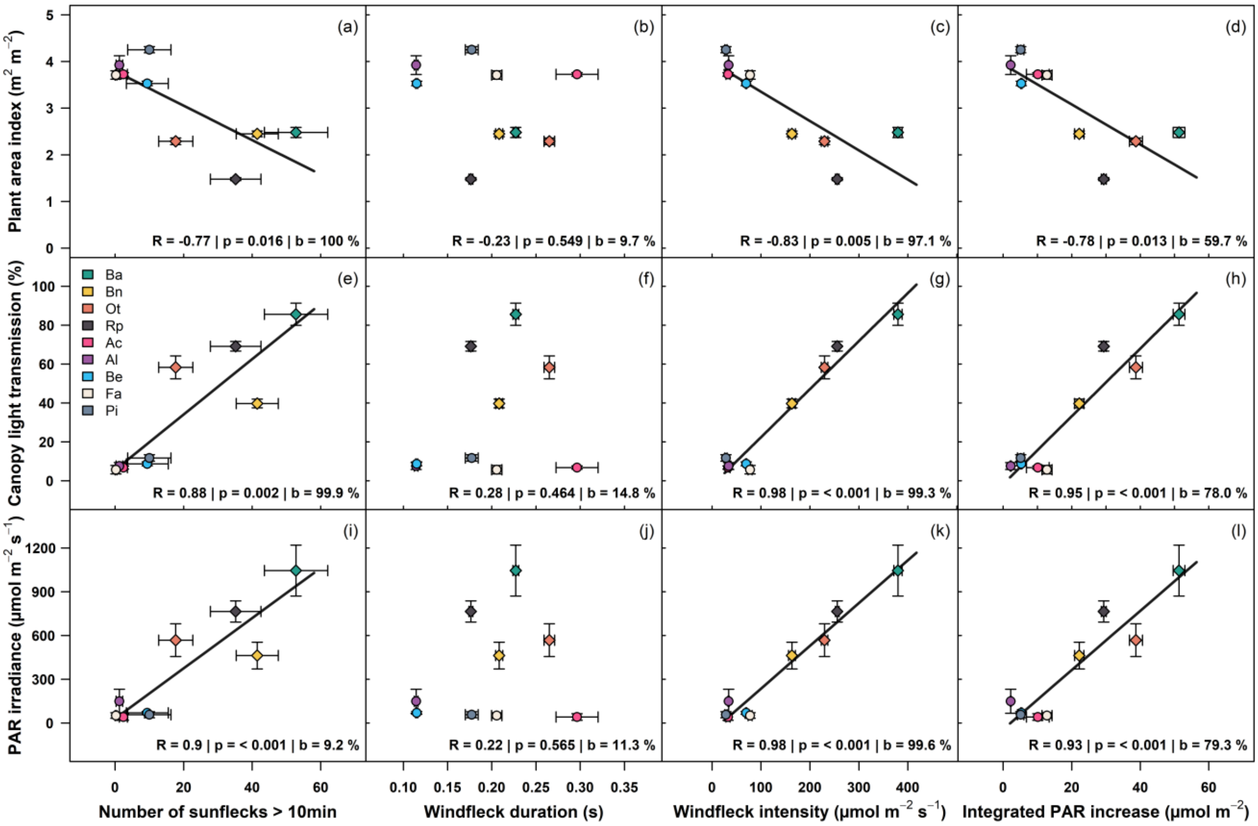

Figure 7: Canopy-specific correlations between architectural traits and windfleck properties in four crop fields (a, c, e, ; Ba: barley in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba;* Ot: oat in orange, *Avena sativa;* Rp: rapeseed in black, *Brassica napus*) and five forest stands (b, d, f; Ac: *Acer platanoides* in pink, Al: *Alnus incana* in purple, Be: *Betula pendula* in blue, Fa: *Fagus sylvatica* in white, Pi: *Picea abies* in grey) measured in Helsinki. Leaf angle (a-d) and canopy light transmission (e-f) were correlated with windfleck intensity (a-b) and clustering (c-f). Values are means ± standard error Pearson correlation coefficient, *p* values, and the percent of *p* values < 0.05 in the bootstrap analysis (*b* value) are reported. Windfleck clustering was calculated over the whole measurement period, as such they couldn't be included in bootstrap analyses.

