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1 **TITLE**

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

3

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21

22 **SUMMARY**

- 23 • Wind-induced movement in the canopy produces rapid fluctuations in irradiance, called  
24 “windflecks”. They create a dynamic environment for photosynthesis that bears little  
25 resemblance to the stable controlled conditions under which plants are typically measured.
- 26 • We recorded time-series of irradiance to assess the diversity of windfleck properties (intensity,  
27 duration, frequency, clustering, spectral composition) in canopies of four crops and five tree  
28 species. We also measured traits associated with leaf morphology and canopy architecture,  
29 which could be associated with canopy-specific differences in windflecks.
- 30 • Distinct features of windfleck properties were identified both between and among crop and  
31 tree canopy. Windflecks in crops were generally more intense and longer, baseline irradiance  
32 was much higher than even the peak irradiance during a windfleck in a forest. The change of  
33 spectral composition during a windfleck was species-specific. Overall, irradiance fluctuations  
34 in denser canopies were less frequent and less intense; as found with increasing canopy depth  
35 and plant height.
- 36 • Our systematic exploration of how canopy structure dictates light dynamics, provides new  
37 insight into windfleck creation. Coupled with progress in elucidation of the mechanisms of  
38 photosynthetic induction, this knowledge should improve our capacity to model canopy  
39 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  
45 exception rather than the norm (Kaiser *et al.*, 2018; Murchie & Ruban, 2020; Durand *et al.*, 2022).  
46 Even under a clear sky at the very top of a canopy, a light breeze will cause leaves to move and change  
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;  
50 Hubbart *et al.*, 2018). Improving plant performance by accelerating the response of photosynthesis to  
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),  
60 Ribulose 1,5-bisphosphate regeneration (Sassenrath-Cole & Pearcy, 1994), stomatal opening (Allen  
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  
66 stomata open (Zeiger *et al.*, 1985), and the frequent intermittent brief occurrence of shade may prevent  
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, CO<sub>2</sub>  
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 CO<sub>2</sub> burst after illumination, which can offset the overall CO<sub>2</sub> assimilated (Vines *et al.*,  
74 1983; Pearcy, 1990). These processes are often neglected in models, and yet the degree to which they  
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

78 changes in spectral composition, can we hope to understand how these photosynthetic processes alter  
79 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,  
86 stand density and branching patterns, as well as leaf shape, size, and orientation (Falster & Westoby,  
87 2003), create the 3D canopy architecture determining the penetration of light through the canopy and  
88 thus its interception by leaves (Burgess *et al.*, 2017). In recent years, there has been increasing  
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 al.*  
91 *et 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 al.*  
94 *et al.*, 1989). Therefore, the arrangement of species that compose the canopy will likely affect the light  
95 fluctuations found therein, impacting the light environment in the understorey.

96 Historically, most research on light fluctuations, where brief periods of high irradiance  
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 al.*  
100 *et 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  
102 induced by sun and clouds (generally longer than 30 s). Sunflecks are notorious for being hard to  
103 define, and are often characterized as periods of irradiance above an arbitrary threshold contingent  
104 on the surrounding shade (e.g.  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  in Miyashita *et al.*, 2012;  $300 \mu\text{mol m}^{-2} \text{s}^{-1}$  in Roden  
105 & Pearcy, 1993, 70% of the irradiance at the top of the canopy in Barradas *et al.*, 1998). This makes  
106 comparison between studies and canopies difficult, as for example  $50 \mu\text{mol m}^{-2} \text{s}^{-1}$  could correspond  
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.  
114 To allow for best comparison, measurements were done in a short period of time, allowing similar  
115 environmental conditions (cloudless sky, similar solar angle), and phenological stages. Using our  
116 published method, we then characterized the properties of these light fluctuations, hereafter called  
117 windflecks. We also recorded longer light fluctuations (> 1 min.) using hemispherical pictures,  
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*

125 We conducted this experiment at the University of Helsinki, Finland (60.227 N, 25.018  
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*,  
128 L.), rapeseed (*Brassica napus*, L.), barley (*Hordeum vulgare*, L.), and broad bean (*Vicia faba*, L.), as  
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  
131 conditions of the crops can be found in Table 1. We also measured in an experimental European beech  
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 *Light measurements*

137 We measured spectral irradiance with a CCD array spectroradiometer Maya 2000 Pro  
138 (Ocean insights, Dunedin, FL, USA) using a cosine diffuser (D7-H-SMA, Bentham Instruments Ltd.,  
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  
142 10,000 scans, each scan comprised of 1,377 wavelengths in the range 280-898 nm measured  
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  
146 communication between the software and the operating system. All times-series were recorded from  
147 June 30<sup>th</sup> to July 14<sup>th</sup> 2021 ( $n = 8-16$ ), before the panicle and grains of the oats, and the stalks and  
148 heads of the barley turned yellow. Rapeseed was measured first and beans last, both during their early  
149 flowering stages. Measurements were recorded at mid-canopy depth in the crops, and at 50-cm above  
150 the ground in forest stands. In the beech stand, we also recorded at every meter from 0 to 4 m in  
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)  
152 which can be placed inside dense canopies, equidistant from stems, on a small tripod without affecting  
153 the canopy structure. After each time-series was recorded, we took two additional control recordings  
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  
157 polycarbonate cap (blocking 280-400 nm radiation) over the diffuser (Aphalo & Ylianttila, 2022).  
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 “*oacquire*”  
161 and “*photobiology*” R packages (Aphalo, 2015; Aphalo & Ylianttila, 2022) to process the raw  
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,  $\Delta_{PAR}$ ), for each point  $n$  at time  $t$  in the time series and its  
167 following measurement  $n + 1$  as:

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

169  $\Delta_{PAR}$  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  $5 \mu\text{mol m}^{-2} \text{s}^{-1}$ , 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.

174 We calculated windfleck duration as the time between the start and end of a windfleck,  
175 and its intensity as the difference in PAR irradiance between the peak and the baseline, taken as the  
176 lowest PAR irradiance at either the start or end of the windfleck. This approach avoids potential  
177 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)  
181 and 1 (most clustered). The integrated increase in PAR irradiance caused by the windfleck was  
182 calculated as the total integrated PAR irradiance during the windfleck, from which the residual PAR  
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),  
185 and red:far-red (R:FR) spectral photon ratios were calculated (UV-A: 315-400nm; PAR: 400-700nm;  
186 blue: 420-490nm; green: 500-570nm; red: 620-680nm; far-red: 700-750nm).

