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1 **TITLE**

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

3

4 AUTHORS

- 5 Maxime Durand¹ and T. Matthew Robson^{1,2}
- 6
- 7 ¹ Organismal and Evolutionary Biology (OEB), Viikki Plant Science Centre (ViPS), Faculty of
- 8 Biological and Environmental Sciences, University of Helsinki, 00014, Finland.
- 9 ² National Forestry School, University of Cumbria Ambleside, LA22 9BB, UK

10

11 CORRESPONDING AUTHOR

- 12 Maxime Durand:
- 13 Email: maxime.durand@helsinki.fi
- 14 Phone: (+358) 40 636 1664
- 15

16 **ORCID**

- 17 Maxime Durand: 0000-0002-8991-3601
- 18 T. Matthew Robson: 0000-0002-8631-796X
- 19

20 LENGTH

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22 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.
- 40

41 KEY-WORDS

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

43 INTRODUCTION

44 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). 45 Even under a clear sky at the very top of a canopy, a light breeze will cause leaves to move and change 46 47 the relative angle of incidence of sunlight, affecting the irradiance they receive and the leaf boundary-48 layer conductance. In such conditions, those plants that can respond faster to fluctuations in the 49 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 50 51 light fluctuations has received increasing interest in recent years (Murchie et al., 2009; Kaiser et al., 52 2018; Slattery et al., 2018; Long et al., 2022). This is regarded as a way to, in principle, mitigate 53 climate-related declines in agricultural plant productivity (Asseng et al., 2014), and the rising 54 worldwide demand for food (Ort et al., 2015). Better models that account for the dynamic response 55 of photosynthesis to fluctuating environments will also allow us to predict canopy net carbon 56 assimilation more accurately and how it is impacted by global changes.

57 Multiple physiological processes, operating at different time scales, in plant canopies 58 are affected by changes in irradiance (Way & Pearcy, 2012). Patterns of light fluctuations, in terms 59 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 60 61 & Pearcy, 2000), and the rate of non-photochemical quenching (Murchie & Ruban, 2020). These 62 limitations control the efficiency at which the subsequent period of high light can be used. Even brief 63 light fluctuations will affects these relatively slow (15-45 min duration) processes, dictating the 64 induction state of the photosynthetic machinery, and ultimately determining photosynthetic rates. For 65 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 66 67 the accumulation of photoprotection. Over a shorter time-scale (< 1 min), the efficiency at which 68 photosynthesis can use brief light fluctuations (its momentary induction state), such as those induced 69 by wind, will depend on several processes. First, the build-up of Ribulose 1,5-bisphosphate reaches 70 a non-limiting state 1-2 min after illumination (Sassenrath-Cole & Pearcy, 1992). Second, CO₂ 71 assimilation is sustained for several seconds post-illumination due to residual photosynthetic 72 metabolic pools (McAlister, 1939; Laisk et al., 1984). Third, pools of photorespiratory metabolites 73 can induce a CO₂ burst after illumination, which can offset the overall CO₂ assimilated (Vines et al., 1983; Pearcy, 1990). These processes are often neglected in models, and yet the degree to which they 74 75 affect long-term photosynthetic rates in fluctuating light environments will depend on the duration, 76 frequency and intensity of light fluctuations (Pons & Pearcy, 1992; Roden & Pearcy, 1993b; Kaiser 77 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).

80 To date, exploration of the probable links between canopy structure and the properties 81 of light fluctuations has received little attention (Way & Pearcy, 2012; Smith & Berry, 2013). Yet, 82 we know that light distribution in the canopy is shaped by the morphological, architectural, and 83 mechanical traits of the species that compose it, which interact with environmental factors such as 84 the sun position, clouds and the wind. For example, a higher leaf area in the upper canopy will 85 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, 86 87 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 88 89 recognition of the effect of wind on plant productivity, especially in crops, creating movement in the 90 canopy that depends on the mechanical properties of stems and leaves (de Langre, 2008; Burgess et 91 al., 2016). In contrast, the lignified stems of trees present a stronger resistance to wind, meaning that 92 wind-induced movements will be stronger around the petiole axis (Roden & Pearcy, 1993a). Forest 93 canopies, being taller than crop canopies, also generate more penumbra (or partial shade; Smith et 94 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. 95

Historically, most research on light fluctuations, where brief periods of high irradiance 96 97 are often called sunflecks, has been focused on solar-induced movements (e.g. helio- and photo-98 tropisms) in understorey species in forests (Atkins & Poole, 1937; Evans, 1956; Pearcy, 1990; 99 Chazdon & Pearcy, 1991). Light fluctuations were much more rarely examined in crops (Pearcy et 100 al., 1990; Barradas et al., 1998). More recently, light fluctuations induced by wind have been dubbed 101 "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 102 define, and are often characterized as periods of irradiance above an arbitrary threshold contingent 103 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 104 & Pearcy, 1993, 70% of the irradiance at the top of the canopy in Barradas *et al.*, 1998). This makes 105 comparison between studies and canopies difficult, as for example 50 μ mol m⁻² s⁻¹ could correspond 106 107 to a shade environment in one canopy but the peak of a sunfleck in another. We recently devised a 108 method of tracking light fluctuations that provides a more generic and repeatable means to define 109 sunflecks as brief periods of high irradiance relative to the background shade environment, based on 110 motifs in time-series of irradiance (Durand et al., 2021a). This allows us to describe key features of 111 windflecks, consistently in any canopy.

