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4 **Note and Comments**

5

6 **Title:**

7 Reduction of photosynthesis before midday depression occurred: leaf photosynthesis of

8 *Fagus crenata* in relation to canopy position and a number of days after rainfall.

9

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19 **Abstract**

20 We investigated an effect of canopy position and a number of days after rainfall on
21 reduction of photosynthetic rate in a *Fagus crenata* forest in summer 2008, during days
22 when midday depression was not apparent. We compared in-situ photosynthetic rate and
23 photosynthetic rate that was calculated by photosynthetic light response curves
24 measured in the morning. The ratio, in-situ photosynthesis divided by the
25 curve-estimated value, declined towards the end of each day for the upper leaves, but
26 not for the lower leaves. Total photosynthesis was reduced only for the upper leaves by
27 12% during five days after the rainfall.

28

29 **Key words:** Photosynthesis; stomatal conductance; net primary production; temperate
30 forest; *Fagus crenata* Blume.

31

32 **Introduction**

33 Temperate forests are carbon sinks against climate change (Granier et al. 2000; 2002;
34 Luysaert et al. 2008; Saigusa et al. 2008; Kato and Tang 2008; Ito 2008; 2010; Koyama
35 & Kikuzawa 2010a; Joo et al. 2011). The “big leaf model” extended single-leaf
36 responses (Farquhar 1989) into whole-plant responses under the same scheme, and
37 proposed simple relations predicting ecosystem carbon gain based on an optimization
38 hypothesis (Sellers et al. 1992; Dewar et al. 1996; Haxeltine and Prentice 1996;

39 Terashima et al. 2005; Koyama and Kikuzawa 2009; 2010b). Recently, the big leaf
40 model was validated even under fluctuating light intensity, both theoretically (Koyama
41 and Kikuzawa 2010b), and empirically (Rosati and DeJong 2003; Rosati et al. 2004;
42 Posada et al. 2009; Koyama and Kikuzawa 2010b). However, there have also been
43 countless results showing that the optimization was not always realized (Field 1983;
44 Hirose and Werger 1987; Meir et al. 2002; Posada et al. 2009). One possible explanation
45 for this discrepancy is that photosynthesis is not only limited by light, but also by other
46 factors (Mooney and Gulmon 1979; Meir et al. 2002; Niinemets and Valladares 2004).
47 Even when light is plentiful, both stomatal and non-stomatal limitation plays important
48 roles for reducing in-situ photosynthetic rate for trees (Ishida et al. 1999a; Muraoka et al.
49 2000; Niinemets et al. 2004; Valladares and Pearcy 2002; Misson et al. 2010). In this
50 study, we will demonstrate that photosynthesis of upper leaves on *Fagus crenata* forest
51 was not solely determined by light, but also by stomatal limitation.

52 Leaf stomatal conductance is controlled by many factors. External environment
53 such as air humidity (Jarvis 1976; Tenhunen et al. 1987; Ball et al. 1987; Harley and
54 Tenhunen 1991; Leuning 1995; see review by Damour et al. 2010) controls stomata via
55 increment of transpiration (Mott and Parkhurst 1991; Mott and Peak 2010). However,
56 Damour et al. (2010) concluded that in addition to those leaf-level responses, including
57 an effect of soil water condition is needed. Tazaki et al (1980) reported that upper leaves
58 of mulberry tree showed no midday depression in the second day after the last rainfall,

59 but apparent depression occurred in the eighth day. Nakai et al. (2010) also reported in
60 the experiment of *Salix gracilistyla* cuttings, that the longer the drought treatment, the
61 more stomatal limitation on photosynthesis. However, those studies did not investigate
62 the difference of stomatal limitation between canopy positions.

