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4   **Original Research Paper**

5

6   **Title**: Geometrical similarity analysis of photosynthetic light response curves, light

7   saturation and light use efficiency.

8

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18   **Running title:** Similarity of photosynthetic light response curves

19

Abstract

Light absorption and use efficiency (LAUE mol mol^{-1}, daily gross photosynthesis per daily incident light) of each leaf depends on several factors, including a degree of light saturation. It is often discussed that upper canopy leaves exposed to direct sunlight are fully light-saturated. However, we found that upper leaves of three temperate species, a heliophytic perennial herb *Helianthus tuberosus*, a pioneer tree *Alnus japonica* and a late-successional tree *Fagus crenata*, were not fully light-saturated even under full sunlight. Geometrical analysis of the photosynthetic light response curves revealed that all the curves of the leaves from different canopy positions, as well as from the different species, can be considered as different parts of a single non-rectangular hyperbola. The analysis consistently explained how those leaves were not fully light-saturated. Light use optimization models, called big leaf models, predicted that the degree of light saturation and LAUE are both independent of light environment. From these, we hypothesized that the upper leaves should not be fully light-saturated even under direct sunlight, but instead should share the light limitation with the shaded lower-canopy leaves, so as to utilize strong sunlight efficiently. Supporting this prediction, within a canopy of *H. tuberosus*, both the degree of light saturation and LAUE were independent of light environment within a canopy, resulting in proportionality between the daily photosynthesis and the daily incident light among the leaves.

Keywords: scaling, big leaf model, *Helianthus tuberosus*, *Alnus japonica*, *Fagus*

40 *crenata*.

41

42 **Introduction**

43 Total light energy flux per given land area is limited. Hence, efficiency of conversion

44 from light energy into photosynthate, called light use efficiency, is the most important

45 factor which determines productivity of plant canopies (Murchie et al. 2008; Posada et

46 al. 2009). There are several definitions for light use efficiency (see Gower et al. 1999).

47 In this study, we will use a word "daily light absorption and use efficiency" for each leaf

48 (LAUE) (mol mol^{-1}), defined as daily sum of gross carbon gain per unit area of one leaf

49 (mol m^{-2} d^{-1}) divided by daily sum of incident PPFD on that leaf (mol m^{-2} d^{-1}). Although

50 LAUE is also one of the previous definition of light use efficiency (e.g. Rosati and

51 DeJong 2003), we will use LAUE to distinguish it from light use efficiency of Gower et

52 al. (1999), which was calculated on absorbed photon basis.

53 LAUE depends on several factors, including light saturation of leaves (Sinclair

54 and Horie 1989; Faurie et al. 1996; Hikosaka et al. 1999), photoinhibition (Werner et al.

55 2001; Pearcy et al. 2005) and other environmental factors such as drought or heat stress

56 (Niinemets and Valladares 2004). Being a determinant of LAUE, light saturation of each

57 leaf is one of the important determinants of canopy photosynthesis (Murchie et al. 2008).

58 Despite its importance, there has been no consensus of intra-canopy distribution of light

59 saturation. It is often suggested that upper canopy leaves exposed to direct sunlight are

fully light-saturated (Hirose and Bazzaz 1998; Kull 2002; Falster and Westoby 2003;

Niinemets and Valladares 2004; Eichelmann et al. 2005), while shaded lower leaves are

limited with light (Hirose and Bazzaz 1998; Kull 2002). Other studies reported that

leaves under full sunlight may not be fully light-saturated (Mooney et al. 1976;

Björkman 1981; Green and Kruger 2001). Therefore a quantification of light saturation

for leaves from different positions in a canopy is needed. Light-use optimization models,

called "big-leaf models", predicted that all the leaves on a single plant are

light-saturated or light-limited to the same degree within each day (Sellers et al. 1992;

Kull and Jarvis 1995; Anten et al. 1995; Terashima et al. 2005). The big leaf models

therefore predict that all the photosynthetic apparatus on a single plant are equally

utilized, so that none of them are overloaded with incoming light resources. Under that

condition, all the light resource within a canopy will be utilized with the same efficiency,

albeit the light gradient still exists (Sellers et al. 1992; Kull and Jarvis 1995; Dewar et al.

1998; Rosati and DeJong 2003; Posada et al. 2009). Importantly, those models predicted

that when shaded lower canopy leaves experience light limitation, well-lit upper leaves

should also experience light limitation to the same degree. Hence we hypothesize that

upper canopy leaves should not be fully light-saturated under full sunlight to achieve

this optimal condition.

In this study, we will report that upper leaves of three temperate species do not

show light saturation even under full sunlight (i.e. photosynthetic photon flux density

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80   (PPFD) 1500 – 2000 μmol m^{-2} s^{-1}). The three species are a heliophytic perennial herb

81   *Helianthus tuberosus*, a pioneer tree *Alnus japonica* and a late-successional tree *Fagus*

82   *crenata*. Firstly, we will demonstrate that those photosynthetic responses are the first

83   empirical evidence for the geometrical similarity of non-rectangular hyperbolae

84   (Farquhar 1989; Anten et al. 1995; Kull and Jarvis 1995). This also implies that the

85   non-saturation is not species-specific, but should be universal for leaves with high

86   photosynthetic capacity. Secondly, we tested the hypothesis that the degree of light

87   saturation is controlled to be independent of light environment within the canopy for *H.*

88   *tuberosus*, as predicted by the big leaf models. The applicability of the big leaf models

89   has been questioned for actual canopies, in which PPFD diurnally changes (de Pury and

90   Farquhar 1997). Therefore, we extended the big leaf models into the one which is

91   applicable for canopies under a dynamic light regime.