112 We recorded time-series of irradiance at very high frequency to describe with 113 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 114 environmental conditions (cloudless sky, similar solar angle), and phenological stages. Using our 115 published method, we then characterized the properties of these light fluctuations, hereafter called 116 windflecks. We also recorded longer light fluctuations (> 1 min.) using hemispherical pictures, 117 118 hereafter defined as sunflecks. We then investigated their potential relationships with leaf 119 morphological and canopy architectural traits. We aimed to: (1) characterize windfleck properties in 120 both crop and tree canopies, (2) examine how the spectral composition is modified during a 121 windfleck, and (3) identify the main canopy architectural traits that drive the patterns of light 122 fluctuations.

123 MATERIALS & METHODS

124 Study site and plant material measured in 2021

We conducted this experiment at the University of Helsinki, Finland (60.227 N, 25.018 125 126 E, 10 m above sea level) at Viikki Experimental Farm and Viikki Field Plots for the crop species, and 127 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 128 129 well as pure stands of Norway maple (Acer platanoides, L.), silver birch (Betula pendula, Roth.), 130 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 131 132 stand (Fagus sylvatica, L.) planted in 2010. The stand is composed of trees from four provenances: 133 Blaviksliarna southern Sweden, Eichelberg and Rindelpholz in Germany, and Montejo de la Sierra, 134 in Spain. The plot was thinned by removing half of the trees in May 2020 (for more information, see 135 Durand *et al.*, 2022).

136 Lig

Light measurements

137 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., 138 139 Reading, UK) attached to a fiber-optic cable (FC-UV400-2 400µm, Avantes, Leatherhead, UK). The 140 Finnish Radiation and Nuclear Safety Authority calibrated the spectrometer in April 2021 (STUK; 141 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 142 143 simultaneously, with an integration time of 10 ms. Each set thus made up a 100s-long time-series. 144 We used the "high-speed acquisition" routine of the SpectraSuite software (Ocean insights, v2.0.162),

145 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 146 June 30^{th} to July 14^{th} 2021 (n = 8-16), before the panicle and grains of the oats, and the stalks and 147 heads of the barley turned yellow. Rapeseed was measured first and beans last, both during their early 148 149 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 150 151 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 152 the canopy structure. After each time-series was recorded, we took two additional control recordings 153 154 to correct for stray light and dark signal. The first recorded the baseline noise, which was subtracted 155 from the measurements, by placing a darkening cap over the diffuser to block all UV and visible 156 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). 157 158 We recorded all data within three hours of solar noon (at about 13:30) from 10:30 to 15:30, local time 159 in the absence of clouds. Above-canopy measurements were recorded between one and three times 160 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 161 162 spectrometer counts into irradiance values, and perform the corrections mentioned above.

163

Windfleck detection and properties

164 The method used to detect and measure windfleck properties is detailed in Durand *et* 165 *al.* (2021a). Briefly, we calculated the rate of change between two time points along the measured 166 time-series of PAR irradiance (400-700 nm, Δ_{PAR}), for each point *n* at time *t* in the time series and its 167 following measurement *n* +1 as:

168
$$\Delta_{PAR} = \frac{PPFD_{n+1} - PPFD_n}{t_{n+1} - t_n}$$
Eqn. 1

169 Δ_{PAR} has the property of crossing 0 when PAR irradiance switches from decreasing to 170 increasing, and likewise in reverse. This allowed us to pinpoint the start, peak and end of a windfleck 171 and associated PAR irradiances. Potential windflecks corresponded with an increase in PAR 172 irradiance larger than 5 µmol m⁻² s⁻¹, or represented an increase in PAR irradiance between peak and 173 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

178 between the end of a windfleck and the start of the next windfleck, and the overall frequency (F) as 179 the total number of windflecks recorded divided by the combined duration of all time-series. We also 180 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 181 calculated as the total integrated PAR irradiance during the windfleck, from which the residual PAR 182 183 irradiance (the linearly interpolated PAR irradiance between the start and end of a windfleck) was 184 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; 185 186 blue: 420-490nm; green: 500-570nm; red: 620-680nm; far-red: 700-750nm).

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Canopy architecture

188 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 189 sensor combined with a circular fisheye lens (Sigma 4.5 mm f2.8 EX DC HSM, Sigma Corporation 190 191 of America, USA). All photographs were taken in RAW format, at 10 cm above the ground using a 192 tripod under overcast sky. ISO was fixed at 100 and aperture at F22, varying only shutter speed to 193 adjust exposure. We produced a sharpened gamma-corrected and contrast-stretched blue channel 8bit jpeg from the RAW files following Macfarlane et al. (2014). Photographs were analyzed with the 194 195 Hemisfer software (Schleppi et al., 2007) following the weighted ellipsoidal method from Thimonier 196 et al. (2010) and using the non-linearity and canopy clumping corrections (Chen & Cihlar, 1995; 197 Schleppi et al., 2007). This allowed us to estimate mean tilt angle of the leaves, plant area index (PAI, 198 *i.e.* leaf area index without correction to remove stems), and canopy light transmission. Hereafter, we 199 designate as sunflecks the period for which the sensor experienced direct sunlight, by contrast to the 200 spectrometer method described above to record windflecks. The distribution of sunfleck duration can 201 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 202 30th to July 14th, the same as for the light measurements, and used an automatic thresholding according 203 to Nobis & Hunziker (2005). Finally, we also measured plant height (n = 10), as well as leaf width, 204 205 and length (n = 50) in all canopies sample at mid-canopy height (crops) or green freshly fallen (trees).