63 Within a single canopy, a limiting factor for photosynthesis may differ among
64 different positions. Firstly, leaves from different positions within a canopy themselves
65 differ morphologically, chemically, anatomically and physiologically. This is observed
66 in *Fagus crenata* (Uemura et al. 2000; Yamasaki and Kikuzawa 2003; Iio et al. 2005;
67 2009; Koyama and Kikuzawa 2010ab), other temperate deciduous trees (Niinemets
68 1995; 2010; Koyama and Kikuzawa 2010b; Yoshimura 2010) and temperate evergreens
69 (Hozumi and Kirita 1972; Katahata et al. 2007). Also, leaves on higher position may
70 have smaller water reserves (Jarvis 1976) and / or longer water pathway from root
71 (Ryan et al. 2006). Hence, it is expected that a degree of stomatal limitation of
72 photosynthesis should differ among different canopy positions. However, in most of the
73 previous studies, the effect of canopy position was not investigated (cf. Tazaki et al.
74 1980; Zotz and Winter 1996; Muraoka et al. 2000; Ishida et al. 1999a; 2000; Valladares
75 et al. 2008; Misson et al. 2010; Nakai et al. 2010). For other studies which investigated
76 different canopy positions, the temporal pattern in relation to soil water conditions was
77 not investigated (cf. Muraoka and Koizumi 2005; Iio et al. 2009). To date, knowledge
78 on the interaction between soil water condition and canopy position is very limited (cf.

79 Niinemets et al. 2004). Regarding the above argument, it is necessary to simultaneously
80 investigate both of the above two factors (Niinemets and Valladares 2004). The aim of
81 this study is to elucidate spatial and temporal pattern of efficiency of photosynthetic rate
82 under field condition in a Japanese beech forest (*Fagus crenata* Blume). We tested the
83 following two hypotheses. (1) Daytime reduction of photosynthesis was apparent for the
84 upper leaves, but not for the lower leaves. (2) This reduction was interactively affected
85 by the soil water condition. There will be no apparent reduction in daily photosynthetic
86 rate just after a rainfall, but will be a significant reduction when the number of days
87 after the last rainfall increased.

88

89 **Methods**

90 Species and Site

91 *Fagus crenata* Blume is a late-successional deciduous canopy tree distributed in
92 mountainous regions in Japan (Matsui et al. 2004). The site was a 15-year-old plantation
93 in the Ishikawa Prefectural Forest Experiment Station (36°25'N, 136°38'E, elevation
94 220 m), which is located at the foot of Mt. Hakusan. At the plantation, 130 trees were
95 planted in 1995 in the area of 171 m². Those trees were grown by seeds from Mt.
96 Hakusan (Jiro Kodani, personal communication), and hence they should belong to the
97 Japan Sea coast haplotypes (cf. Okaura and Harada 2002). The stand height and the
98 mean DBH were around 6 m and 4.7 cm in 2008, respectively. The canopy was closed

99 and there was almost no vegetation on the forest floor.

100 The site climate was one of the typical Japan Sea coast regions, characterized
101 by heavy snowfall in winter. The measurement was conducted from 27 July to 1 August
102 2008, when the summer rainy season was finished. Mean annual temperature and mean
103 annual precipitation are 13.0 °C and 2438 mm, respectively (2003 – 2007). Mean
104 temperature in August was 25.0 °C (2003 – 2007), being the hottest month. However, in
105 August there usually was no severe drought in that region, and rainfall typically occurs
106 at least in every one week (Koyama K, personal obs.). Mean monthly precipitation was
107 184 mm (2003 – 2007), which was slightly lower than the mean monthly precipitation
108 (203 mm). The mean temperature and total precipitation in 2008 was 12.8 °C and 2229
109 mm, respectively. The mean temperature and the total precipitation in August 2008 was
110 24.2 °C and 182 mm, respectively, being not greatly different from the normal years.
111 The above data were from the Annual Report of the Ishikawa Prefectural Forest
112 Experiment Station (2003 – 2008).

113

114 Photosynthesis measurement

115 A total of 91 mm rainfall was observed within two days in 27 and 28 July 2008 at the
116 site (data from the Ishikawa Prefectural Forest Experiment Station, by courtesy of Dr.
117 Jiro Kodani). There was no rain during successive measurement days as confirmed by a
118 plastic funnel-top container set above the canopy. The measurements were conducted on