92

93   **Model**

94   Daily light absorption and use efficiency (LAUE mol mol^{-1}) was defined as daily sum of

95   gross carbon gain per unit area of one leaf (mol m^{-2} d^{-1}) divided by daily sum of incident

96   PPFD on that leaf (mol m^{-2} d^{-1}):

97

98   $$\text{LAUE} = \sum_{t=0}^{24h} P_{(t)} \, / \, \sum_{t=0}^{24h} I_{(t)} \qquad (\text{mol mol}^{-1}) \qquad\qquad \text{Eq. 1}$$

100    $P_{(t)}$ (µmol m^{-2} s^{-1}) and $I_{(t)}$ (µmol m^{-2} s^{-1}) indicate instantaneous gross photosynthetic rate

101   and incident PPFD for each leaf at each moment (t). We defined LAUE by gross

102   photosynthesis, not by net photosynthesis. Gross LAUE provides information of the

103   efficiency of conversion from light energy into photosynthate, and should always be

104   negatively correlated with the incident PPFD level and with the degree of light

105   saturation. Net LAUE can be affected both by photosynthesis and respiration, and it can

106   increase with incident PPFD when light is very low (cf. Tooming 1970; Hirose and

107   Bazzaz 1998; Kadaja and Tooming 2004). In such cases, the increasing net LAUE does

108   not mean that light is more efficiently converted into photosynthate.

109   Photosynthetic light response for each leaf is assumed to be expressed by the

110   non-rectangular hyperbola (Marshall and Biscoe 1980):

111

112    $$P_{(t)} = \frac{\Phi I_{(t)} + P_{\max} - \sqrt{(\Phi I_{(t)} + P_{\max})^2 - 4\theta\Phi I_{(t)}P_{\max}}}{2\theta} \quad \text{(µmol m}^{-2}\text{ s}^{-1}) \qquad \text{Eq. 2}$$

113

114    $P_{\max}$ indicates light-saturated gross photosynthetic rate, defined as $P_{(t)}$ when $I_{(t)}$

115   approaches infinity. ϕ (µmol µmol^{-1}) and θ (dimensionless) indicate the initial slope and

116   the convexity, respectively. Our first objective was to test the following geometrical

117   similarity of photosynthetic light response curves (Farquhar 1989; Anten et al. 1995;

6

118   Kull and Jarvis 1995). Two curves with different P_{max} (37.5 and 5.6 µmol m^{-2} s^{-1}) were

119   shown in Fig. 1ab. Both curves have the same initial slope ($\phi = 0.062$ µmol µmol^{-1}) and

120   convexity ($\theta = 0.55$, no dimension). Although they share the common slope and

121   convexity, the leaf with high P_{max} does not show light saturation even under PPFD 2000

122   µmol m^{-2} s^{-1} (Fig. 1a), while the leaf with low P_{max} shows light saturation at that PPFD

123   (i.e. achieving photosynthetic rate that is close to P_{max}) (Fig. 1b). Those two curves can

124   be understood as different parts of two geometrically similar curves, which differed in

125   size (= P_{max}) but not in shape (Fig. 1c). As being similar, they become congruent when

126   normalized to the same size. This normalization can be achieved by reducing each curve

127   by a factor of its size (P_{max}), in both vertical and horizontal directions (Fig. 1d). This

128   similarity is given by (Farquhar 1989; Anten et al. 1995; Kull and Jarvis 1995):

129

130    $$\frac{P_{(t)}}{P_{max}} = \left\{ \frac{\Phi \frac{I_{(t)}}{P_{max}} + 1 - \sqrt{(\Phi \frac{I_{(t)}}{P_{max}} + 1)^2 - 4\theta\Phi \frac{I_{(t)}}{P_{max}}}}{2\theta} \right\} \qquad \text{Eq. 3}$$

131

132   Eq. 3 shows that the relation between ($I_{(t)} / P_{max}$) and ($P_{(t)} / P_{max}$) for the two curves are

133   expressed in the same normalized non-rectangular hyperbola with the asymptotic line

134    $P_{(t)} / P_{max} = 1$ (Fig. 1d). All the symbols are on the same normalized non-rectangular

135   hyperbola. Strictly, this similarity occurs when initial slope and convexity of curves are

136   invariant (Farquhar 1989; Kull and Jarvis 1995; Anten et al. 1995). The two vertical

137   axes in Fig. 1d show difference of positions on the normalized curve among the two

138   leaves when PPFD = 2000 μmol m^{-2} s^{-1}. It is clear that the leaves with different P_{max}

139   conduct photosynthesis at different positions on the same normalized curve under the

140   same PPFD. Therefore, light regime *per se* is not suitable to quantify light saturation for

141   leaves with different P_{max}. In contrast, $P_{(t)}$ relative to P_{max} (i.e. $P' = P_{(t)} / P_{max}$) indicates

142   a relative position on the same non-rectangular hyperbola. We will call $P_{(t)}$ / P_{max}

143   "relative photosynthetic rate", and use it as an indicator of light saturation equally for

144   leaves with different P_{max}. Our first aim was to test whether the phenomenon shown in

145   Fig. 1d will be observed for the three species.

146   Relative photosynthetic rate ($P_{(t)}$ / P_{max}) indicates a degree of light saturation at

147   each moment. The simple big leaf models predict that this value will be constant for

148   leaves throughout a canopy at every moment during a day (Sellers et al. 1992; Anten et

149   al. 1995; Kull and Jarvis 1995). However, this prediction has been questioned for actual

150   canopies, in which light environment diurnally fluctuates (de Pury and Farquhar 1997).