206

Statistical analysis

207 We used Type II ANOVA to test for significant differences between canopy species in 208 light fluctuations and canopy architectural traits. Normality and homoscedasticity were checked 209 graphically. We performed *post-hoc* pairwise contrast analyses to test for differences among factor 210 levels, and adjusted p values to control the false discovery rate. Significant differences were 211 considered at p < 0.05 for all tests. These tests were made using R 4.2.1 (R Core Team, 2022) with

212 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 213 214 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 215 216 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 217 218 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 219 220 expected that 5% of the random pairings would result in a correlation with a p value < 0.05, thus only 221 *b* values higher than 5% would provide evidence of a possible correlation between the two variables.

222 **RESULTS**

223 Variability of canopy architecture at the species level

224 There were generally large difference between the canopy architecture of trees and 225 crops (Fig. 1), although a single genotype per species was examined. PAI was 1.75 times higher in 226 the tree species than in the crops, with an average canopy light transmission of 63% in the crops but 227 only 8.2% in the tree stands. Leaves were generally erectophile in the crops $(72.2 \pm 1.9^{\circ})$ but more planophile in the tree stands ($32.4 \pm 2.6^\circ$, Fig. 1e). Among the crop species, only the rapeseed canopy 228 229 showed a PAI significantly lower (by 39%) than the other three canopies (Fig. 1a). This was despite rapeseed being the tallest crop canopy $(75.3 \pm 3.9 \text{ cm}, \text{Fig. 1b})$. The bean canopy had the most 230 231 planophile leaves $(57.1 \pm 1.7^{\circ})$ and barley the most erectophile ones $(85.6 \pm 1.8^{\circ})$, which resulted in beans having the lowest (39.7 \pm 2.2%) and barley highest (85.6 \pm 5.7%) canopy light transmission 232 233 among crops (Fig. 1d). Barley had very long leaves (Fig. 1c), 1.25, 4.6 and 4.0 times longer than oat, 234 bean and rapeseed respectively, which had wider leaves (Fig. 1f).

235 Among the trees, PAI was much more similar across stands, with only the spruce stand 236 having a PAI 16% higher than the maple, birch and beech stand (p < 0.007, Fig. 1a). We could not detect significant differences in canopy light transmission (p = 0.08), but spruce leaves were the most 237 238 erectophile (48.6 \pm 2.1°) and beech leaves the most planophile (19.8 \pm 8.2°). The beech stand being the youngest, it was also the shortest $(5.6 \pm 1.4 \text{ m})$, followed by the maple, spruce, alder, and birch 239 240 as the tallest stand (20.6 \pm 6.0 m, Fig. 1b). 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. 1c-f). On 241 242 the contrary, the spruce leaves were the smallest, both in length and width, but had the higher length 243 to width ratio (11.7).

244

Species-specific windfleck properties

245 Overall, the baseline and peak irradiance was 7.0 and 6.4 times higher in the crops than 246 in the tree stands (respectively, Table 2). This resulted in windflecks being much more intense, by 5.3 times, in the crop (on average $266.4 \pm 3.2 \,\mu\text{mol}\,\text{m}^{-2}\,\text{s}^{-1}$) than in the tree canopies ($60.6 \pm 1.0 \,\mu\text{mol}$) 247 m⁻² s⁻¹, p < 0.001). Windfleck duration was on average longer in the crop (206.4 ± 0.2 ms) than in 248 the tree stands (132.3 \pm 0.1 ms, p < 0.001), although this was species dependent. This led to an 249 integrated PAR increase of $34.6 \pm 0.7 \,\mu\text{mol} \,\text{m}^{-2}$ per windfleck on average in the crops, compared to 250 only 5.6 \pm 0.2 µmol m⁻² per windfleck in the tree stands. Differences of time interval between 251 252 windfleck, windfleck frequency and clustering was strongly species-specific, rather than being 253 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 254 stands for those lasting less than 10 min, and 7.4 times as numerous when considering those lasting 255 256 more than 10 min.

257 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 258 was a similar trend for the peak irradiance of the windflecks. This led to windflecks being 2.3, 1.7 259 and 1.5 times more intense in the barley canopy compared to bean, oat and rapeseed, respectively 260 261 (Fig. 2a). Due to a smaller difference in windfleck duration than intensity between canopies, the 262 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, 263 264 and oat. Along with a lowest average time between windflecks, this resulted in a windfleck frequency 265 in rapeseed that was 1.5, 2.5 and 2.4 times lower than in the barley, bean, and oat canopy respectively 266 (Fig. 2c). Overall, windflecks in the bean and oat canopies tended to be more clustered together than 267 in the other canopies (Table 2). For longer sunflecks, we found that those lasting less than 10 min 268 occurred most often in the rapeseed canopy, but those lasting more than 10 min were more frequent 269 in the barley.

270 The ranking among tree species was the same for both baseline and peak irradiance 271 during windflecks, with the highest irradiance in beech followed by birch, spruce, maple and alder 272 stands (Fig. 3). Yet, irradiance increased by 82.2% during a windfleck in the alder stand, but only by 273 37.2% in the spruce stand, resulting in a similar windfleck intensity in the maple, alder and spruce 274 stand, but still on average 2.3 times lower than that of birch or beech stands (Fig. 3a). Maple had one of the least intense windflecks, but they were also the longest, 2.6 times as long as the shortest 275 276 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 277

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.