119 the 1st, the 3rd and the 5th day after the last rainfall on 28 July. We used two portable
120 photosynthesis systems (LI-6400, LI-COR, Lincoln, USA), with CO₂ supply inside the
121 chambers kept at 350 ppm. Four leaves on the upper part of the canopy (i.e. “the upper
122 leaves”) were selected from one branch at the height of 5.7 m. Those were accessed by a
123 scaffolding tower. Another four leaves on the lower canopy (i.e. “the lower leaves”)
124 were selected from one branch on an adjacent tree at the height of 1.5 m, as there were
125 no accessible lower leaves on the same tree. For each position (the upper and lower),
126 incident photosynthetically active photon flux density (PPFD) were measured for seven
127 times with 1 - 2 hours intervals during daytime (8:30 - 16:00) with a quantum sensor
128 (IKS-27, KOITO Kogyo, Yokohama, Japan) placed above the branch of those leaves.
129 Hence, the angle of each leaf was not considered in this study. Net photosynthetic rates
130 of those intact leaves at each moment were measured by the two LI-6400s under the
131 PPFD of the same intensity just recorded on those leaves on each occasion, which were
132 supplied by the LED light sources (LI-6400-02B). On each occasion, the PPFDs were
133 kept constant until the equilibration of the leaves (typically, 20 - 40 min). Leaf
134 conductance to H₂O (*g*) (mol m⁻² s⁻¹), leaf temperature, and vapor pressure deficit based
135 on leaf temperature (VPD) (kPa) were simultaneously calculated by the LI-6400s. In the
136 following, we will regard *g* as equivalent to leaf stomatal conductance, assuming that
137 leaf boundary layer resistance was negligible. Immediately after each occasion of the
138 photosynthetic measurement, dark respiration rate was measured with zero light.

139 We simultaneously measured one photosynthetic light response curve for each
140 of the same sample leaves with the same LI-6400s. Those measurements were
141 conducted from 9:30 to 11:30 a.m., intermittently between the in-situ photosynthesis
142 measurements described above. For the lower leaves, all the four leaves were measured
143 on the 1st day. For the upper leaves, as we could not finish the measurement on the 1st
144 day, each two of the four leaves were measured on the 1st and the 3rd day. On each
145 measurement, the leaves were firstly induced by $\text{PPFD} = 1500 \mu\text{mol m}^{-2} \text{s}^{-1}$ until
146 equilibration. Then, PPFD was changed from higher to lower (2000, 1500, 1000, 750,
147 500, 250, 125, 63, 32 and $0 \mu\text{mol m}^{-2} \text{s}^{-1}$) with the LEDs. On each occasion of the
148 change, PPFD was kept constant until the equilibration of the leaves. During those
149 light-response measurements, leaf temperatures were not controlled and ranged $28.6 \text{ }^\circ\text{C}$
150 $- 33.2 \text{ }^\circ\text{C}$ and $28.1 \text{ }^\circ\text{C} - 31.9 \text{ }^\circ\text{C}$ for the upper and the lower leaves, respectively.

151

152 Data analysis

153 Diurnal course of in-situ gross photosynthetic rate ($P_{\text{g_mes}}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$) for each leaf
154 was calculated as the sum of net photosynthesis and dark respiration rate at each
155 moment. We set another open-sky PPFD sensor set above the canopy during the
156 measurement days, and we set $P_{\text{g_mes}}$ at the dawns and the sunsets as both zeros (i.e.
157 when the open-sky PPFD became zero) on each day. Daily photosynthesis for each leaf
158 was estimated by interpolations of those $P_{\text{g_mes}}$ values.

159 We alternatively calculated hypothetical diurnal courses of gross
160 photosynthetic rate, estimated solely by the diurnal change of the light intensity. Each
161 net photosynthetic rate during the light-response measurement (from PPFD 0 to 2000
162 $\mu\text{mol m}^{-2} \text{s}^{-1}$, see above) were converted to gross photosynthetic rate by adding dark
163 respiration rate (PPFD = 0). Then, non-rectangular hyperbola (Marshall and Biscoe
164 1980) was fitted by KaleidaGraph 4 (Synergy Software, Reading, USA) ($r^2 > 0.997$):

165

$$166 \quad P_{g_{cv}} = \frac{\phi I + P_{\max} - \sqrt{(\phi I + P_{\max})^2 - 4\theta\phi I P_{\max}}}{2\theta} \quad (\mu\text{mol m}^{-2} \text{s}^{-1}) \quad \text{Eq. 1}$$