151   Daily LAUE should depend on a fraction of light energy utilized at each degree of light

152   saturation ($P_{(t)}$ / P_{max}) on that day. Hence, we calculated the mean of this distribution as

153   an indicator of daily light saturation. We therefore defined quantum-weighted average

154   of light saturation ($_{ave}(P_{(t)}$ / $P_{max})_{quanta}$) as:

155

156 $$\text{ave}(P_{(t)}/P_{\max})_{\text{quanta}} = \frac{\sum\limits_{t=0}^{24h} I_{(t)}(P_{(t)}/P_{\max})}{\sum\limits_{t=0}^{24h} I_{(t)}}$$ Eq. 4

157

158 It indicates "on average under what degree of light saturation, incident light quanta on

159 that leaf were utilized". When large amount of light energy is supplied in short

160 sunflecks, it would not affect the unweighted time-average of $P_{(t)}/P_{\max}$ (i.e. leaves are

161 not frequently light-saturated), whilst it would greatly affect the $\text{ave}(P_{(t)}/P_{\max})_{\text{quanta}}$ (i.e.

162 most of the light quanta incident on that leaf were utilized on light-saturated phase). The

163 latter should be more mechanistically linked to LAUE of each leaf, which is the present

164 focus. Our extended big leaf model predicts that $\text{ave}(P_{(t)}/P_{\max})_{\text{quanta}}$ to be similar within

165 a canopy. This means that all the light energy were utilized on average under the similar

166 degree of light saturation, irrespective of canopy position. This will result in the similar

167 daily LAUE within the canopy. Our second objective was to test this hypothesis for *H.*

168 *tuberosus*.

169

170 **Materials and methods**

171 Species and site

172 *Helianthus tuberosus* L. is a naturalized perennial herb introduced from North America

173 and distributed throughout Japan (Shimizu 2003). It is a C_3 species (Singsaas et al.

174   2001). It grows in disturbed open sites and reaches about 2 m height. They flower in

175   autumn and all the aboveground parts die at the beginning of winter, leaving new tubers.

176   *Alnus japonica* Steud. is a pioneer deciduous tree, which invades mesic sites such as

177   riversides and swamps (Kikuzawa 1983). *Fagus crenata* Blume is a late-successional

178   deciduous tree distributed in mountainous region (Okaura and Harada 2002).

179   The two study sites are in Ishikawa Prefecture in central Japan, an area with a

180   warm temperate climate. The site for *H. tuberosus* was the experimental farm station of

181   Ishikawa Prefectural University situated in a lowland plain (36° 30' N, 136° 35' E, 39 m

182   a.s.l.). Mean annual temperature and mean annual precipitation are 14.3 ^{o}C and 2161

183   mm, respectively (2002 - 2008, IPU-1, Ishikawa Prefectural University). We established

184   an experimental plot in the garden. There were no tall objects surrounding the plots, and

185   the plants received full sunlight during daytime. Twenty-five tubers were planted in the

186   1 m^2 plot in the garden in December 2007. Those tubers were taken from the previous

187   year's plot of Koyama and Kikuzawa (2009). A total of 35 stems (one to four stems per

188   tuber) germinated in April 2008. Six stems from the outermost layer were damaged and

189   bent by a windstorm in July 2008, and in the following experiment we have investigated

190   a stem which was surrounded by unaffected stems. Weeds in the plot were frequently

191   removed. No fertilizer was supplied. The stand height was 1.8 m on the measurement

192   day. The site for *A. japonica* and *F. crenata* was the Ishikawa Prefectural Forest

193   Experiment Station, which is located at the foot of Mt. Hakusan (36˚25'N, 136˚38'E,

10

194　200 m a.s.l.). Mean annual temperature and mean annual precipitation are 13.0 $^{\circ}$C and

195　2438 mm, respectively (2003 - 2007, Annual Report of the Ishikawa Prefectural Forest

196　Experiment Station). For *A. japonica*, a naturally-established stand on an abandoned

197　paddy field was investigated. The stand age was estimated to be around 50 - 60 years

198　old, according to a land-use record. The trees in the stand reached around 20 m forming

199　a closed canopy. The site for *F. crenata* was 16-years-old plantation, which is within 50

200　m from the *A. japonica* stand. There were 130 trees in 171 m^2 area, and the stand height

201　was around 6 m, forming a closed canopy.

202

203　Leaf samples

204　Only fully-expanded leaves were measured in this study. For *H. tuberosus*, fifteen

205　leaves from the different positions of one plant in the interior of the stand were

206　measured on 17-Aug-2008. The day was about one month before the first appearance of

207　inflorescence, and new leaves were expanding successively from the apex. For *A.*

208　*japonica*, fifteen leaves just after their full expansion from the different positions of one

209　tree were accessed by a scaffolding tower, and were measured on 25-May-2009. For *F.*

210　*crenata*, of total eleven leaves were measured on 18-May or on 6-Jun in 2007, or on

211　28-May-2009. Upper leaves of one individual were accessed by another scaffolding

212　tower and were measured. As there were no accessible lower leaves on that tree, leaves

213　on the lower position of an adjacent tree were measured from the ground.