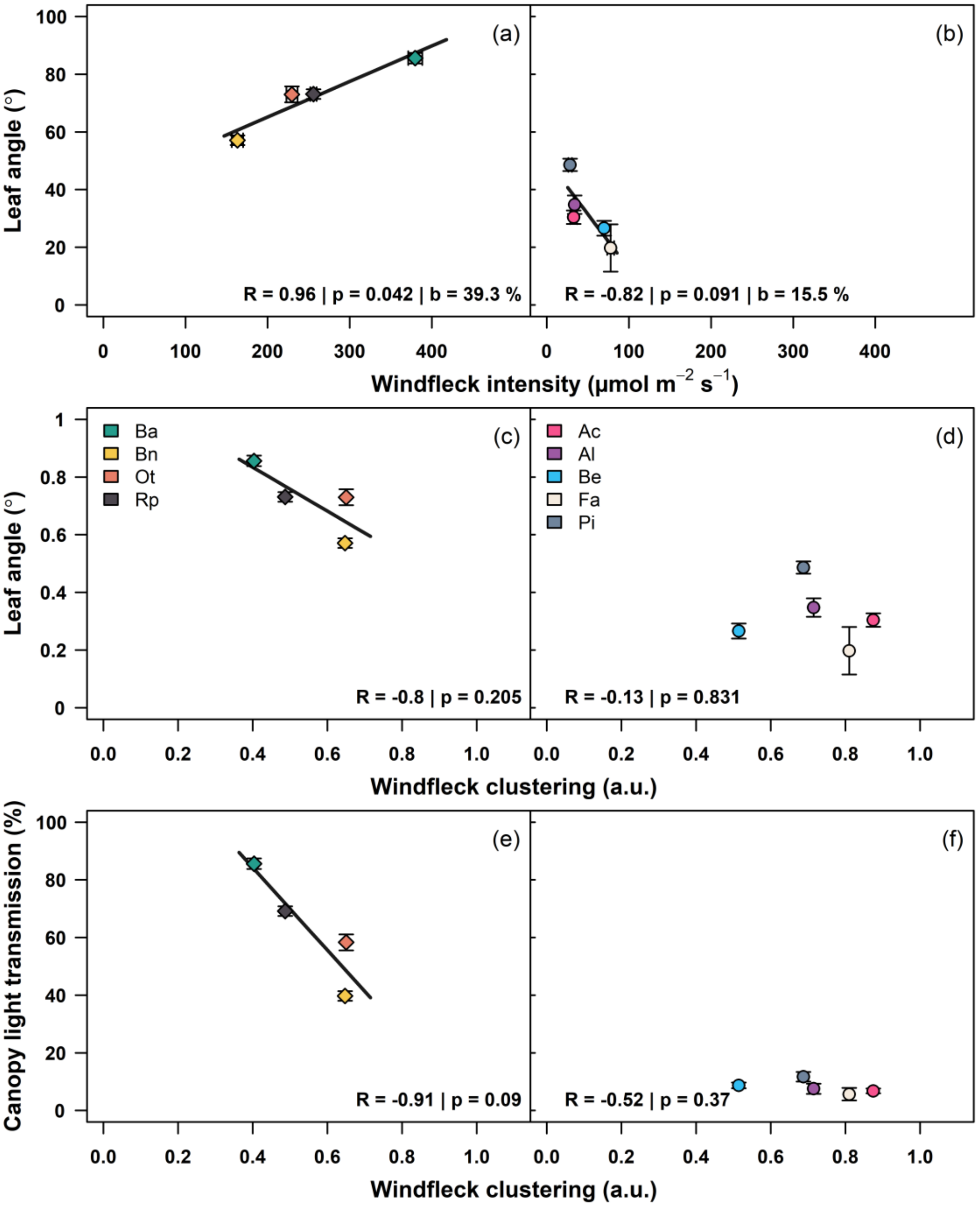

Figure 8: Crop-specific correlations between architectural traits and windfleck properties (Ba: barley in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba;* Ot: oat in orange, *Avena sativa;* Rp: rapeseed in black, *Brassica napus*) measured in Helsinki. Plant height (a-c), leaf length (d-f) and width (g-i) were correlated with windfleck duration (a, d, g), intensity (b, e, h) and integrated increase in PAR irradiance due to the windfleck (c, f, i). Values are means ± standard error. Pearson correlation coefficient, *p* values, and the percent of *p* values < 0.05 in the bootstrap analysis (*b* value) are reported.