167

168 In Eq. 1, $P_{g_{cv}}$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$) indicates a curve-estimated gross photosynthetic rate at
169 each incident PPFD intensity (I , $\mu\text{mol m}^{-2} \text{s}^{-1}$). P_{\max} indicates maximum gross
170 photosynthetic rate of that leaf when I approaches infinity. The other two parameters, ϕ
171 ($\mu\text{mol } \mu\text{mol}^{-1}$) and θ (dimensionless) indicate initial slope and convexity, respectively.
172 The curve-estimated photosynthetic rate ($P_{g_{cv}}$, $\mu\text{mol m}^{-2} \text{s}^{-1}$) at each time was estimated
173 by substituting the same incident PPFD as was used in the in-situ photosynthetic rate
174 described above into Eq.1 with each different set of parameters P_{\max} , ϕ and θ for each
175 different leaf. We used each single set of parameters for each leaf, such that same
176 photosynthetic light response curves were assumed throughout the five measurement
177 days. In other words, we hypothetically fixed conditions of the leaves at the time of

178 light-response curve measurements, and only PPFD was changed as the same way as
179 the actual diurnal courses.

180

181 Efficiency of photosynthesis

182 Actual photosynthetic rate (P_{g_mes}) should be under the effect of diurnal change of both

183 light intensity and all the other factors. In contrast, hypothetical P_{g_cv} should be

184 independent of diurnal change of the factors other than light. Then, the ratio between the

185 above two values (P_{g_mes} / P_{g_cv}) will be interpreted as diurnal change of efficiency of

186 photosynthesis, as affected by the non-light limitation. This ratio should be reduced,

187 when in-situ photosynthesis at that moment (P_{g_mes}) was reduced by non-light factors.

188 Note that P_{g_cv} (and hence P_{g_mes} / P_{g_cv} as well) also depends on the non-light factors at

189 the time of the measurement of the photosynthetic light response curve, but was

190 independent of “diurnal change” of non-light factors, as we fixed each leaf at one

191 particular time of the day. Because of this, P_{g_mes} / P_{g_cv} can be higher than unity, when

192 photosynthesis was limited less compared with the time of the measurement of

193 photosynthetic light response curves.

194

195 Statistics

196 Linear regressions and Pearson’s correlation coefficients (r) were calculated by SPSS

197 13.0J for Windows (SPSS Japan Inc, Tokyo, Japan).

198 Results

199 Upper leaves had higher maximum gross photosynthetic rate (P_{g_max}) and dark
200 respiration rate (Table 1), which is consistent with the previous studies (Iio et al. 2005;
201 Koyama and Kikuzawa 2010b). Diurnal course of in situ gas exchange rate (P_{g_mes})
202 basically followed incident PPFD both for the upper and the lower leaves, except in the
203 afternoon on the fifth day (Fig. 1a). There were no apparent “midday” depressions for
204 the both positions. The only visible difference was found in the upper leaves on the 5th
205 day, in which afternoon photosynthetic rate was apparently lower than that in the
206 morning. Diurnal course of VPD and leaf temperature showed similar pattern as that of
207 PPFDs (Fig. 1c). Leaf conductance to H_2O (g) tended to decline towards the end of
208 each day (Fig. 1b). This trend was evident on all the days for the upper leaves, but only
209 on the 5th day for the lower leaves. The actual in-situ daily gross photosynthetic rate
210 averaged over the three measurement days was 0.35 and 0.042 ($\text{mol m}^{-2} \text{day}^{-1}$) for the
211 upper and lower leaves, respectively.

212 Although “midday depression” was not apparent, a clear difference was
213 detected between canopy positions when we compare P_{g_mes} / P_{g_cv} (Fig. 2). For the
214 upper leaves P_{g_mes} / P_{g_cv} linearly declined towards the end of each day. In contrast, for
215 the lower leaves P_{g_mes} / P_{g_cv} only fluctuated around the mean value for all the days.
216 The slope of the decline of the upper leaves became steeper (i.e. more negative), as the
217 number of days after the last rain increased (Fig. 3). The P_{g_mes} / P_{g_cv} were strongly and

218 positively correlated with leaf conductance to H₂O for the upper leaves, but there were
219 no consistent relationships for the lower leaves (Fig. 4).