214

215   Measurement of photosynthesis

216   Photosynthetic rate of each leaf was measured with one or two portable infrared gas

217   analyzers (LI-6400, LI-COR, Lincoln, USA). The PPFD was supplied with an LED

218   light source (LI-6400-02B) inside the chamber. Leaves were firstly induced by PPFD =

219   1500 μmol m^{-2} s^{-1} until equilibration. Then, PPFD was changed from higher to lower

220   (2000, 1500, 1000, 750, 500, 250, 125, 63, 32 and 0 μmol m^{-2} s^{-1}). On each occasion of

221   the change, PPFD was kept constant until the equilibration of the leaves. CO_2

222   concentrations inside the chamber were maintained at 350 μmol mol^{-1}. Gross

223   photosynthetic rate at each PPFD was calculated as the sum of each value and dark

224   respiration rate, which was measured under zero light. For *H. tuberosus*, the

225   measurement was conducted between 7:00 and 14:30. The day was cloudy, and the air

226   temperature inside the chamber ranged between 24.9 $^{\circ}$C - 31.8 $^{\circ}$C. The plants were

227   watered to saturation in the evening before measurement was taken. For *A. japonica*, the

228   measurement was conducted between 9:00 and 15:00 on a cloudy day. The air

229   temperature inside the chamber ranged between 18.4 $^{\circ}$C - 23.7 $^{\circ}$C. The plant was

230   watered by rainfall during the night before the measurement, and continually by an

231   adjacent natural stream. For *F. crenata*, the measurements were conducted between 7:30

232   and 14:30 in a cloudy day or in an early morning of a sunny day. The air temperature

233   inside the chamber ranged between 22.4 $^{\circ}$C - 26.4 $^{\circ}$C. For each dataset, the

234   non-rectangular hyperbola (Eq. 2) was fitted ($r^2 > 0.995$ for all the leaves), and the three

235   parameters (P_{max}, Φ and θ) were estimated by Levenberg-Marquardt algorithm using

236   KaleidaGraph 4 (Synergy Software, Reading, USA). To estimate the normalized

237   photosynthetic light response curve (as in Fig. 1d), each PPFD ($I_{(t)}$) (from 0 to 2000

238   μmol m^{-2} s^{-1}) and the gross photosynthetic rate under that PPFD ($P_{(t)}$) were divided by

239   P_{max} of that leaf. The normalized non-rectangular hyperbola (Eq. 3) was fitted for all

240   those normalized data pooled within each species, as well as for all the data pooled from

241   the three species.

242

243   Measurement of incident light

244   Diurnal course of incident PPFD was estimated for all the 15 leaves of *H. tuberosus*.

245   Small photodiodes (G1118, Hamamatsu Photonics, Hamamatsu, Japan) were used to

246   estimate PPFD on the leaves (Nishimura et al. 1998; Nishimura and Ito 2003). Each

247   photodiode had been calibrated against a quantum sensor (IKS-27, Koito, Yokohama,

248   Japan). For each leaf, the photodiode was mounted on the center of the leaf blade with

249   adherent tapes, so that its light-sensitive surface was set parallel to the leaf adaxial

250   surface. They were connected to a voltage logger (Thermodac-F, Eto Denki, Tokyo,

251   Japan) by light leading wires. Because the photodiode was light (weight 150 mg), and

252   because we adhered the wires to the stem to avoid putting extra load on the leaf, there

253   were no signs of additional leaf bending. In 18-Aug-2008, which was a clear sunny day,

254   incident PPFD on each leaf at each moment ($I_{(t)}$) was recorded every 10 minutes for 24

255   hours. Using the photosynthetic light response curves, instantaneous gross

256   photosynthetic rate at that moment ($P_{(t)}$) was estimated for each leaf.

257

258   **Results**

259   For all the three species, photosynthetic rates of the upper leaves at PPFD 1500 – 2000

260   µmol m^{-2} s^{-1} were substantially less than P_{max}, indicating that the leaves were not fully

261   light-saturated (Fig. 2, upper). The phenomenon was the most evident in the upper

262   leaves of *H. tuberosus*, which have higher P_{max} (32.5 – 37.5 µmol m^{-2} s^{-1}) than the other

263   two species, *A. japonica* (18.5 – 19.5 µmol m^{-2} s^{-1}) and *F. crenata* (14 – 19.5 µmol m^{-2}

264   s^{-1}). In contrast, the lower leaves with low P_{max} showed light-saturation (i.e. they

265   achieved photosynthetic rate nearly equal to P_{max}) under the same PPFD range (Fig. 2,

266   lower). For all the three species, there were weak positive correlation between the initial

267   slope and P_{max}, though it was significant only for *A. japonica* (Fig. 3). Correlation

268   between the convexity and P_{max} was negative, but non-significant for all the three

269   species (Fig. 3). When normalized, all the data within each species almost coincided on

270   a single non-rectangular hyperbola ($r^2 > 0.995$, Fig. 4abc). When all the dataset of the

271   three species were normalized, they almost coincided on the single non-rectangular

272   hyperbola ($r^2 = 0.996$, Fig. 4d).

273   In the *H. tuberosus* canopy, the lower leaves episodically received sunflecks

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274   (Fig. 5). Although the peak value of PPFD was greater for the upper leaves than the

275   lower leaves, the daily maxima of $P_{(t)} / P_{max}$ were similar or somewhat smaller for the

276   upper than that of the lower (Fig. 5). Strong negative correlation between LAUE and the

277   quantum-based average ($_{ave}(P_{(t)} / P_{max})_{quanta}$) was observed (Fig. 6a). The degree of light

278   saturation with which light quanta were utilized ($_{ave}(P_{(t)} / P_{max})_{quanta}$) was independent

279   of light environment within a canopy (Fig. 6b). Consequently, LAUE was not

280   significantly correlated with the daily incident PPFD ($p = 0.86$), and hence the daily leaf

281   photosynthesis was proportional to the daily incident light (Fig. 6c).