### 187 *Canopy architecture*

188 We took hemispherical photographs at 10 measurement points for crops species, and 5  
189 for forest stands, using a Canon Eos 800D (Canon Inc., Japan) camera with a CMOS 24 MP image  
190 sensor combined with a circular fisheye lens (Sigma 4.5 mm f2.8 EX DC HSM, Sigma Corporation  
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 8-  
194 bit jpeg from the RAW files following Macfarlane *et al.* (2014). Photographs were analyzed with the  
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  
202 Gap Light Analyser software (Simon Fraser University, BC, Canada). We considered the period June  
203 30<sup>th</sup> to July 14<sup>th</sup>, the same as for the light measurements, and used an automatic thresholding according  
204 to Nobis & Hunziker (2005). Finally, we also measured plant height ( $n = 10$ ), as well as leaf width,  
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”  
213 (Hothorn *et al.*, 2008). Windfleck properties cannot be directly paired with canopy architecture at the  
214 individual measurement level, thus to test for a correlation we had to use species means. This had the  
215 effect of reducing our statistical power, as each species is considered as a single replicate even though  
216 it is informed by a large number of observations. To address this problem, we randomly paired  
217 windfleck properties and canopy architecture at the species level 100,000 times (similar to a bootstrap  
218 with replacement), and calculated a value “*b*” representing the percentage of random pairings that  
219 gave a *p* value < 0.05, following Durand *et al.* (2020). If two variables are uncorrelated, it would be  
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  
228 planophile in the tree stands ( $32.4 \pm 2.6^\circ$ , Fig. 1e). Among the crop species, only the rapeseed canopy  
229 showed a PAI significantly lower (by 39%) than the other three canopies (Fig. 1a). This was despite  
230 rapeseed being the tallest crop canopy ( $75.3 \pm 3.9$  cm, Fig. 1b). The bean canopy had the most  
231 planophile leaves ( $57.1 \pm 1.7^\circ$ ) and barley the most erectophile ones ( $85.6 \pm 1.8^\circ$ ), which resulted in  
232 beans having the lowest ( $39.7 \pm 2.2\%$ ) and barley highest ( $85.6 \pm 5.7\%$ ) canopy light transmission  
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  
237 detect significant differences in canopy light transmission ( $p = 0.08$ ), but spruce leaves were the most  
238 erectophile ( $48.6 \pm 2.1^\circ$ ) and beech leaves the most planophile ( $19.8 \pm 8.2^\circ$ ). The beech stand being  
239 the youngest, it was also the shortest ( $5.6 \pm 1.4$  m), followed by the maple, spruce, alder, and birch  
240 as the tallest stand ( $20.6 \pm 6.0$  m, Fig. 1b). The maple leaves were the widest (more than 2.7 times  
241 wider than the other trees), the longest, and the only ones that were wider than long (Fig. 1c-f). On  
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).

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  
247 5.3 times, in the crop (on average  $266.4 \pm 3.2 \mu\text{mol m}^{-2} \text{s}^{-1}$ ) than in the tree canopies ( $60.6 \pm 1.0 \mu\text{mol}$   
248  $\text{m}^{-2} \text{s}^{-1}$ ,  $p < 0.001$ ). Windfleck duration was on average longer in the crop ( $206.4 \pm 0.2 \text{ ms}$ ) than in  
249 the tree stands ( $132.3 \pm 0.1 \text{ ms}$ ,  $p < 0.001$ ), although this was species dependent. This led to an  
250 integrated PAR increase of  $34.6 \pm 0.7 \mu\text{mol m}^{-2}$  per windfleck on average in the crops, compared to  
251 only  $5.6 \pm 0.2 \mu\text{mol m}^{-2}$  per windfleck in the tree stands. Differences of time interval between  
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  
254 between June 30<sup>th</sup> to July 14<sup>th</sup> to be 3.9 times more numerous in the crop canopies than in the tree  
255 stands for those lasting less than 10 min, and 7.4 times as numerous when considering those lasting  
256 more than 10 min.

257 Among crop canopies, barley had the highest baseline irradiance, twice as high as in the  
258 bean canopy, and 47%, and 9% higher than the oat and rapeseed canopies, respectively (Fig. 2). There  
259 was a similar trend for the peak irradiance of the windflecks. This led to windflecks being 2.3, 1.7  
260 and 1.5 times more intense in the barley canopy compared to bean, oat and rapeseed, respectively  
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  
263 duration was shortest in the rapeseed canopy, by 28%, 18%, and 50% compared to the barley, bean,  
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  
275 of the least intense windflecks, but they were also the longest, 2.6 times as long as the shortest  
276 windflecks of the alder stand. This led to maple and beech stands having the highest average  
277 integrated PAR increase per windfleck, the former due to longer windflecks, and the latter due to

278 more intense ones (Table 2). The maple stand also had the least frequent windflecks, with an average  
279 time between windflecks being at least 2.6 times as long as in the other stands. This pattern was in  
280 part due to a higher degree of windfleck clustering in the maple stand, while the least clustering was  
281 found in the birch stand where windflecks were shortest and most frequent. Some long sunflecks were  
282 present in the forest stands, unlike the crops canopies. The maple stand had the most sunflecks shorter  
283 than 10 min, and the spruce stand the least (Fig S2). For sunflecks longer than 10 min, the intra-group  
284 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 ( $p <$   
293  $0.002$ ; 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*

304 We recorded a large number of windflecks at each canopy height, allowing high  
305 statistical power, even when correlations are relatively weak. For example, there was a minor  
306 reduction in windfleck duration compared to their distribution, from  $0.89 \pm 0.01$  s at the ground level  
307 to  $0.64 \pm 0.02$  s at 4 m (Fig. 5a). Yet, the range of windfleck durations was large, with 50% of  
308 windflecks either longer than 1.2 s or shorter than 0.5 s at ground level. While at 4 m, 50% of  
309 windflecks were either longer than 0.8 s or shorter than 0.4 s. The correlation was also weak, although  
310 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  $480.0 \pm 17.6$   
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 ( $R > 0.88$ ;  $p <$   
323  $0.002$ , Fig. 6e-i), windfleck intensity ( $R > 0.98$ ,  $p < 0.001$ , Fig. 6g-k), and the integrated increase in  
324 PAR per windfleck ( $R > 0.93$ ,  $p < 0.001$ , Fig. 6h-l). Windfleck duration was neither correlated with  
325 PAI, canopy light transmission, nor the average PAR irradiance ( $p > 0.46$ , Fig. 6b-f-j) or sunfleck  
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 ( $R = -0.82$ ,  $p =$   
331  $0.09$ , Fig. 7b). Sunfleck clustering produced a negative trend with leaf angle ( $R = -0.8$ ,  $p = 0.21$ ) and  
332 canopy light transmission ( $R = -0.91$ ,  $p = 0.09$ ) in the crops, but not among the tree species ( $p > 0.37$ ,  
333 Fig. 7c-f).