220

221 **Discussion**

222 We found a clear difference between canopy positions; only the upper leaves showed
223 declining trends in photosynthetic efficiency (Fig. 2). We estimated the percentage loss
224 of daily gross photosynthetic rate due to this decline as follows. When P_{g_mes} / P_{g_cv} of
225 one particular time (say, 15:00) on one day was 0.85, while P_{g_mes} / P_{g_cv} of the earliest
226 morning within that day was 1.1 (see Fig. 2 upper), we calculated the ratio $1.1 / 0.85 (=$
227 $1.3)$. It means that leaves in the earliest morning can conduct 1.3 times more
228 photosynthesis than the actual leaf exists at 15:00 under the same PPFD observed at
229 15:00. Then, we calculated product of this ratio and P_{g_mes} on each time on each day. It
230 is the estimation of hypothetical photosynthetic rate conducted by a leaf, being “fixed”
231 at the condition of that in the earliest morning, whilst PPFD on that leaf was changed as
232 the same way as the actual diurnal course. Finally, we calculated potential gross daily
233 photosynthetic rate by the interpolation of those values as the same manner as the above
234 actual ones. Compared with those potential values, actual gross daily photosynthetic
235 rates were 12% and 1% less for the upper and the lower leaves, respectively. Hence, the
236 reduction was modest for the upper leaves, and did not exist for the lower leaves. Those
237 results supported the hypothesis that photosynthesis is constrained more greatly for the

238 upper leaves than the lower leaves (Jarvis 1976; Niinemets et al. 2004).

239 Among the upper leaves, P_{g_mes} / P_{g_cv} decreased towards the end of each day.

240 This result supported Jarvis (1976), who suggested that water reserves within branches

241 or stems were gradually exhausted in upper canopies towards the end of each day. This

242 diurnal decline became steeper, as the number of days after the rainfall increased (Fig.

243 3). Then, the visible reduction of photosynthetic rate was eventually observed in the

244 afternoon on the fifth day (Fig. 1a). Those results are consistent with the study of a

245 mulberry tree (Tazaki et al. 1980), which showed that midday depression was not

246 evident until the second day after the last rainfall, but it was apparent from one week

247 after the rainfall. Those results were consistent with the classical scheme of the

248 periodical decline of soil water potential from morning to sunset within each day, with

249 the absolute water availability decreases as days after the last rain proceeds (Slatyer

250 1967). Kikuzawa et al. (2004) reported 46.5% reduction of daily photosynthesis for the

251 sun leaves of *Alnus sieboldiana*, when the apparent midday depression occurred. Our

252 results (12% loss without visible midday depression) suggests that a reduction of

253 photosynthesis does not abruptly rises up to 46% when an apparent midday depression

254 is observed, but it gradually increases from the onset of a rainless period. This indicates

255 that there may be no threshold condition for a midday depression. Hence, our results

256 depicted more general pattern than that of Tazaki et al. (1980), since it showed reduction

257 of photosynthesis before “midday depression” was apparent.

258 Stomatal limitation was expected to be higher for the upper leaves, which were
259 exposed to high light environment (Niinemets and Valladares 2004). In addition, leaves
260 on the higher position may have smaller water reserves (Jarvis 1976), longer water
261 pathway from root (Ryan et al. 2006) and, specifically for tall trees, less water potential
262 due to gravitation (Ishii et al. 2008; Nabeshima and Hiura 2008). Another mechanism
263 suggested that sunlit upper leaves may have more water supplies by a selective
264 investment of water into favorable sunlit leaves (Sprugel et al. 2002). In this study (6 m
265 height), the gravitational effect should be negligible. However, we could not separate
266 each of those confounding effects, as we selected upper and lower leaves from different
267 individuals. Hence, before generalizing our results to other forests, mechanistic
268 measurements including investigation of water supply on each position is needed to
269 separate those factors.

270 We did not measured photoinhibition. Actual reduction is caused by both
271 stomatal limitation and photoinhibition (Ishida et al. 1999abc; 2000; 2001; Muraoka et
272 al. 2000; Werner et al. 2001; Valladares and Pearcy 2002; Yamazaki et al. 2007; Misson
273 et al. 2010). Uemura et al. (2005) discussed that the reduction of photosynthesis in
274 another *Fagus crenata* forest was due to photoinhibition, rather than stomatal closure.
275 Our results showed that at least some part of reduction of photosynthesis was related to
276 stomatal closure, which did not violate the conclusion by those studies.