285 Changes of spectral composition during a windfleck

286 The ratio of UV-A to PAR generally decreased from the baseline to the peak of the 287 windfleck, by as much as 22% in the barley canopy, whereas in the beech and spruce canopy, UV-288 A:PAR was lowest, and increased by 6% and 30% during windflecks. The lowest baseline B:G ratio 289 was also in the beech stand, where it increased by 14% on average during a windfleck, while other 290 canopies had either a similar or lower B:G ratio during a windfleck. For all canopies, the average B:R 291 ratio decreased by 10% and the R:FR ratio increased by 31% during a windfleck. In general, a smaller 292 baseline ratio was correlated with a larger increase (or a smaller decrease) during the windfleck (p < p293 0.002; Fig. S1).

294 In barley, UV-A radiation and blue light did not increase as much as green or red light, 295 and there was a modest increase of R:FR in a windfleck (Table 3, Fig. 4). The other crops showed a 296 similar trend, with rapeseed having the smallest proportional change of spectral composition overall. 297 In maple, while the shortwave part of the spectrum showed small changes of spectral composition, 298 there was a large increase in red light, leading to a large reduction in B:R and increase in R:FR in a 299 windfleck. In alder and birch, this increase extended to the green light as well, cause a reduced B:G 300 during the windfleck, unlike in maple (Table 3). We recorded the largest relative increase of both 301 blue and red, compared to green, in the beech canopy, while in the spruce there was a relative increase 302 in UV-A radiation but minor changes in the blue, green and red regions.

303

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. 5a). 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

- 311 coefficient of correlation (R) of -0.06. Still, a stronger correlation was found with windfleck intensity 312 (R = 0.42, Fig. 5c), which increased from $102.3 \pm 4.4 \mu \text{mol m}^{-2} \text{ s}^{-1}$ at ground level to 480.0 ± 17.6 313 $\mu \text{mol m}^{-2} \text{ s}^{-1}$ at 4 m. This led to a similar, albeit weaker, positive correlation between the integrated 314 PAR increase per windfleck and canopy height (R = 0.25). In general, with height in the beech 315 canopy, windflecks tended to be shorter, more frequent, and much more intense (Fig 5).
- 316

Relationships between canopy architecture and the properties of light fluctuations therein

317 The architecture of the canopy was generally well correlated with the properties of 318 windflecks, even though our statistical power was reduced by using species means. We found PAI to 319 be negatively correlated with the number of sunflecks longer than 10 min (R = -0.77, p = 0.02, Fig. 320 6a), the intensity of windflecks (R = -0.83, p = 0.005, Fig. 6b), and the integrated increase in PAR 321 per windfleck (R = -0.78, p = 0.013, Fig. 6d). Both canopy light transmission and the average PAR 322 irradiance were positively correlated with the number of sunflecks longer than 10 min (R > 0.88; p < 1000.002, Fig. 6e-i), windfleck intensity (R > 0.98, p < 0.001, Fig. 6g-k), and the integrated increase in 323 324 PAR per windfleck (R > 0.93, p < 0.001, Fig. 6h-l). Windfleck duration was neither correlated with PAI, canopy light transmission, nor the average PAR irradiance (p > 0.46, Fig. 6b-f-j) or sunfleck 325 326 frequency (data not shown). In general, denser canopies produce fewer long sunflecks than sparser 327 canopies, and less intense windflecks, but of similar duration and frequency to sparser canopies. Some 328 correlations could only be detected in either the crops or the tree canopies but not both. For example, 329 average leaf angle was positively correlated with windfleck intensity in the crops (R = 0.96, p = 0.04, 330 Fig. 7a), but only a relatively weak negative tendency was found in the forest stands (R = -0.82, p =0.09, Fig. 7b). Sunfleck clustering produced a negative trend with leaf angle (R = -0.8, p = 0.21) and 331 332 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**). 333

334 We found correlations between windfleck properties and architecture in the crop fields. 335 Among the crop canopies, plant height was negatively correlated with windfleck duration (R = -0.93, 336 p = 0.07, Fig. 8a). The significance of this correlation (p value) was marginally above the threshold 337 of 0.05. Yet, more than 21% of random pairings between plant height and windfleck duration had a 338 p < 0.05, providing more evidence of a possible link between the two variables. This pattern was 339 repeated but with a weaker trend for plant height and the integrated increase in PAR per windfleck 340 (Fig. 8c). Windfleck intensity was neither correlated with plant height, leaf length nor width (p > 10.25), but leaf length was positively related to the integrated increase in PAR per windfleck (R = 0.96, 341 342 p = 0.044, Fig. 8f), due to similar positive trends with windfleck duration and intensity (Fig. 8d-e). By contrast, there was a negative trend between leaf width and both windfleck duration (R = -0.89, 343

Fig. 8g) and the integrated increase in PAR per windfleck (R = -0.82, Fig. 8i). 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).