282

283   **Discussion**

284   We found that the upper canopy leaves were not fully light-saturated even under full

285   sunlight. This phenomenon is explained by the geometrical similarity of photosynthetic

286   light response curves (Fig. 1, Fig. 4). This similarity was predicted by mathematical

287   models (Farquhar 1989; Anten et al. 1995; Kull and Jarvis 1995), but has not been

288   tested empirically. When photosynthetic capacity of a leaf is high, full sunlight (PPFD

289   1500 - 2000 μmol m^{-2} s^{-1}) caused incomplete light saturation (Fig. 2). We observed this

290   phenomenon among different C_3 species from different successional stages, implying

291   that the result is not species-specific. Models show that all the photosynthetic light

292   response curves exactly coincide with each other, when the initial slope (ϕ) and the

293   convexity (θ) are invariant (Farquhar 1989; Anten et al. 1995; Kull and Jarvis 1995).

294 Instead, we observed weak positive correlation between ϕ and $P_{\max}$, and weak negative

295 correlation between θ and $P_{\max}$ for all the three species, which are consistent with the

296 result of Hirose and Werger (1987). Nonetheless, the similarity of the normalized curves

297 (Fig. 4) indicates that the overall shape of the curves was mainly determined by $P_{\max}$ as

298 shown in Fig. 1. Also, strong correlation between LAUE and $_{\text{ave}}(P_{(t)} / P_{\max})_{\text{quanta}}$ (Fig.

299 6a) showed that relative position on the normalized curve, on which light quanta were

300 utilized, is a qualitatively reliable parameter to evaluate light saturation for leaves with

301 different $P_{\max}$. Hence, even though the slope and the convexity were not strictly

302 invariant, our analysis based on the similarity of the curves was useful as a good

303 approximation.

304   For *H. tuberosus* canopy, we further demonstrated that the non-saturation of the

305 upper leaves is an effective strategy to utilize light resource. The daily maxima of $P_{(t)} /$

306 $P_{\max}$ was similar or somewhat greater for the lower leaves than the upper (Fig. 5). The

307 quantum-based average for relative photosynthetic rate ($_{\text{ave}}(P_{(t)} / P_{\max})_{\text{quanta}}$) was

308 independent of light environment (Fig. 6b). Hence we found no evidence that the

309 well-lit upper leaves were more light-saturated than the lower leaves. Consequently,

310 LAUE was independent of light environment (Fig. 6c), which is consistent with the

311 other reports (Rosati and DeJong 2003; Rosati et al. 2004; Posada et al. 2009). The

312 previous big leaf models assumed that PPFD on each leaf relative to that above the

313 canopy is constant within each day (e.g. Sellers et al. 1992; Anten et al. 1995; Kull and

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314   Jarvis 1995). Although this condition can be predicted by assuming all-diffuse radiation

315   (Monsi and Saeki 2005), leaves receive direct sunbeam, which causes great fluctuation

316   of PPFD on their surfaces (Fig. 5, Pearcy 1983; Tang et al. 1988; Pearcy et al. 1994). It

317   has been recognized that the use of diurnally-averaged irradiance is invalid to estimate

318   light saturation for each leaf (de Pury and Farquhar 1997; Thornley 2002; Hirose 2005;

319   Niinemets and Anten 2009). For this reason, the applicability of the big leaf models has

320   been questioned (de Pury and Farquhar 1997). However, we showed that the leaves

321   acclimated their P_{max}, such that the incident light energy was on average utilized with

322   the similar degree of light saturation under variable light environment. It is in good

323   agreement with the sugar sensing models (Dewar et al. 1998; Ono et al. 2001) and/or

324   the cytokinin sensing models (Boonman et al. 2007), both of which predicted that leaves

325   can adjust their P_{max} according to daily-integrated carbon gain, under dynamic PPFD.

326   Therefore, the big leaf models can be developed further by incorporating the models of

327   direct beam radiation (e.g. Sinclair and Horie 1989; Goudriaan and van Laar 1994;

328   Pearcy and Yang 1996; Thornley 2002).

329   Efficient light utilization in general is achieved not only by physiological

330   acclimation of P_{max}, but also by morphological acclimation of the leaves as well (Pearcy

331   et al. 2005; Posada et al. 2009). Leaf elevation angle determines PPFD on a leaf surface

332   as well as transmission deeper into the canopy (Kuroiwa 1970). Sun-exposed leaves

333   avoid light saturation by a combination of high P_{max} and leaf inclination (Valladares and

334 Pearcy 2002; Falster and Westoby 2003). In *H. tuberosus* canopy, the upper leaves were

335 almost horizontal (Koyama K, personal obs.), and therefore the efficient light utilization

336 was mainly achieved by their high P_{max}. However, for other species with inherently low

337 P_{max}, such as *Fagus crenata*, physiological acclimation should be accompanied by

338 morphological acclimation such as leaf or branch inclination, to avoid light saturation.

339 Reduction of light saturation by both physiology and morphology can also be

340 considered as a defense against photoinhibition (Ishida et al. 2001; Valladares and

341 Pearcy 2002; Falster and Westoby 2003; Pearcy et al. 2005). Hence, the non-saturation

342 of the upper leaves (Fig. 2), which reduced excess light energy on those leaves, may

343 also have alleviated photoinhibition as well.