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 ( $p >$   
341  $0.25$ ), but leaf length was positively related to the integrated increase in PAR per windfleck ( $R = 0.96$ ,  
342  $p = 0.044$ , Fig. 8f), due to similar positive trends with windfleck duration and intensity (Fig. 8d-e).  
343 By contrast, there was a negative trend between leaf width and both windfleck duration ( $R = -0.89$ ,

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

346 Those relationships across the tree stands were weaker than in field crops, and often  
347 driven by a single species (*e.g.* the much shorter tree height of the beeches, or the much larger leaf  
348 width of the maples), which we decided not to consider in detail (see Fig. S2 for a corresponding Fig.  
349 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  
356 tall forests canopies than in crops (Smith *et al.*, 1989; Pearcy, 1990). Indeed, the least intense  
357 windflecks were recorded in the spruce canopy which is highly clumped, and less susceptible to wind,  
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)  
363 also found windflecks in soybean canopies to be shorter and more frequent than those in forest  
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.

370 There is a dearth of studies investigating the diversity of light fluctuation patterns in  
371 plant canopies. Kaiser *et al.* (2018) found ten times more sunflecks in Durum wheat (*Triticum durum*,  
372 Desf.) than in white mustard (*Sinapis alba*, L.) during the same time period: these sunflecks were also  
373 longer and more intense. A comparison of sunflower (*Helianthus annuus*, L.), wheat (*Triticum*  
374 *aestivum*, L.), and maize (*Zea mays*, L.) canopies detected only marginal differences (Peressotti *et*  
375 *al.*, 2001). There are some differences between those windfleck properties among oat, barley and  
376 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  
385 meant that at the time of measurement the bean canopy was nearly 20 cm taller, switching from the  
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  
389 a similar pattern of windflecks becoming less intense, and less frequent further away from the top of  
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  
418 along with variations in spectral composition. While the potential physiological effects these changes  
419 have on photosynthesis remain to be determined, penetration and absorption of light is wavelength  
420 dependent (Brodersen & Vogelmann, 2010). Green light penetrates deeper in the mesophyll  
421 (Terashima *et al.*, 2009; Smith *et al.*, 2017) than blue or red because it is less efficiently absorbed by  
422 chlorophylls, but is it still the case when light is predominantly green, as is the case in shade? To our  
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  
428 which ultimately limit species' spatial distribution. Combinations of species in agroforestry systems,  
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.

432 Generally, UV-A:PAR was lower during the peak of a windfleck than at the baseline,  
433 except in the beech and spruce canopies. This general decline is in agreement with evidence of lower  
434 UV-B to PAR ratio in sunflecks compared to shade (Flint & Caldwell, 2002; Hartikainen *et al.*, 2018;  
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  
448 similar impact of differential scattering. This can have meaningful consequences for the functional  
449 traits, survival, and thus community composition of understorey and overstorey vegetation. A large  
450 array of leaf traits are regulated by UV and blue light (Siipola *et al.*, 2015; Wang *et al.*, 2020), via  
451 photoreceptors like phototropins, cryptochromes 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*

455 As a canopy gets denser and darker, sunflecks become less frequent, and windflecks  
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,  
461 1977; Earles *et al.*, 2017). The low light of a tree canopy induces physiological acclimation that make  
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).  
471 Whether leaves prioritize temporary bursts of high light, or the more reliable but lower quality shade  
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.

474 A greater leaf width in the crops was related to shorter windflecks. We know that greater  
475 leverage is gained when a force is exerted at a longer distance from a fulcrum (the support about  
476 which a lever turns, see the law of levers; Davidovits, 2008). Therefore, it is possible that wider leaves  
477 flutter more rapidly around the midrib, creating faster fluctuations of irradiance. In crops, canopies  
478 with a larger leaf angle were associated with more intense windflecks, but in contrast this trait in tree  
479 canopies led to windflecks of reduced intensity. The larger leaf angles of crop canopies would lead



480 to larger gaps in the canopy, increasing the penetration of direct light (Falster & Westoby, 2003).  
481 Such an effect may not occur in canopies with a more planophile leaf orientation (such as our tree  
482 canopies), and where an increase of leaf angle may tilt the leaves in the direction of the sun, actually  
483 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  
492 (Burgess *et al.*, 2021), but further research is needed to assess its extent. We found that the change  
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  
502 photosynthesis. This will require a combined approach, to disentangle the complex interaction  
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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512

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  
714 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.

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719 **TABLES**

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

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

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724 **Table 2:** Summary of windfleck properties in crop fields (*Hordeum vulgare*, *Vicia faba*, *Avena sativa*, *Brassica napus*) and tree stands (*Acer*  
725 *platanoides*, *Alnus incana*, *Betula pendula*, *Fagus sylvatica*, *Picea abies*) in Helsinki. Windfleck frequency and clustering were calculated over the  
726 whole measurement period, as such they couldn't be included in statistical analyses, all other properties differed significantly among stands. Values  
727 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  
728 in Fig. S3. Letters represent statistically significant differences between groups tested by *post-hoc* pairwise comparisons ( $p < 0.05$ ).