350 **DISCUSSION**

351

Considerable disparity between light fluctuations in crops and forests

352 One of the striking differences we found regarding windflecks, was that their intensity 353 in forests was considerably lower than that in crops. The windfleck peak was often lower in tree 354 canopies than the baseline irradiance in the crops (Fig. 2b, Fig. 3b). Penumbral effects amplify as the 355 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 356 windflecks were recorded in the spruce canopy which is highly clumped, and less susceptible to wind, 357 358 with its more rigid needle-shaped leaves (Table 2). While this result has been predicted, from 359 measurements in a soybean (Glycine max, L.) canopy (Pearcy et al., 1990), to our knowledge our 360 study is the first systematic examination and quantification of this pattern. It should be noted that our 361 measurements in crops were performed within the canopy, but further below in the trees. We could 362 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 363 364 understories. Here, we showed that this pattern is not consistent among field crops, rather windfleck 365 duration and frequency seem to be species-specific (Table 2), although an assessment of genotypic 366 variation is needed before a definitive conclusion can be reached. This finding is somewhat 367 unexpected, as the woody stems of trees makes them more resistant to wind. Instead, the 368 biomechanics of the petioles in trees seem to play as much of a role as the stems of crops, in 369 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 377 same method to detect windflecks in both studies. In summer 2020, we found windflecks in the barley 378 canopy to be more intense, shorter, and less frequent than in the oat canopy, which is similar to our 379 current results. However, while in 2020 the broad bean canopy generated windflecks with the highest 380 intensity, duration and frequency, measurements from 2021 found broad beans to have the lowest 381 intensity, duration, and frequency (Table 2, Durand et al., 2021a). Differences in the stage of canopy 382 development at the time of measurement may be partially responsible for the inconsistency between 383 the measurements in the two consecutive years, as the barley and oats canopies were planted six and 384 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 385 386 shortest crop in 2020, to the tallest crop in 2021. A time course of measurements in a common bean 387 (Phaseolus vulgaris, L.) canopy found windflecks to become shorter as the canopy grew taller 388 (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 389 390 the canopy (see Fig. 5). Windfleck duration also decreased with height within the canopy, but 391 decreased with plant height in crops (Fig. 6a) suggesting that each imply the specific patterns of light 392 fluctuations. These considerations may also explain why the relatively young and short beech canopy 393 produced windflecks of high intensity and duration compared to the other tree canopies measured 394 (Fig. 1b). A better understanding of the impact of plant height, and depth in the canopy would be 395 gained if future studies focus their attention on genotypic variability in plant height, and 396 developmental stages.

397

Canopy-dependent changes in spectral irradiance of windflecks

398 Since a full record of spectral irradiance can be accessed for each time-point of the time-399 series we used to detect windflecks, we could specifically examine the change in spectral composition 400 during a windfleck. Comparison of regions of the spectrum allowed for smaller, but more precise, 401 differences between the baseline and the peak of the windfleck to be identified, than was possible 402 from comparing only the spectral integral, i.e. PAR (e.g. as in Durand *et al.*, 2021a).

403 Spectral composition of solar radiation in the canopy can be highly variable 404 (Hartikainen et al., 2018; Hovi & Rautiainen, 2020). In part, this depends on the structural and 405 biochemical composition of the leaves affecting their optical properties (Gates, 1965), but also on 406 canopy properties such as leaf area and angle (Asner, 1998). These features partly explain the 407 diversity of spectral composition we found between canopies. The B:R and R:FR spectral photon 408 ratios we recorded were higher than those reported in Hertel et al. (2011), although in both studies 409 the ratios were higher in the spruce than in the beech canopy. While generally windflecks provide 410 disproportionately more blue and red light within canopies as shade is depleted in these wavelengths, 411 we found that changes in spectral composition during a windfleck were characteristic to each canopy 412 type. This means that differences in spectral composition, resulting from overstorey structure and 413 species with different leaf optical properties, could be detected during a windfleck. This could 414 differentially affect those understorey species that are thought to exploit the brief fluctuating 415 irradiances provided by windflecks for photosynthesis, with the efficiency of this process depending 416 on spectral composition (Brodersen & Vogelmann, 2010; Smith *et al.*, 2017).

417 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 418 419 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 420 421 (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 422 423 knowledge, no study investigated whether diffuse light that is enriched in green and far-red light 424 penetrates as deeply or deeper in the mesophyll than direct solar radiation. The pertinence of this 425 question is also dependent on the location of chloroplasts which will condition the potential to use 426 light at various depth in the mesophyll. These differences in spectral composition may also more 427 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, 428 429 where one plant grows under the shade of another, may also benefit from a specific coupling of 430 overstorey/ canopy species that, through their leaf traits and canopy architecture, creates a better light 431 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, 432 433 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; 434 435 Burgess et al., 2021; Durand et al., 2021a). Moreover, the ratio of UV over PAR commonly increases 436 with height in the canopy (Yang et al., 1993; Grant, 1997; Deckmyn et al., 2001; Burgess et al., 437 2021). This could be partly attributable to a higher relative absorption of UV radiation than PAR by 438 leaves, leading to a larger increase of UV than PAR with height in the canopy (Day et al., 1994; Grant 439 et al., 2003). This would mean that the effect of a sunfleck on UV:PAR would be different at the top 440 and bottom of a canopy. A higher scattering probability of shortwave radiation (e.g. UV-B, UV-A 441 and blue light) in the atmosphere (Durand et al., 2021b), results in diffuse light that is enriched in UV 442 radiation compared to direct light (Flint & Caldwell, 2002). At the top of the canopy, the direct and 443 diffuse radiation incident on leaves is mainly scattered by the atmosphere, and coming from all 444 directions of the sky. This results in relatively high UV:PAR. By contrast, the light incident on leaves 445 during a windfleck at the bottom of a canopy mainly originates from a direction close to the solar

446 disc, where UV radiation is comparatively depleted. In all the canopies we measured, B:R always 447 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 448 449 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 450 451 photoreceptors like phototropins, cryptochomes and UVR8, among others (Rai et al., 2019). They 452 may impact cross-tolerance to stress (Jansen et al., 2019), and even affect flowers and fruit visibility 453 to animals (Endler, 1993).