344   The normalized curves of the three species coincided with each other on the

345 single curve (Fig. 4d), suggesting the possibility that our analysis is applicable for

346 interspecific comparison. This results is consistent with Singsaas et al. (2001), who

347 showed that initial slopes of photosynthetic light response curves were mostly invariant

348 among C_3 plants. Although an analysis with larger data set including many species is

349 needed, it would have the following implication. P_{max} has been regarded as a

350 representative value of a leaf's potential carbon gain (cf. Mediavilla and Escudero 2003;

351 Wright et al. 2004; Kitajima et al. 2005; Ishida et al. 2008; He et al. 2009; Hikosaka and

352 Shigeno 2009; Karagatzides and Ellison 2009; Nagano et al. 2009; Reich et al. 2009;

353 Santiago and Kim 2009; Sardans et al. 2010). However, the mechanistic link between

354 P_{max} and time-integrated carbon gain remains unclear (Kruger and Volin 2006). Based

355 on our geometrical analysis, we suggest that P_{max} represents a "scale" of similar

356 photosynthetic light response curves (Fig. 1c), which determines sizes of photosynthetic

357 rate under any PPFD. Therefore, it would be a qualitative indicator of magnitude of

358 *in-situ* photosynthetic rate.

359   There were several limitations of our results. Firstly, other stress factors that

360 reduce LAUE were not considered. In general, LAUE is determined not solely by light

361 availability, but also by other environmental stresses, such as water limitation and

362 photoinhibition (Werner et al. 2001; Valladares and Pearcy 2002). Hence there are

363 light-use vs. stress constraints within plant canopies (Niinemets and Valladares 2004).

364 We deliberately chose the situation in which water limitation dose not affect LAUE

365 significantly. Actual plants' behaviors can be considered as a summation of simple

366 models and site-specific factors (Koyama and Kikuzawa 2009). Hence applications of

367 our analysis to more complex systems need modifications by incorporating other factors.

368 Secondary, we ignored an effect of photosynthetic induction time. Estimating

369 photosynthetic rate by photosynthetic light-response curves measured under steady-state

370 condition would have overestimated the daily carbon gain, because doing so assumes

371 that the leaves were fully-induced at each moment (cf. Chazdon and Pearcy 1986;

372 Pearcy et al. 1994). The magnitude of this effect varies among species (Pearcy et al.

373 1994; 1997). Pearcy et al. (1997) estimated that the effect was relatively small for a

374 soybean canopy, while it was large for an understory plant *Alocasia macrorrhiza*. From

375 our field observation, the multi-layered canopy of a sun-plant *H. tuberosus* seems to be

376 more similar to that of the soybean than the *Alocasia*. However, it should be emphasized

377 that those studies clearly indicate that the accuracy of our estimate may be largely

378 affected by this effect, and the same method may not be suitable for other species.

379 Leaf anatomy affects photosynthetic light responses (Terashima and Hikosaka

380 1995; Terashima et al. 2005). Within thick leaves the chloroplasts in lower cell layers

381 receive less irradiance than the upper chloroplasts (Terashima and Saeki 1983;

382 Terashima et al. 2009). The anatomy of leaves is known to differ between sun- and

383 shade- leaves (Oguchi et al. 2003; 2008; Terashima et al. 2006; Niinemets 2007), as

384 well as among species (Oguchi et al. 2005; Shipley et al. 2006). Those differences are

385 likely to cause difference in patterns of light saturation among leaves with different leaf

386 morphology (Kull and Kruijt 1998; Green and Kruger 2001; Terashima et al. 2009). We

387 suggest that those phenomena are not mutually exclusive to our results. We found the

388 dissimilarity of the degree of light saturation under the same PPFD among different

389 leaves (Fig. 2), which is equivalent to the similarity of the photosynthetic light response

390 curves under the different PPFD (Fig. 4). Hence, difference in morphology or chemistry

391 should exist inside the leaves for the different responses under the same PPFD. Those

392 divergent responses resulted in the similarity of photosynthetic light response curves

393 and light use efficiency observed among different light regimes.

394

404

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572 **Fig. 1** Two non-rectangular hyperbolae for photosynthetic light response curves with

573 (**a**) high and (**b**) low photosynthetic capacity (P_{max} = 37.5 and 5.6 µmol m^{-2} s^{-1},

574 respectively) and with the same initial slope (ϕ = 0.062 µmol µmol^{-1}) and convexity (θ

575 = 0.55). The open circles and crosses were plotted at PPFD = 2000, 1500, 1000, 750,

576 500, 250, 125, 63, 32 and 0 µmol m^{-2} s^{-1}. The top of each panel was positioned to

577 coincide with the asymptotic line of the curve. The height of each asymptotic line was

578 defined as light-saturated gross photosynthetic rate (P_{max}). (**c**) Geometrical similarity

579 of the two curves. The two curves shown in panel-a and b only differed in size but not

580 in shape. The three dashed arrows show that the curves with the common shape were

581 magnified in those directions with the origin (O) being the center of similitude, and

582 with P_{max} being the magnification ratio for each curve. (**d**) As being similar, they

583 became congruent when normalized to the same size. This can be achieved by reducing

584 each curve by a factor of its size (P_{max}) in both vertical and horizontal directions (see

585 Eq. 3). As they differ in size, they conduct photosynthesis at different part of the curve

586 under the same PPFD range. The two additional axes below panel-d show

587 corresponding absolute PPFD level. The two points (P1) and (P2) shown in all the

588 panels indicate the positions on the curves when PPFD 2000 µmol m^{-2} s^{-1} on the

589 absolute scale. Two vertical arrows in panel-d show why the degree of light saturation

590 under PPFD 2000 µmol m^{-2} s^{-1} differed between the two curves in panel-a and b.

591   **Fig. 2** Photosynthetic light response curves. *Upper*: upper canopy leaves. *Lower*: lower

592   canopy leaves. Figures in parenthesis next to the species names show the stand heights,

593   and those appear on the panels show leaf heights from the ground. One representative

594   leaf from each canopy position and species was shown. The top of each panel is

595   positioned to coincide with the asymptotic line of the curve, of which Y-intercept is

596   defined as light-saturated gross photosynthetic rate (P_{max}).