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

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

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

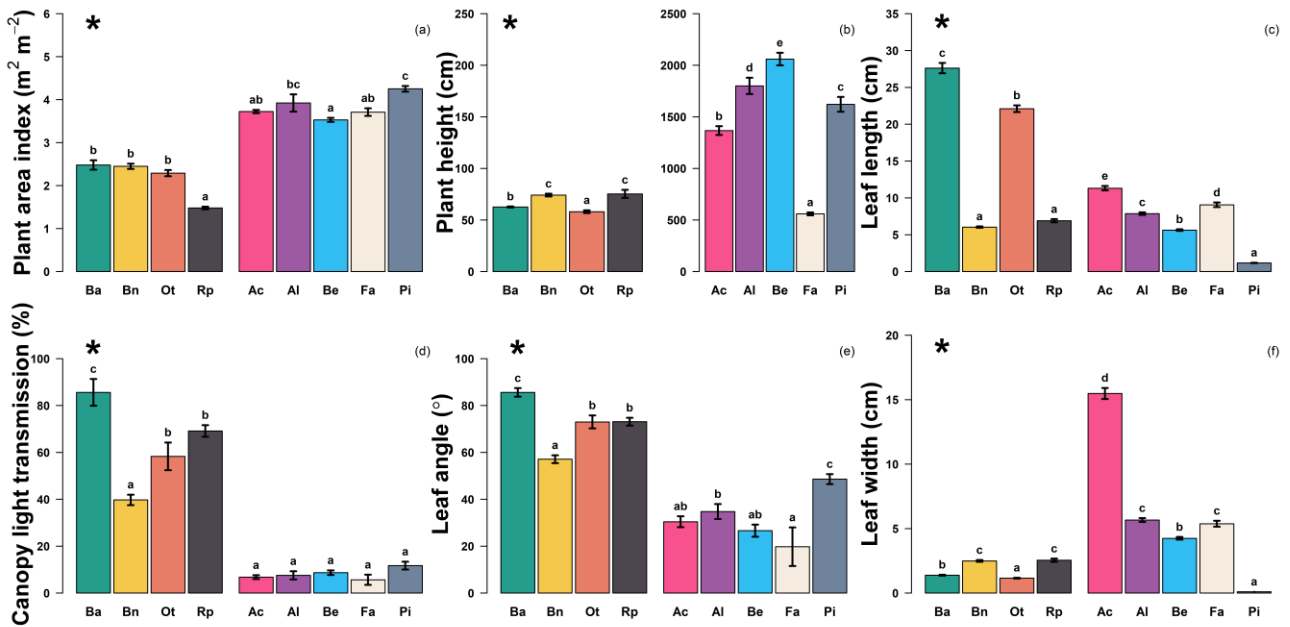
741 UV-A: 315-400nm ; PAR: 400-700nm; blue: 420-490nm ; green: 500-570nm ; red: 620-680nm ; far-red: 700-750nm

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744 **FIGURES**

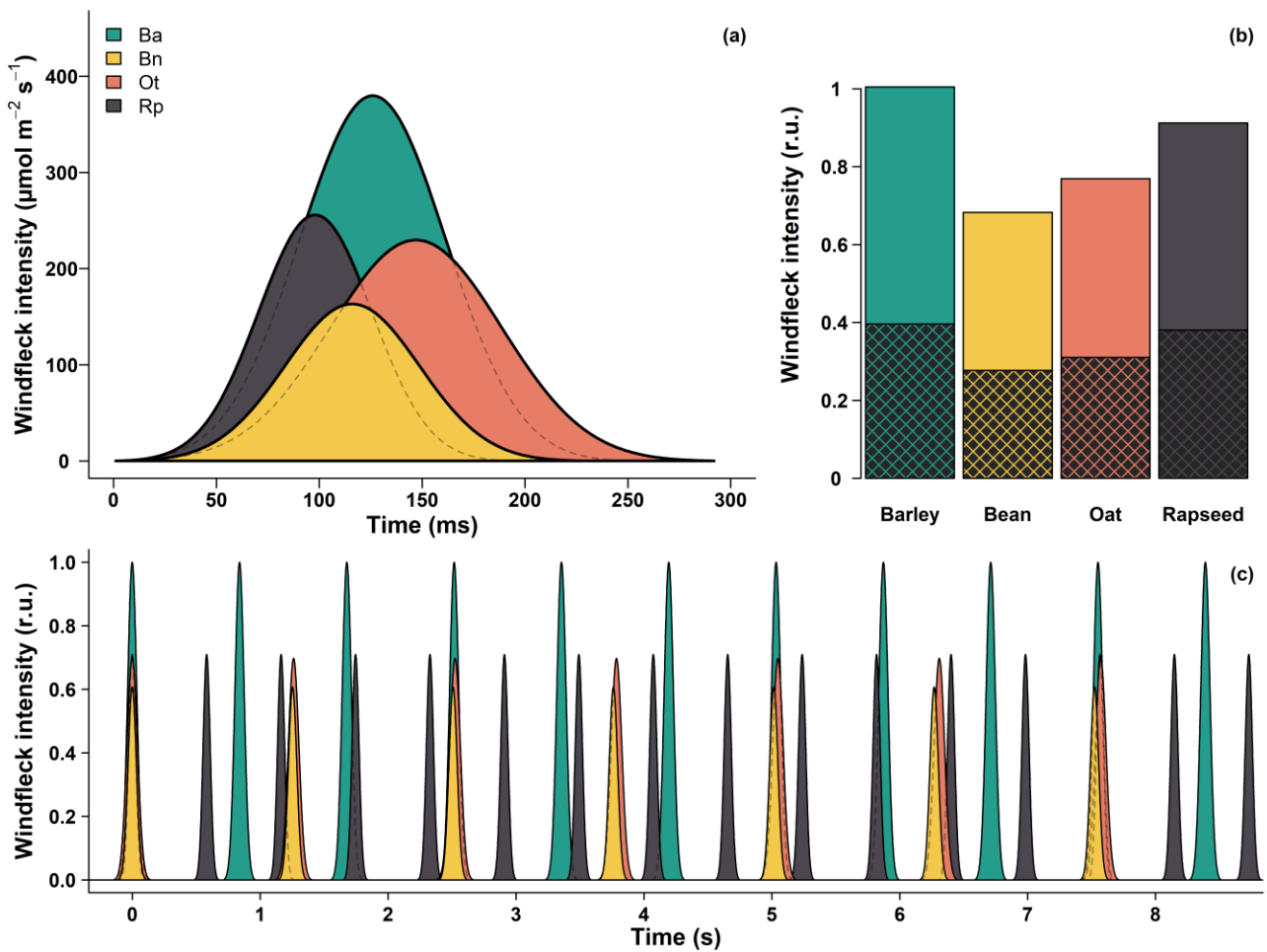
745 **Figure 1:** Canopy architectural traits measured in crop fields (Ba: barley, *Hordeum vulgare*; Bn:  
 746 bean, *Vicia faba*; Ot: oat, *Avena sativa*; Rp: rapeseed, *Brassica napus*) and tree stands (Ac: *Acer*  
 747 *platanoides*, Al: *Alnus incana*, Be: *Betula pendula*, Fa: *Fagus sylvatica*, 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  
 750 and 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 ( $p < 0.05$ ).