454

How canopy architecture shapes the light fluctuations within

As a canopy gets denser and darker, sunflecks become less frequent, and windflecks 455 456 intensity fades (Fig. 1). This diminishes the potential photosynthetic gains from light fluctuations, 457 because a higher proportion of the total available light will come in the form of shade, rather than 458 transient patches of high light. This is especially the case at the bottom of a canopy, where windfleck 459 intensity is reduced compared to the upper layers (Fig. 5). Because they are acclimated to shade, 460 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 461 462 them slower to react to a change of light conditions (Durand et al., 2022). These factors reduce their 463 capacity to use flecks of light efficiently. Yet, shade light is of lower spectral quality as well as lower 464 irradiance level, because it is enriched in green and far red wavelengths that are absorbed less 465 efficiently by chlorophylls (Terashima et al., 2009), and it is more diffuse, which penetrates the 466 mesophyll less deeply than direct light (Cui et al., 1991; Gorton et al., 2010). As an example, blue 467 gum (Eucalyptus tereticornis, Sm.) trees often have a sparse canopy, which allows lower leaves to 468 maintain photosynthetic induction and benefit from sunflecks (Campany et al., 2016), whereas the 469 lower leaves of beech trees, acclimated to deep shade, have a reduced photosynthetic capacity and 470 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 471 472 light will likely depend on the species' physiology contingent on its functional strategy, and its 473 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).

484 *Conclusion*

485 Most studies of photosynthesis are done under steady light conditions, especially those 486 in controlled environments. This means that we lack knowledge of natural patterns of light 487 fluctuations, how canopy architecture affects them, and related plant responses. This research is 488 needed if we want to better apply laboratory findings to the field, and find ways to improve canopy 489 photosynthesis. In this study, we described the diversity of light fluctuation occurring in plant 490 canopies, and outlined major differences between crops and forest windflecks. While this study 491 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 492 493 in spectral composition during a windfleck is dependent on the species that forms the canopy, and 494 that canopy density and architecture affect the properties of light fluctuations. Leaf morphology 495 seemed to play an important role in creating different types of light fluctuations.

496 Although this study found that short fluctuations are omnipresent in all types of 497 canopies, one should not consider inconsequential longer changes in light (> 1 min), that involves 498 other processes such as stomatal movements. Light has a certain fractal quality where rapid 499 fluctuations symphonize with longer changes, each involving different processes that affect the 500 overall photosynthetic dynamic. Still, the ubiquitous nature of windflecks provides a strong incentive 501 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 502 503 between wind patterns, the biomechanics of plant movements, and the resulting the light fluctuations 504 in plant canopies, to grasp the benefits of them dancing in the wind.

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513 **CONFLICT OF INTEREST**

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

516

517 AUTHOR CONTRIBUTION

- 518 M.D. and T.M.R. contributed to the data collection, experimental design, the data analysis and 519 interpretation. Both authors contributed to the writing of the manuscript.
- 520

521 DATA AVAILABILITY

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

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711 Legend for Supplementary Information

- 712 **Table S1:** Dataset used for statistical analysis (see separate Excel file).
- 713 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.
- 715 Fig. S2: Tree-specific correlations between architectural traits and windfleck properties
- 716 **Fig. S3**: Distribution of sunfleck durations per species.
- 717
- 718

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	Soil type Fertiliser	
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 4 th)	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 \pm 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).

729	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	$708.5\pm9.7~g$	$1088.3\pm10.5\ h$	$379.8\pm8.5~f$	$227.1\pm3.3~d$	$0.61 \pm 0.04 \ c$	1.61	0.4	$51.3\pm1.7~g$	$437.8\pm41.1\ d$	$52.8\pm9.2\ c$
	Vicia faba	$350.9\pm5.9\ d$	$514.2\pm9.4~e$	$163.3\pm7.0\ c$	$208.3\pm4.0\ c$	$1.04\pm0.09\;d$	0.77	0.65	$22.2\pm1.4\ d$	$383.4\pm23.3\ cd$	$41.5\pm6.1\ c$
	Avena sativa	$481.8\pm8.1~e$	$711.6\pm10.6\;f$	$229.8\pm 6.8\;d$	$265.1\pm6.0\;e$	$1.00\pm0.07\;d$	0.92	0.65	$38.7\pm1.9\ f$	$634.5 \pm 43.5 \text{ e}$	$17.7\pm5\ ab$
	Brassica napus	$646.3\pm4.2~f$	$902.2\pm6.4~g$	$255.8\pm3.8~e$	$176.3\pm2.3~b$	$0.41\pm0.01\ b$	2.23	0.49	$29.4\pm0.7~\text{e}$	$1413.0 \pm 35.0 \; f$	35.2 ± 7.4 bc
	Acer platanoides	57.5 ± 7.6 ab	$90.1 \pm 8.8 \text{ ab}$	32.6 ± 4.1 a	$296.4\pm23.8~f$	$4.29\pm0.79\;f$	0.15	0.87	10.1 ± 3.3 bc	$269.8\pm71.1\ bc$	2.4 ± 1.2 a
	Alnus incana	$41.1\pm1.7~a$	$74.9\pm2.3~a$	$33.8\pm1.3\ a$	114.4 ± 2.1 a	$0.55\pm0.06\;c$	1.68	0.72	$2.2\pm0.1\ a$	$123.2\pm16.4\ ab$	$1.2\pm0.9~a$
	Betula pendula	$100.8 \pm 1.3 \ c$	$170.5\pm2.3~c$	$69.7\pm1.4\ b$	$115.0\pm1.1~a$	$0.30\pm0.02\ a$	3.24	0.51	$5.3\pm0.2\ b$	$260.4\pm11.5\ bc$	$9.4\pm6.1~a$
	Fagus sylvatica	$113.0\pm5.3~c$	$190.7\pm7.7~d$	$77.7\pm4.1\ b$	$205.6\pm5.8\;c$	$1.14\pm0.14\ d$	0.53	0.81	$12.8\pm1.5\;c$	$141.8\pm47.4\ ab$	0.2 ± 0.2 a
	Picea abies	$76.0\pm3.7\;b$	$104.3\pm4.8\ b$	$28.4\pm2.3\ a$	$177.3\pm7.3\ b$	$1.67\pm0.13~\text{e}$	0.46	0.69	$5.1 \pm 1.0 \; \text{ab}$	$101.0\pm15.4\ a$	$10.0\pm6.3\;a$

