1 **Original Research Paper**

2

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

4 saturation and light use efficiency.

5

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

16

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*

37   *crenata.*

38

39   **Introduction**

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

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

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

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

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

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

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

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

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

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

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

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

52   2001; Pearcy et al. 2005) and other environmental factors such as drought or heat stress

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

70   1998; Rosati and DeJong 2003; Posada et al. 2009). Importantly, those models predicted

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

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

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

74   this optimal condition.

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

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

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

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

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

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

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

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

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

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

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

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

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

88   applicable for canopies under a dynamic light regime.

89

90   **Model**

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

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

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

94

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

96

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

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

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

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

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

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

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

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

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

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

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

108

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

110

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

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

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

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

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

116   shown in Fig. 1ab. Both curves have the same initial slope (ϕ = 0.062 µmol µmol^{-1}) and

117   convexity (θ = 0.55, no dimension). Although they share the common slope and

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

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

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

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

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

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

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

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

126

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

128

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

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

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

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

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

7

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

152

153 $$\text{ave}(P_{(t)} / P_{\text{max}})_{\text{quanta}} = \frac{\sum\limits_{t=0}^{24h} I_{(t)}(P_{(t)} / P_{\text{max}})}{\sum\limits_{t=0}^{24h} I_{(t)}}$$ Eq. 4

154

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

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

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

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

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

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

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

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

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

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

165 *tuberosus*.

166

167 **Materials and methods**

168 Species and site

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

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

171   2001). It grows in disturbed open sites and reaches about 2 m height. They flower in

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

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

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

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

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

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

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

179   a.s.l.). Mean annual temperature and mean annual precipitation are 14.3 $^\circ$C and 2161

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

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

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

183   1 m^2 plot in the garden in December 2007. Those tubers were taken from the previous

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

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

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

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

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

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

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

191 200 m a.s.l.). Mean annual temperature and mean annual precipitation are 13.0 $^{\circ}$C and

192 2438 mm, respectively (2003 - 2007, Annual Report of the Ishikawa Prefectural Forest

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

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

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

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

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

198 was around 6 m, forming a closed canopy.

199

200 Leaf samples

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

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

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

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

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

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

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

208 28-May-2009. Upper leaves of one individual were accessed by another scaffolding

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

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

211

212   Measurement of photosynthesis

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

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

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

216   1500 μmol m^{-2} s^{-1} until equilibration. Then, PPFD was changed from higher to lower

217   (2000, 1500, 1000, 750, 500, 250, 125, 63, 32 and 0 μmol m^{-2} s^{-1}). On each occasion of

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

238 the three species.

239

240 Measurement of incident light

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

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

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

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

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

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

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

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

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

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

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

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

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

254

255 **Results**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

14

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

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

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

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

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

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

277 correlated with the daily incident PPFD (p = 0.86), and hence the daily leaf

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

279

280 **Discussion**

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

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

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

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

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

286 1500 - 2000 μmol m^{-2} s^{-1}) caused incomplete light saturation (Fig. 2). We observed this

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

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

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

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

15

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

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

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

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

295   shown in Fig. 1. Also, strong correlation between LAUE and $_{\mathrm{ave}}(P_{(t)} / P_{\max})_{\mathrm{quanta}}$ (Fig. 6a)

296   showed that relative position on the normalized curve, on which light quanta were

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

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

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

300   approximation.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

325 Pearcy and Yang 1996; Thornley 2002).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

340 also have alleviated photoinhibition as well.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

355 *in-situ* photosynthetic rate.

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

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

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

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

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

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

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

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

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

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

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

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

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

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

370 1994; 1997). Pearcy et al. (1997) estimated that the effect was relatively small for a

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

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

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

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

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

376   Leaf anatomy affects photosynthetic light responses (Terashima and Hikosaka

377 1995; Terashima et al. 2005). Within thick leaves the chloroplasts in lower cell layers

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

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

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

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

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

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

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

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

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

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

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

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

390 and light use efficiency observed among different light regimes.

391

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

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

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

572   = 0.55). The open circles and crosses were plotted at PPFD = 2000, 1500, 1000, 750,

573   500, 250, 125, 63, 32 and 0 μmol m^{-2} s^{-1}. The top of each panel was positioned to

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

594

595

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

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

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

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

600   r-values without asterisk: $p = 0.17 - 0.31$.

601

602

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

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

605   leaves, or **(d)** the different species. A non-rectangular hyperbola was fitted for all the

606   dataset in each panel.

607

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

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

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

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

612

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

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

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

616 $_{ave}(P_{(t)}$ / $P_{max})_{quanta}$ and **(c)** daily gross leaf photosynthetic rate, both in relation to daily

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

618 regression in the panel-c: $Y = - 2.72 \times 10^{-2} + 2.39 \times 10^{-2} X$. The intercept is not

619 significantly different from zero (p = 0.65).

620   **Fig. 1**

Pmax_1=37.5   **a**   Pmax_2 =5.6   **b**

Pt: Gross photosynthetic rate (μmol m⁻² s⁻¹) — y-axis label (a)

P1

P2

PPFD (μmol m⁻² s⁻¹)

c

Pmax_1   H1

P1

Pmax_2

P2 = H2

PPFD_2   PPFD_1
(= 2000 μmol m⁻² s⁻¹)

d

Pt / Pmax

P1   P2

PPFD / Pmax
(μmol m⁻² s⁻¹
/ μmol m⁻² s⁻¹)

400

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

(O: center of simulitude)

(H1 and H2: homothetic points)

Pmax = 37.5

Absolute PPFD
for the leaf of:

(μmol m⁻² s⁻¹)   Pmax = 5.6

621

622

33

623   **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})

624

625 **Fig. 3**

H. tuberosus   *A. japonica*   *F. crenata*

Initial slope (ϕ)

$r = 0.37$ $r = 0.75$* $r = 0.39$

Convexity (θ)

$r = -0.34$ $r = -0.28$ $r = -0.36$

P max (μmol m^{-2} s^{-1})

626

627   **Fig. 4**

a *Helianthus tuberosus*

$r^2 = 0.998$
$\phi = 0.0625$
$\theta = 0.543$

b *Alnus japonica*

$r^2 = 0.995$
$\phi = 0.0629$
$\theta = 0.497$

c *Fagus crenata*

$r^2 = 0.995$
$\phi = 0.0549$
$\theta = 0.575$

d All species

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

$r^2 = 0.996$
$\phi = 0.0602$
$\theta = 0.547$

Pt / Pmax

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

628

36

629   **Fig. 5**

630

631   **Fig. 6**

632

The image shows three scatter plots labeled a, b, c. This is essentially a figure.