277 We used LED light-sources, such that an effect of heat loading (Ishida et al.

278 2000; Uemura et al. 2005; Iio et al. 2009; Vogel 2009) may not have been properly
279 evaluated. Although our method has a clear disadvantage in these points, it has another
280 merit than those using natural sunlight. Diurnal course of incident photosynthetic rate
281 did not show a visible midday depression on the 1st day (Fig 1a), which is consistent
282 with Tazaki et al. (1980). However, when we calculated the P_{g_mes} / P_{g_cv} , the reduction
283 became apparent from the 1st day (Fig. 2). Hence, the reduction was detected only when
284 we evaluated the ratio of the two kind of photosynthetic rates, P_{g_mes} and P_{g_cv} , both of
285 which were measured by the same LEDs, so that were readily comparable.

286 The study period was during the hottest season of one year on one particular
287 ecotype of *Fagus crenata*. However, patterns of photosynthetic limitation should vary
288 among seasons or years (Ishida et al. 1999b; Valladares et al. 2008; Misson et al. 2010).
289 Generally, responses to environment differ among species (Turner et al. 1984; Ishida et
290 al. 1999a; Uemura et al. 2000; 2005; Turnbull et al. 2002; Oguchi et al. 2005; Valladares
291 et al. 2008; Kitaoka et al. 2009; Kamiyama et al. 2010), among ecotypes of *Fagus*
292 *crenata* (Yamazaki et al. 2007; Tateishi et al. 2010), and between microhabitats
293 (Koyama and Kikuzawa 2008; Nagano et al. 2009). A behavior of a plant can be
294 considered as a summation of simple basic principles and those situation-dependent
295 factors (Koyama and Kikuzawa 2009). Simple theories and complex factors are not
296 mutually exclusive, but are compensatory for each other.

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301

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485 **Table 1** The photosynthetic light response curve parameters and dark respiration rate
 486 (R_d) at the time of the curve measurement.

487	Upper	Lower	Units
488 P_{\max}	13.7 ^a	3.8 ^b	$\mu\text{mol m}^{-2} \text{s}^{-1}$
489 ϕ	0.055	0.049	mol mol^{-1}
490 θ	0.21	0.55	
491 R_d	1.8 ^c	0.2 ^d	$\mu\text{mol m}^{-2} \text{s}^{-1}$

493 Different uppercase letters: (a, b) $p < 0.01$ and (c, d) $p < 0.05$ (t - test).

494

495 **Figure Legends (Figs. 1 - 4)**

496 **Fig. 1** Diurnal courses of the parameters. The left, the middle and the right column
 497 shows the 1st, the 3rd and the 5th day after the last rain in 28 July 2008, respectively.
 498 For each parameter but PPFD (one sensor), the mean value of the four leaves on each
 499 position are respectively shown. The error bars indicate the unbiased estimate of the
 500 standard deviation.

501 **a** (*Closed circles*) in situ gross photosynthetic rate of the leaves (P_{g_mes}). (*Open circles*)
 502 PPFD on the branch. **b** Leaf conductance to H_2O (g). **c** (*Open boxes*) leaf temperature.
 503 (*Open circles*) vapor pressure deficit based on the leaf temperature (VPD).

504

505 **Fig. 2** Diurnal course of P_{g_mes} / P_{g_cv} , the ratio between in-situ photosynthetic rate on
506 each time and photosynthetic rate estimated by photosynthetic light response curve,
507 which was measured at one particular time during measurement days for each leaf. Each
508 *open circle* and its error bars indicate mean value and its unbiased standard deviation,
509 respectively, for the four leaves on each canopy position. Solid lines indicate significant
510 linear regressions (* $p < 0.05$, ** $p < 0.01$):

511

512 (1st day) $P_{g_mes} / P_{g_cv} = 1.3 - 2.2 \times 10^{-2}$ Time of day (h).

513 (3rd day) $P_{g_mes} / P_{g_cv} = 1.4 - 2.9 \times 10^{-2} h$.

514 (5th day) $P_{g_mes} / P_{g_cv} = 1.4 - 4.1 \times 10^{-2} h$.