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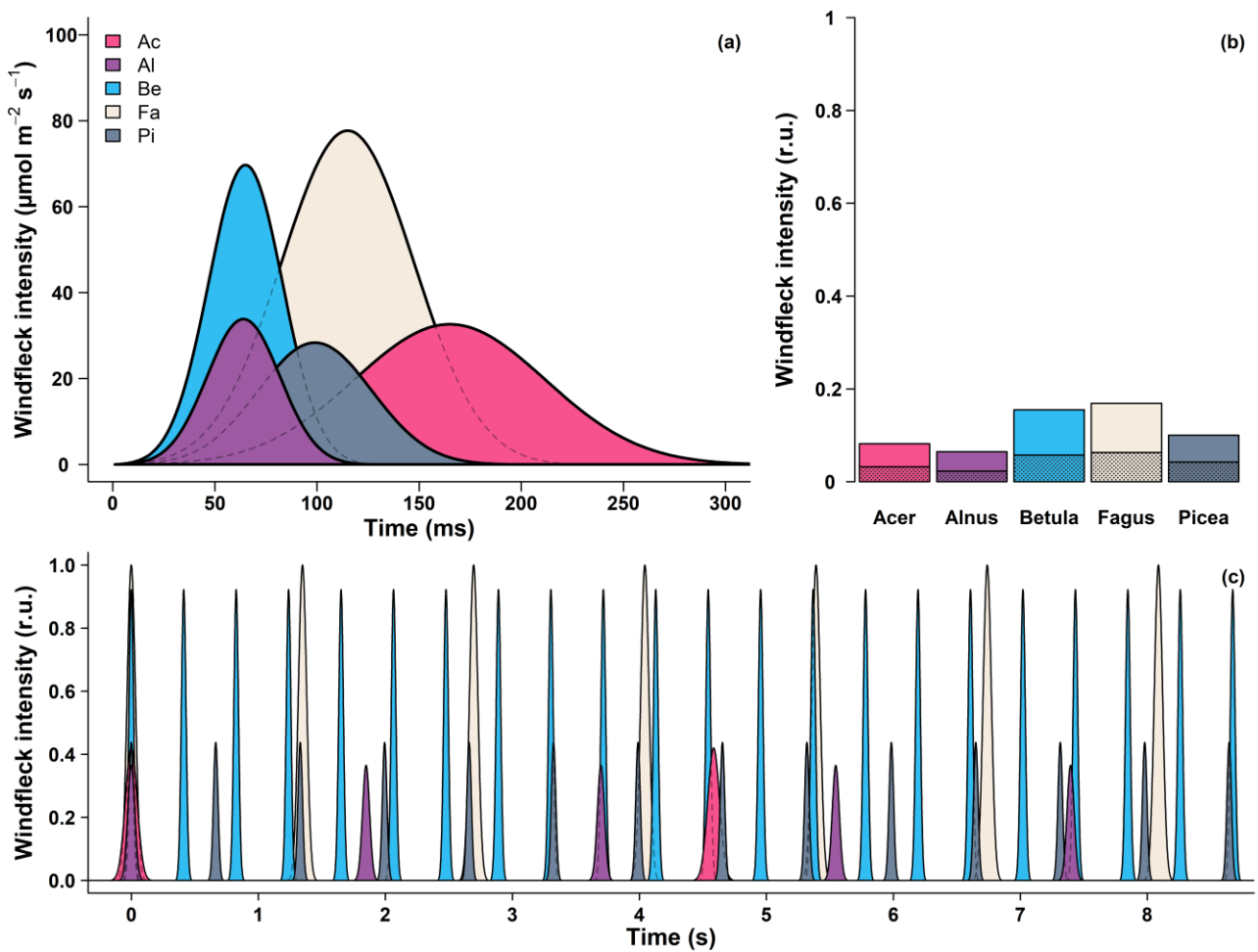
756 **Figure 2:** Typical windfleck properties recorded in the four crop fields (Ba: barley in green, *Hordeum*  
 757 *vulgare*; Bn: bean in yellow, *Vicia faba*; Ot: oat in orange, *Avena sativa*; Rp: rapeseed in black,  
 758 *Brassica napus*) in Helsinki. (a) Typical windfleck calculated using average 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).