Table 3: Summary of windfleck spectral composition in crop fields (*Hordeum vulgare*, *Vicia faba*, *Avena sativa*, *Brassica napus*) and tree stands738(*Acer platanoides*, *Alnus incana*, *Betula pendula*, *Fagus sylvatica*, *Picea abies*) in Helsinki. Values for windfleck peaks and baselines are given739(means \pm standard deviation), as the statistical significance of changes in spectral composition between the baseline and the peak of the windfleck740for each species (*p*). Letters represent statistically significant differences between species tested by *post-hoc* pairwise comparisons (*p* < 0.05).</td>

Species	L	VV-A: PAR	Blue : Green			Blue : Red			Red : Far-red		
	Baseline	Peak p	Baseline	Peak	р	Baseline	Peak	р	Baseline	Peak	р
Hordeum vulgare	$0.158~\pm~0.001~f$	0.123 ± 0.001 d < 0.0	1 0.996 \pm 0.002 h	$0.940 \ \pm \ 0.001 \ h$	< 0.001	$1.559 \pm 0.009 e$	$1.309 \pm 0.005 d$	< 0.001	$1.037 \pm 0.005 ~{\rm f}$	$1.208 \pm 0.003 h$	< 0.001
Vicia faba	$0.138 ~\pm~ 0.001 ~e$	0.123 ± 0.001 d < 0.0	$1 0.909 \pm 0.001 e$	$0.897 \hspace{0.2cm} \pm \hspace{0.2cm} 0.001 \hspace{0.2cm} e$	< 0.001	$1.451 \ \pm \ 0.005 \ d$	$1.325 \ \pm \ 0.004 \ d$	< 0.001	$0.757 \hspace{0.2cm} \pm \hspace{0.2cm} 0.005 \hspace{0.2cm} d$	$0.907 \ \pm \ 0.005 \ d$	< 0.001
Avena sativa	$0.130 \ \pm \ 0.001 \ d$	0.109 ± 0.001 b < 0.0	$0.917 \pm 0.001 \text{ f}$	$0.892 \hspace{0.2cm} \pm \hspace{0.2cm} 0.001 \hspace{0.2cm} de$	< 0.001	$1.384~\pm~0.008~c$	$1.237 ~\pm~ 0.006 ~bc$	< 0.001	$0.907 \pm 0.009 e$	$1.075 \pm 0.007 ~{\rm f}$	< 0.001
Brassica napus	$0.123 ~\pm~ 0.000 ~c$	0.112 ± 0.000 c < 0.0	$0.875 \pm 0.000 \text{ c}$	$0.877~\pm~0.000~c$	0.058	$1.285 ~\pm~ 0.002 ~b$	$1.233 ~\pm~ 0.001 ~b$	< 0.001	0.895 ± 0.003 e	$1.020 \ \pm \ 0.003 \ e$	< 0.001
Acer platanoides	0.127 ± 0.003 cd	$0.117 \pm 0.002 \text{ c}$ 0.0	0.832 ± 0.003 b	$0.846 ~\pm~ 0.002 ~b$	0.021	$1.468 \pm 0.023 \ d$	1.247 ± 0.012 bc	< 0.001	$0.918 \pm 0.136 e$	$1.287 \pm 0.173 i$	< 0.001
Alnus incana	$0.160 \pm 0.001 ~{\rm f}$	0.138 ± 0.001 e < 0.0	$1 0.900 \pm 0.001 d$	$0.888 \pm 0.001 \ d$	< 0.001	$1.732 \pm 0.010 \text{ g}$	$1.399 \pm 0.006 e$	< 0.001	0.283 ± 0.005 a	$0.478 \pm 0.006 \ a$	< 0.001
Betula pendula	$0.174~\pm~0.001~g$	0.149 ± 0.001 f < 0.0	$1 0.937 \pm 0.001 \text{ g}$	$0.921~\pm~0.001~{\rm g}$	< 0.001	$1.660 \pm 0.005 ~{\rm f}$	$1.440 \pm 0.004 ~\rm{f}$	< 0.001	$0.468 \hspace{0.1 cm} \pm \hspace{0.1 cm} 0.003 \hspace{0.1 cm} b$	$0.652 \ \pm \ 0.004 \ b$	< 0.001
Fagus sylvatica	0.067 ± 0.001 a	0.087 ± 0.001 a < 0.0	1 0.715 \pm 0.006 a	0.816 ± 0.003 a	< 0.001	1.181 ± 0.008 a	1.138 ± 0.004 a	< 0.001	$0.491 \pm 0.014 \ c$	$0.759 \pm 0.013 \ c$	< 0.001
Picea abies	$0.085 \hspace{0.2cm} \pm \hspace{0.2cm} 0.001 \hspace{0.2cm} b$	0.090 ± 0.001 a 0.0	$0.915 \pm 0.002 \text{ f}$	$0.905 ~\pm~ 0.002 ~f$	0.002	$1.289 \pm 0.009 b$	$1.258~\pm~0.015~c$	0.033	$1.031 \pm 0.011 ~{\rm f}$	$1.130 \pm 0.010 \text{ g}$	< 0.001