515

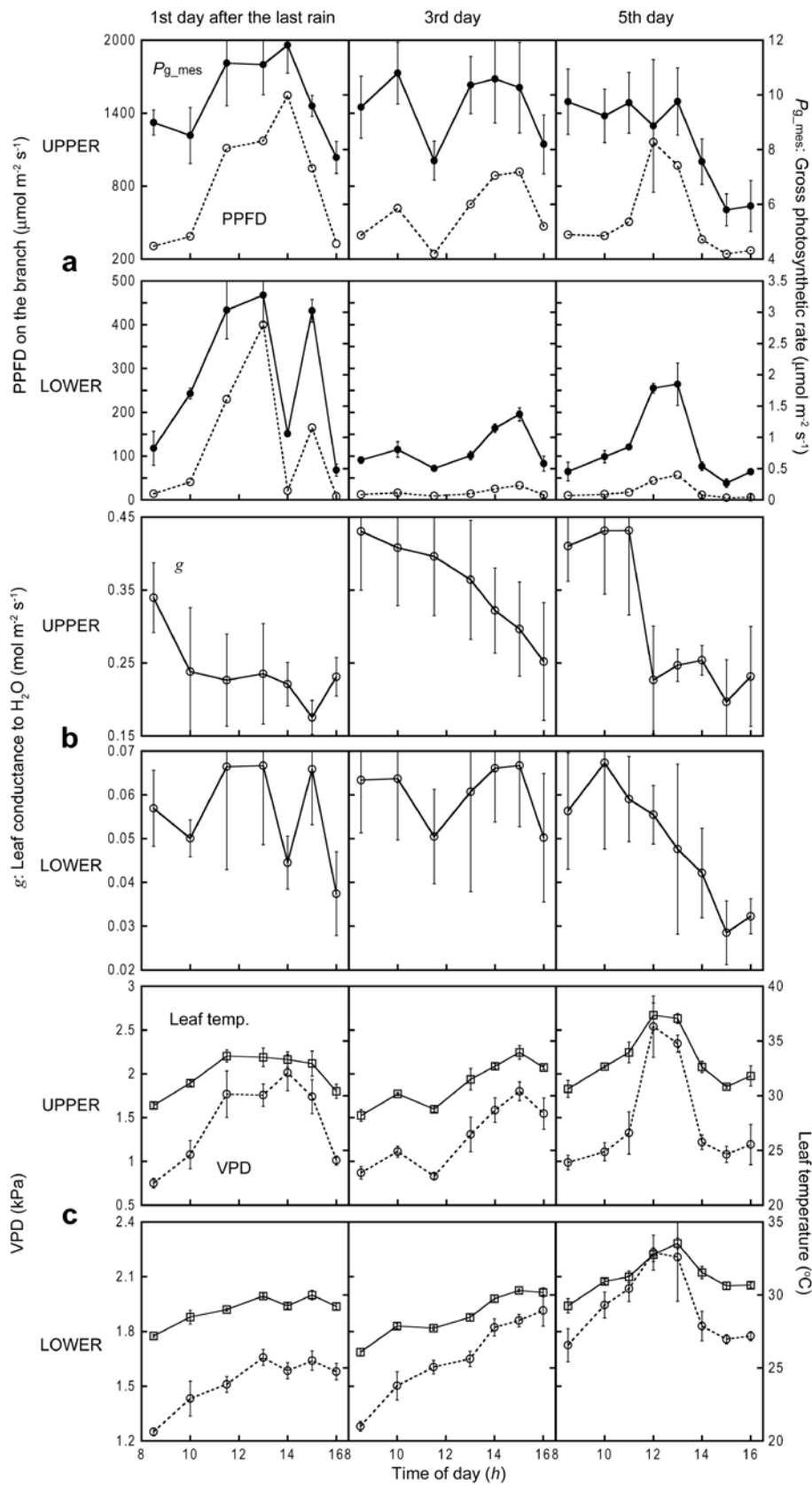
516 **Fig. 3** The slopes of the diurnal decline of P_{g_mes} / P_{g_cv} (i.e. the slopes of the linear
517 regressions for the upper leaves shown in Fig. 2) in relation to number of days after the
518 last rain.