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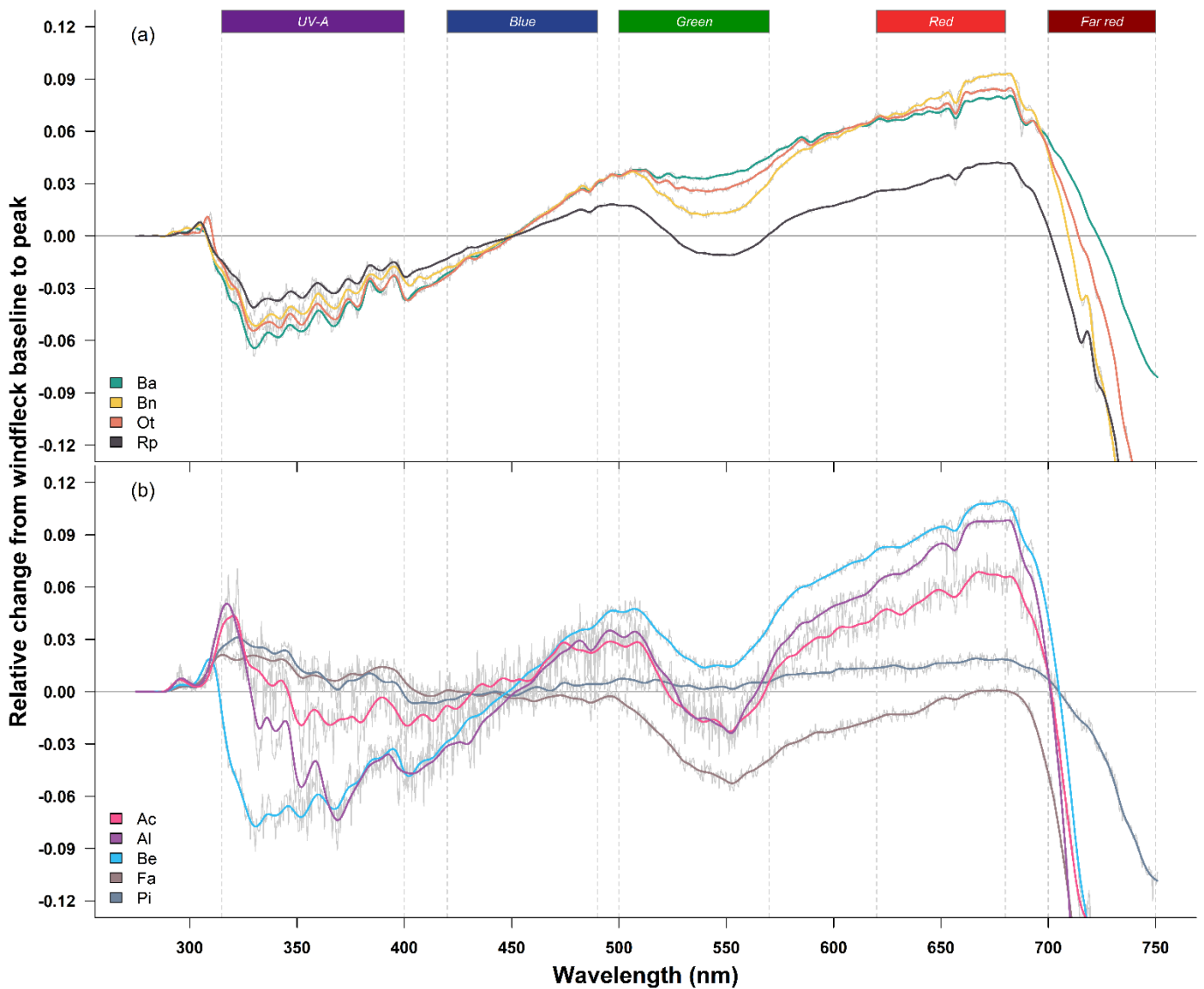
766 **Figure 3:** Typical windfleck properties recorded in the five forest stands (Ac: *Acer platanoides* in  
 767 pink, Al: *Alnus incana* in purple, Be: *Betula pendula* in blue, Fa: *Fagus sylvatica* in white, Pi: *Picea*  
 768 *abies* in grey) in Helsinki. (a) Typical windfleck calculated using average windfleck duration and  
 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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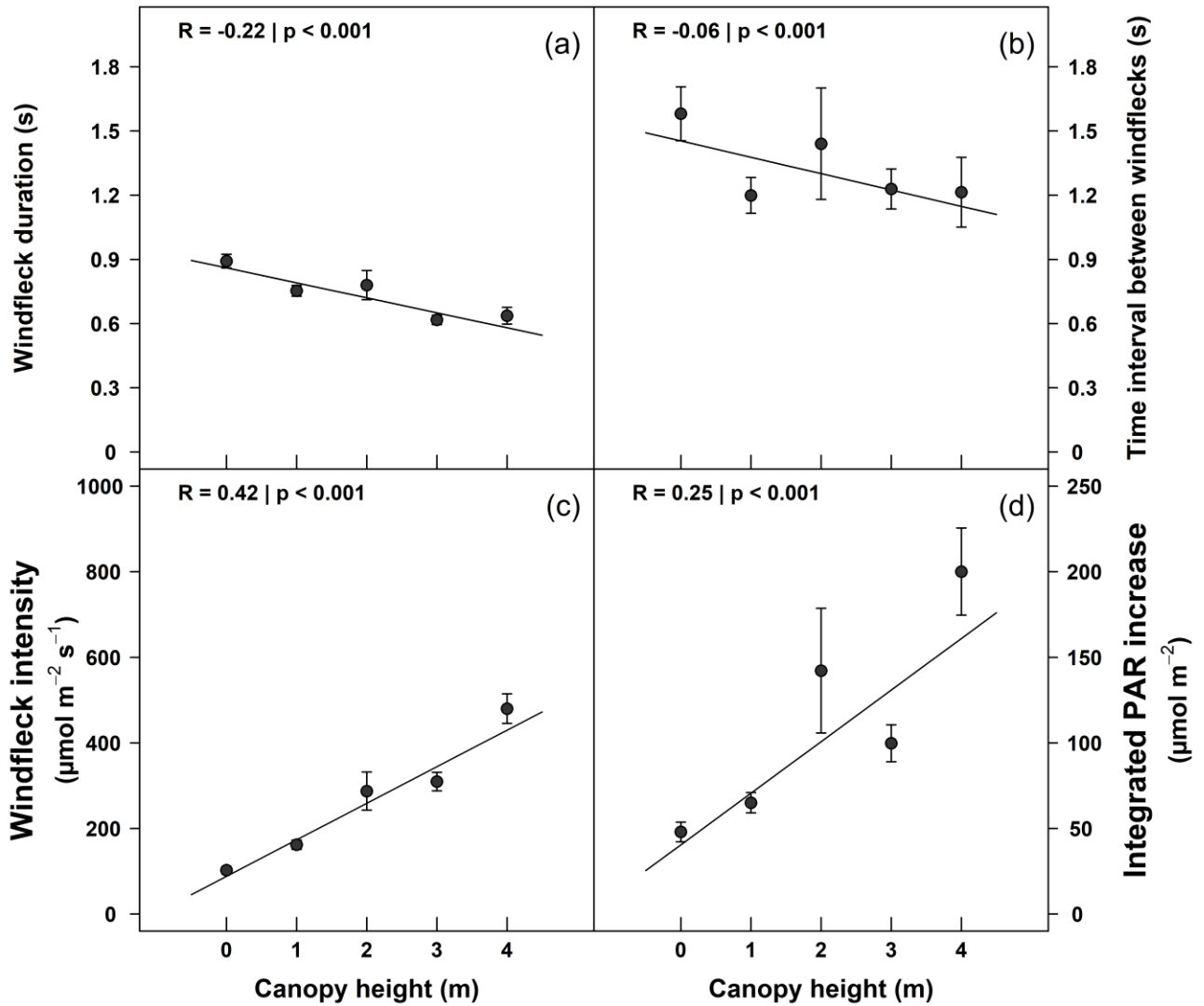
776 **Figure 4:** Relative change in spectral composition during a windfleck in four crop fields (a, Ba: barley  
 777 in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba*; Ot: oat in orange, *Avena sativa*; Rp:  
 778 rapeseed in black, *Brassica napus*) and five forest stands (b, Ac: *Acer 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.  
 783 Positive values reflect an increase of this wavelength during a windfleck, whereas negative values  
 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.