597

598

599   **Fig. 3** Initial slope (ϕ) and convexity (θ) of photosynthetic light response curve in

600   relation to light-saturated gross photosynthetic rate (P_{max}). Each open circle indicates

601   one leaf ($n = 15$, 15 and 11 for *H. tuberosus*, *A. japonica* and *F. crenata*, respectively).

602   Pearson's correlation coefficient (r) was shown on each panel. Asterisk (*): $p < 0.01$.

603   *r*-values without asterisk: $p = 0.17 – 0.31$.

604

605

606   **Fig. 4** The normalized photosynthetic light-response curves observed in the experiment

607   (see Fig. 1d for the format). Different symbols show the data for **(abc)** the different

608   leaves, or **(d)** the different species. A non-rectangular hyperbola was fitted for all the
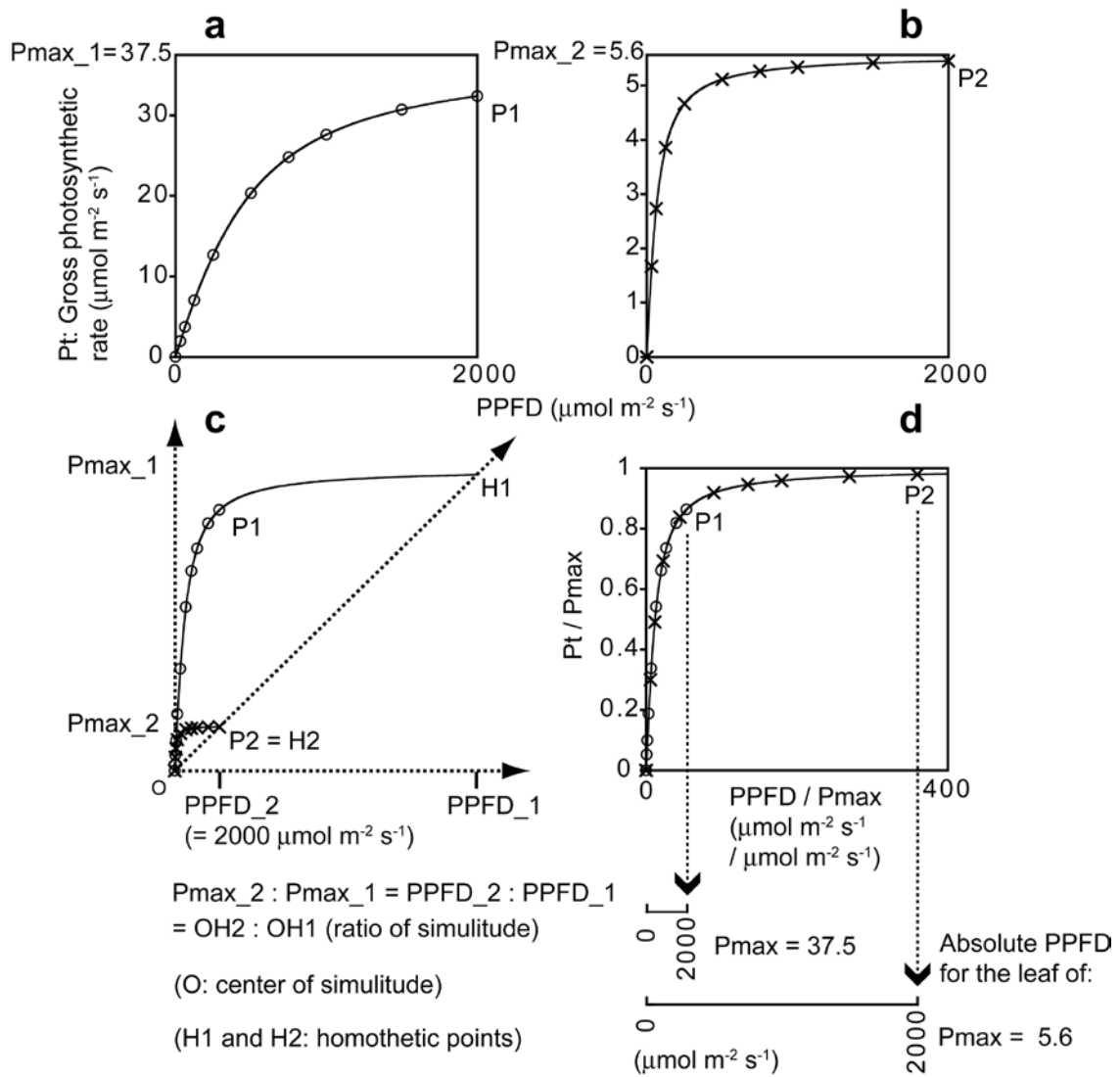
609   dataset in each panel.

610

611 **Fig. 5** Diurnal course of **(a)** PPFD incident on the leaves ($I_{(t)}$) and **(b)** relative

612 photosynthetic rate of the leaves ($P_{(t)} / P_{max}$) of *H. tuberosus* in 18-Aug-2008. Within

613 each position, five different leaves were shown with different symbols. Middle canopy

614 leaves are not shown, as they showed an intermediate pattern between the two.