519

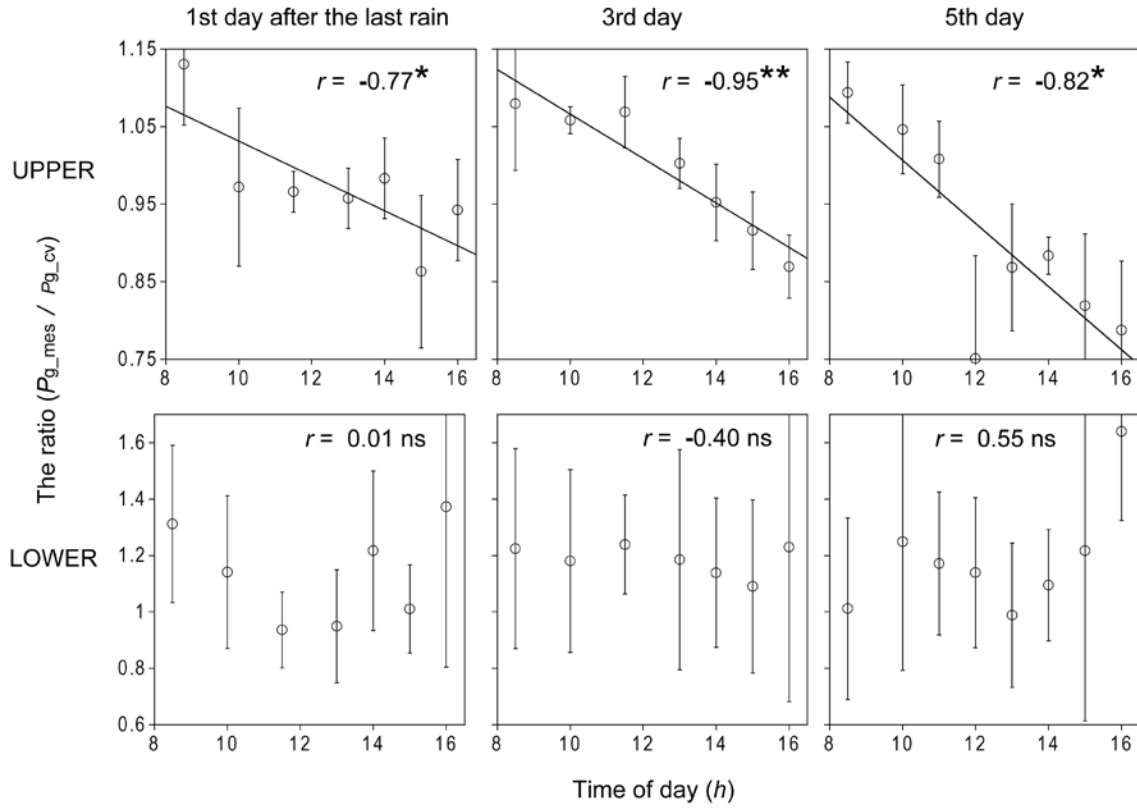
520 **Fig. 4** P_{g_mes} / P_{g_cv} in relation to g . Each *open circle* and its error bar indicate mean
521 value and standard deviation, respectively, for the four leaves in each position.

522 Pearson's correlation coefficients (r) were shown (* $p < 0.05$, *** $p < 0.001$).

523



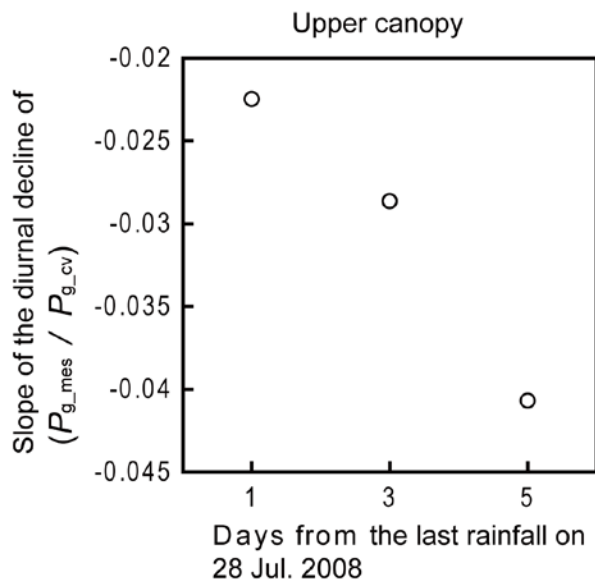
527 Fig. 2



528

529

530 Fig. 3



531

532