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

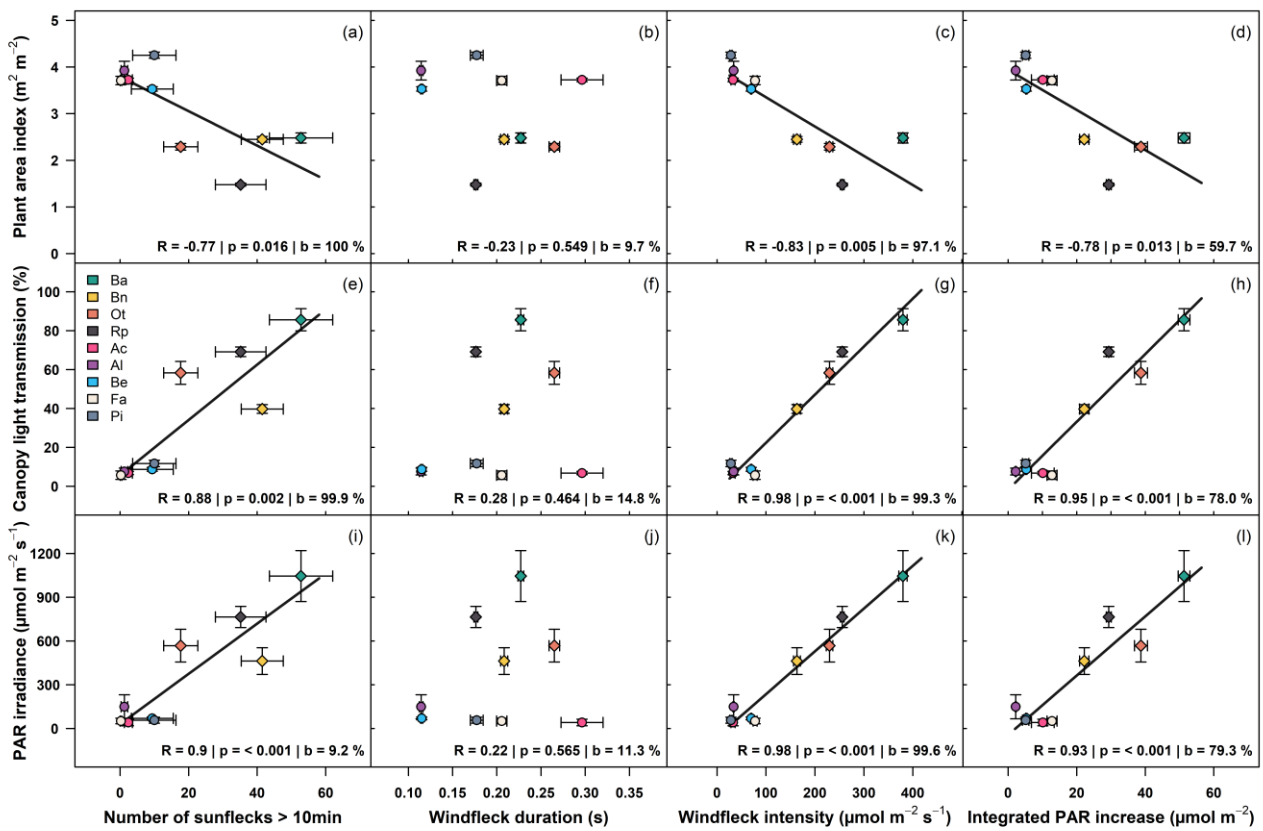


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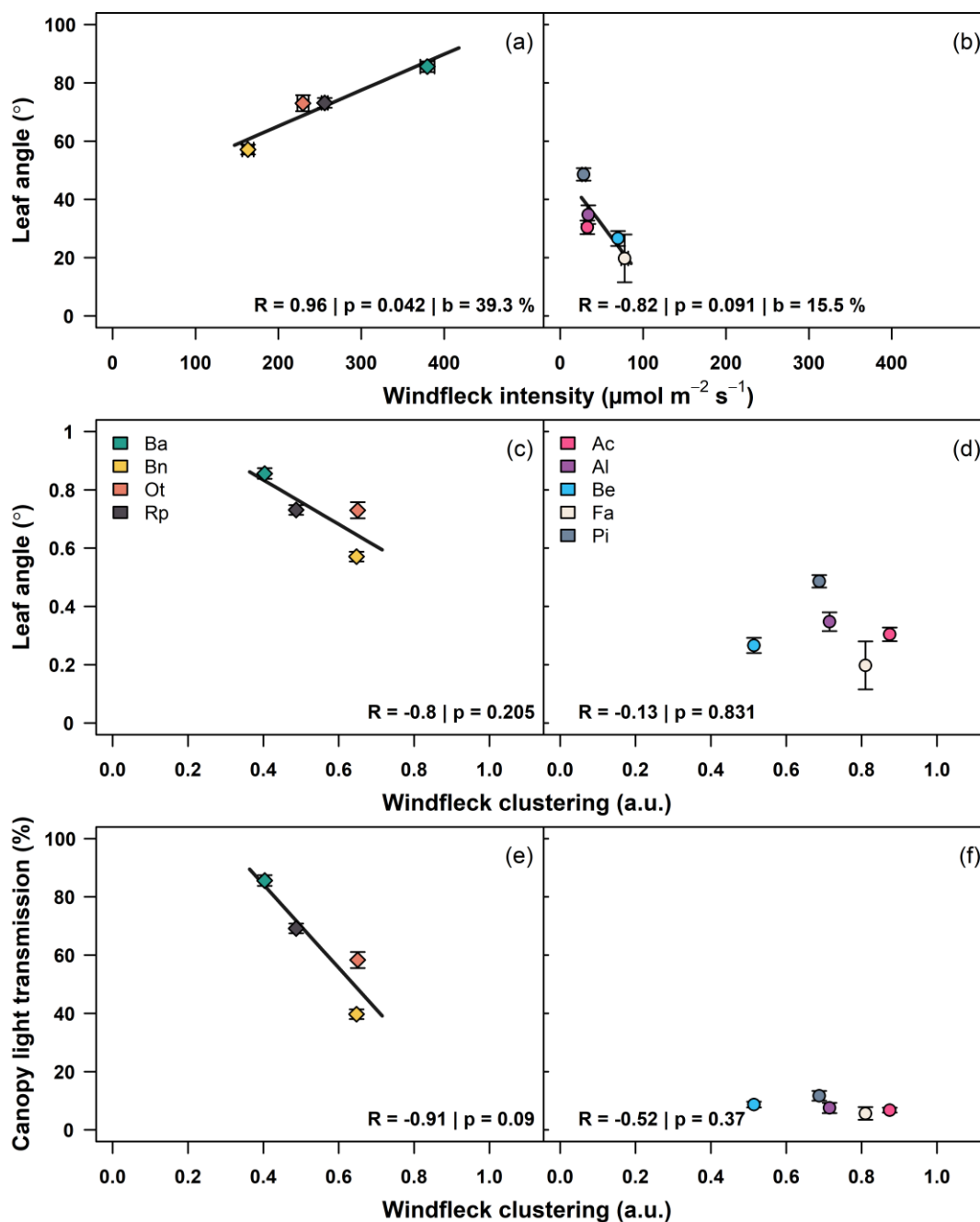
796 **Figure 6:** Correlations between canopy architectural traits and windfleck properties in four crop fields  
 797 (Ba: barley in green, *Hordeum vulgare*; Bn: bean in yellow, *Vicia faba*; Ot: oat in orange, *Avena*  