615

616 **Fig. 6 (a)** Light absorption and use efficiency (LAUE: daily gross photosynthetic rate

617 per unit area of each leaf divided by daily incident PPFD on that leaf) in relation to the

618 quantum-based average of relative photosynthetic rate ($_{ave}(P_{(t)} / P_{max})_{quanta}$) (Eq. 4). **(b)**

619 $_{ave}(P_{(t)} / P_{max})_{quanta}$ and **(c)** daily gross leaf photosynthetic rate, both in relation to daily

620 incident PPFD. For all the panels, each symbol indicates one leaf ($n = 15$). Linear

621 regression in the panel-c: $Y = -2.72 \times 10^{-2} + 2.39 \times 10^{-2} X$. The intercept is not
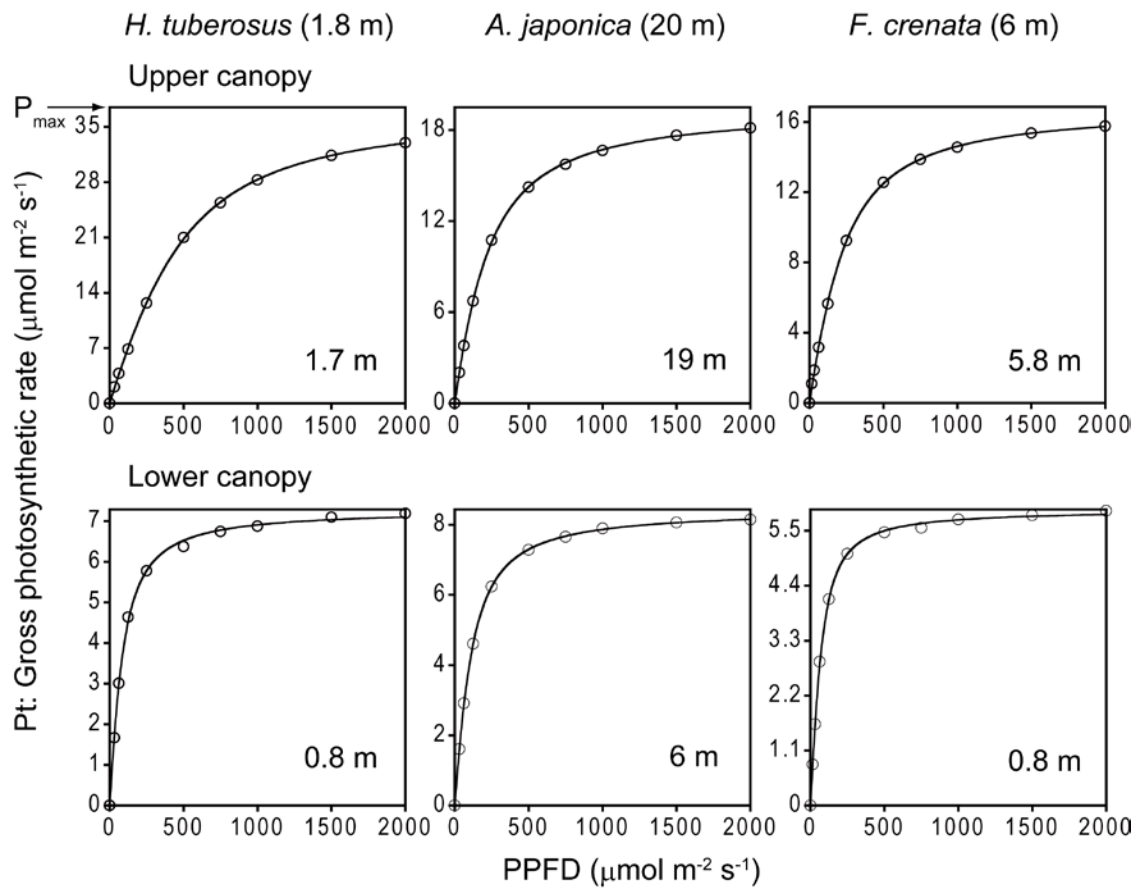
622 significantly different from zero ($p = 0.65$).

623   **Fig. 1**

a

Pmax_1=37.5

Pt: Gross photosynthetic rate (μmol m^{-2} s^{-1})

30

20

10

0

0   2000

P1

b

Pmax_2 =5.6

5

4

3

2

1

0

0   2000

P2

PPFD (μmol m^{-2} s^{-1})

c

Pmax_1

Pmax_2

P1

P2 = H2

H1

O   PPFD_2   PPFD_1
    (= 2000 μmol m^{-2} s^{-1})

Pmax_2 : Pmax_1 = PPFD_2 : PPFD_1
= OH2 : OH1 (ratio of simulitude)

(O: center of simulitude)

(H1 and H2: homothetic points)

d

1

0.8

0.6

0.4

0.2

0

Pt / Pmax

0   400

P1

P2

PPFD / Pmax
(μmol m^{-2} s^{-1}
/ μmol m^{-2} s^{-1})

0

2000

Pmax = 37.5

0

2000

(μmol m^{-2} s^{-1})

Absolute PPFD
for the leaf of:

Pmax = 5.6

624

625

33

626   **Fig. 2**

H. tuberosus (1.8 m)   A. japonica (20 m)   F. crenata (6 m)

Upper canopy

Lower canopy

Pt: Gross photosynthetic rate (μmol m⁻² s⁻¹)

PPFD (μmol m⁻² s⁻¹)

627

628   **Fig. 3**

629

Fig. 4

a *Helianthus tuberosus*

r^2 = 0.998
ϕ = 0.0625
θ = 0.543

b *Alnus japonica*

r^2 = 0.995
ϕ = 0.0629
θ = 0.497

c *Fagus crenata*

r^2 = 0.995
ϕ = 0.0549
θ = 0.575

d All species

○ *H. tuberosus*
● *A. japonica*
× *F. crenata*

r^2 = 0.996
ϕ = 0.0602
θ = 0.547

Pt / Pmax

PPFD / Pmax (μmol m^{-2} s^{-1} / μmol m^{-2} s^{-1})

632 **Fig. 5**

633

634 **Fig. 6**

635