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

744 FIGURES

745 Figure 1: Canopy architectural traits measured in crop fields (Ba: barley, Hordeum vulgare; Bn: 746 bean, Vicia faba; Ot: oat, Avena sativa; Rp: rapeseed, Brassica napus) and tree stands (Ac: Acer 747 platanoides, Al: Alnus incana, Be: Betula pendula, Fa: Fagus sylvatica, Pi: Picea abies) in Helsinki. 748 Traits measured included plant area index (a), plant height (b), leaf length (c), canopy light 749 transmission (d), leaf angle (e), and width (f). Note the different scales of plant height for crops and 750 trees. Values are means \pm standard error (n = 10-50). The asterisk on the top left shows for each trait 751 when there was a significant difference between crop and tree species. Letters represent statistically 752 significant differences between groups (crops and trees were tested separately) tested by *post-hoc* 753 pairwise comparisons (p < 0.05).



Figure 2: Typical windfleck properties recorded in the four crop fields (Ba: barley in green, Hordeum 756 757 vulgare; Bn: bean in yellow, Vicia faba; Ot: oat in orange, Avena sativa; Rp: rapeseed in black, 758 Brassica napus) in Helsinki. (a) Typical windfleck calculated using average windfleck duration and 759 intensity for each species (n = 828 - 2675). The shape of the windfleck followed a normal density 760 distribution. (b) Average windfleck intensity relative to the irradiance at the top of the canopy. 761 Crossed areas show the relative baseline irradiance. (c) Reconstructed time-series of typical 762 windflecks accounting for sunfleck duration and average time interval between windfleck. Windfleck 763 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 766 767 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 768 769 intensity for each species (n = 149 - 4858). The shape of the windfleck followed a normal density 770 distribution. (b) Average windfleck intensity relative to the irradiance at the top of the canopy. 771 Crossed areas show the relative baseline irradiance. (c) Reconstructed time-series of typical 772 windflecks accounting for sunfleck duration and average time interval between windfleck. Windfleck 773 intensities were normalized to the most intense windfleck (in F. sylvatica).



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776 Figure 4: Relative change in spectral composition during a windfleck in four crop fields (a, Ba: barley 777 in green, Hordeum vulgare; Bn: bean in yellow, Vicia faba; Ot: oat in orange, Avena sativa; Rp: 778 rapeseed in black, Brassica napus) and five forest stands (b, Ac: Acer platanoides in pink, Al: Alnus 779 *incana* in purple, Be: *Betula pendula* in blue, Fa: *Fagus sylvatica* in brown, Pi: *Picea abies* in grey) 780 measured in Helsinki. Peak and baseline spectral irradiance were normalized to 450 nm, where 781 irradiance was highest, to highlight difference in composition rather than amount of radiation. The 782 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 783 784 reflect a decrease. We applied a smoothing spline (in color) to each curve (in grey) to emphasize 785 general trends. The wavebands used to calculate spectral ratios in the main text are shown at the top 786 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 \pm standard error of measurements at 7 locations in the stand. Pearson correlation coefficient and *p* values are reported.



794

796 Figure 6: Correlations between canopy architectural traits and windfleck properties in four crop fields 797 (Ba: barley in green, Hordeum vulgare; Bn: bean in yellow, Vicia faba; Ot: oat in orange, Avena 798 sativa; Rp: rapeseed in black, Brassica napus) and five forest stands (Ac: Acer platanoides in pink, 799 Al: Alnus incana in purple, Be: Betula pendula in blue, Fa: Fagus sylvatica in white, Pi: Picea abies 800 in grey) measured in Helsinki. Plant area index (a-d), canopy light transmission (e-h) and median 801 PAR irradiance (i-l) were correlated with the number of sunfleck longer than 10 min (a, e, i), 802 windfleck duration (b, f, j), intensity (c, g, k) and integrated increase in PAR irradiance due to the 803 windfleck (d, h, l). Values are means \pm standard error. Pearson correlation coefficient, p values, and 804 the percent of p values < 0.05 in the bootstrap analysis (b value) are reported.



805

807 Figure 7: Canopy-specific correlations between architectural traits and windfleck properties in four 808 crop fields (a, c, e, ; Ba: barley in green, Hordeum vulgare; Bn: bean in yellow, Vicia faba; Ot: oat 809 in orange, Avena sativa; Rp: rapeseed in black, Brassica napus) and five forest stands (b, d, f; Ac: 810 Acer platanoides in pink, Al: Alnus incana in purple, Be: Betula pendula in blue, Fa: Fagus sylvatica 811 in white, Pi: Picea abies in grey) measured in Helsinki. Leaf angle (a-d) and canopy light transmission 812 (e-f) were correlated with windfleck intensity (a-b) and clustering (c-f). Values are means ± standard 813 error Pearson correlation coefficient, p values, and the percent of p values < 0.05 in the bootstrap 814 analysis (b value) are reported. Windfleck clustering was calculated over the whole measurement 815 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 \pm standard error. Pearson correlation coefficient, *p* values, and the percent of *p* values < 0.05 in the bootstrap analysis (*b* value) are reported.



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