 798 *sativa*; Rp: rapeseed in black, *Brassica napus*) and five forest stands (Ac: *Acer platanoides* in pink,  
 799 *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.



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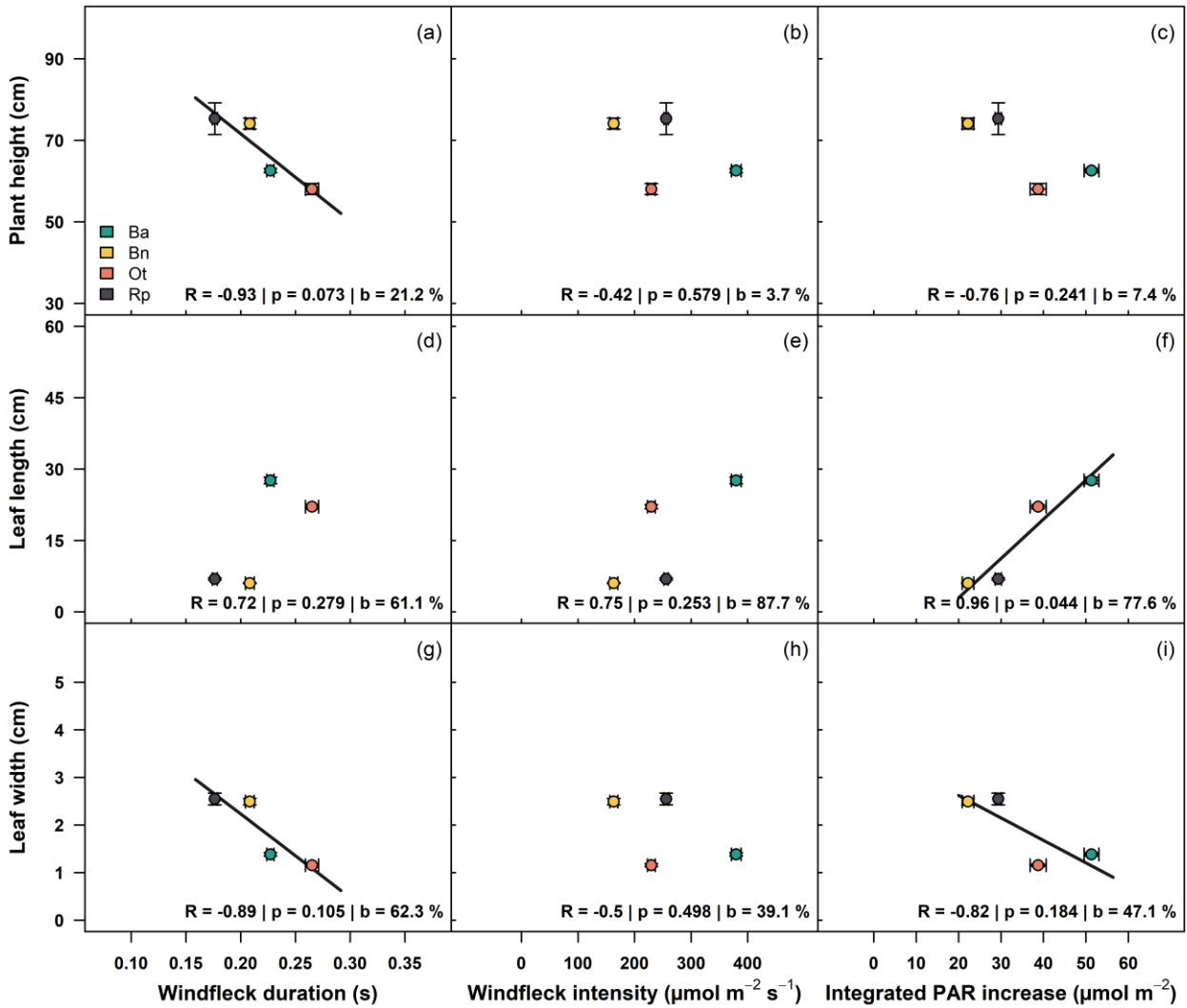
806

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  $\pm$  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.



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



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